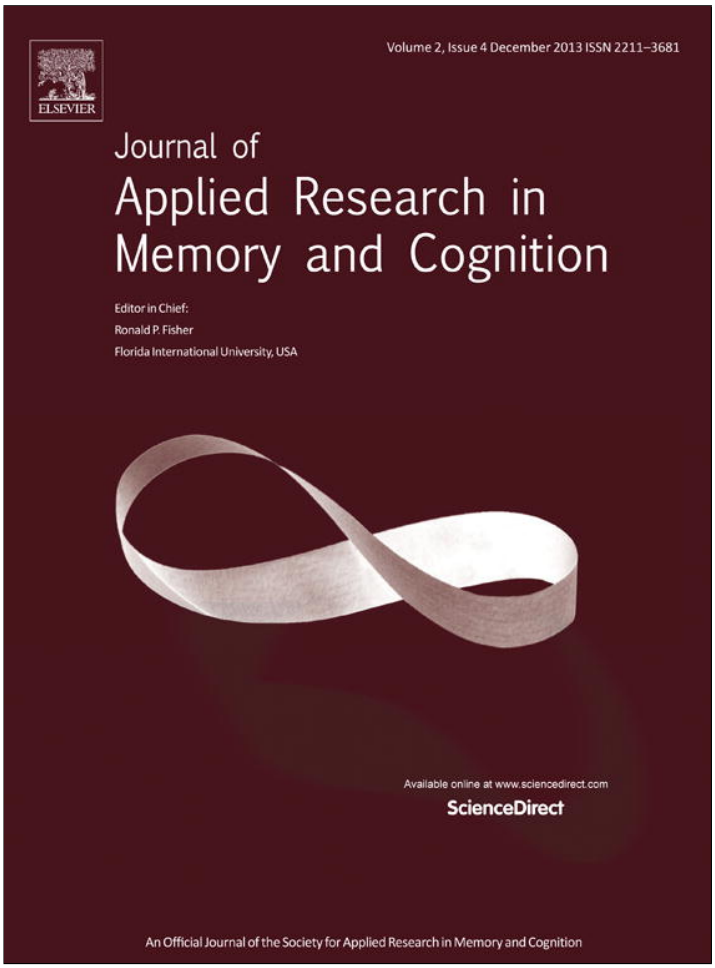

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Commentary

Episodic-like animals, functional faces, and a defense of accuracy

Patrick Douglas Sellers Ii [a,*], Bennett L. Schwartz [b,*]

[a] Department of Psychology, Florida Atlantic University, Boca Raton, FL 33431, United States
[b] Department of Psychology, Florida International University, Miami, FL 33199, United States

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The transformation of past experience into associative relationships and/or mental representation allows even the most simple of organisms to direct current and future behavior based upon lessons learned in the past. Without such abilities, the present moment, in concert with inherited dispositions and reflexes, would be the only sources of information to guide behavior and decision-making. As such, most researchers agree that natural selection shaped the nature of learning and memory (Sherry & Schacter, 1987). The question raised by Klein (2013) is to what ends has evolution sculpted our memory. Klein argues that "memory is *of* the past but *about* the future" (p. 17). Indeed, a dog that comes running to the sound of a bag of treats or a human driver remembering directions to a friend's house demonstrate the future-oriented nature of learning. In both examples, information in the past serves current needs. However, Klein goes further, calling for a reexamination of the assumptions and methodologies that have led human memory research to focus on the past. Klein asserts that natural selection designed memory in a functional capacity, and fitness relevant functionality requires an orientation toward present and future action. His plea is that fitness-based functionality should be the central question of interest in memory research.

The heart of Klein's thesis is the assertion that subjective feelings of pastness associated with episodic memory are a byproduct of future-oriented mental time travel. We agree that this is an important theoretical claim. However, we think that Klein misses evidence that supports his view, especially from the animal memory literature. Indeed, much work on animal memory is inspired by evolutionary concerns or can be interpreted within an evolutionary framework. Our commentary focuses on the likelihood that there may be other requirements placed on episodic memory in addition to future planning, specifically that the past informs social interactions and that within this context accuracy is important. Comparative and social memory research can test functional hypotheses to a greater extent than Klein highlights. Similarly, studies of memory accuracy (the correspondence between memory and the actual earlier event) are critical to understanding underlying processes and modern-world functions (Koriate & Goldsmith, 1996). Acknowledging the existing work on functional memory is a necessary step to integrate Klein's view into the broader literature.

1. Comparative episodic memory

Comparative research on episodic memory in non-human animals demonstrates the likelihood that animals as varied as rodents, birds, and primates have an episodic-like memory system (for a recent review, see Martin-Ordas & Call, 2013). Episodic-like memory in non-humans involves retrieving information about specific events from the past, typically measured by looking for an integrated what/where/when memory (www memory). In contrast, Tulving's (1983, 1993) conception of episodic memory requires the inclusion of autonoetic (self-knowing) awareness, re-experiencing past events with the self as an actor. The human ability for autonoesis extends the abilities to project ourselves into the past and future and thus augment the functionality of an episodic memory system. If animals demonstrate self-awareness of the past it would change

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* Corresponding authors.
E-mail addresses: psellers@fau.edu (P.D.S. Ii), schwartb@fiu.edu (B.L. Schwartz).

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the designation of non-human memory systems from episodic-like to episodic. Many lines of research confirm that, in fact, numerous species can access integrated www information about the past (e.g. Clayton & Dickinson, 1998; Clayton, Yu, & Dickinson, 2001; Kamil, Balda, & Olson, 1994; Martín-Ordás, Haun, Colmenares, & Call, 2010), but methodological limitations prohibit investigation of animals' subjective experience of the self during retrieval. Additionally, only some investigations involve palinscopic retrieval, that is, referring to actions in the past, rather than the current state of the world (see Schwartz, Meissner, Hoffman, Evans, & Frazier, 2004).

The functional utility of animal www-memory is analogous to the functionality of autonoetic episodic memory in humans; both lead to the retrieval of events from the past and the control of present behavior. Indeed, one reason that comparative work tests Klein's idea is that researchers *cannot* engage in subjective investigations with non-humans. The fact that abilities similar to those of humans are observed in a purely functional form in animals accredits the notion that human memory is about future function. This suggests that we should be able to correlate specific memory abilities with specific ancestral functions when specialized abilities map onto specialized functions. Indeed, many animals display such memory abilities. For example, foraging ecology predicts memory in monkeys with an omnivorous species being able to remember over longer retention intervals than a species that feeds only on tree sap (Platt, Brannon, Briese, & French, 1996). Spatial memory is enhanced in polygamous male voles in comparison to monogamous male voles, as the polygamous males have to ranger wider than their monogamous kin (Jacobs, Gaulin, Sherry, & Hoffman, 1990). Finally, food-caching birds show better spatial memory for hidden food when compared to non-caching birds (Balda & Kamil, 2006). These examples illustrate that natural selection often molds memory abilities to functionally meet ecological challenges.

Comparative literatures have the ability to further test Klein's concept of episodic memory. If the subjective experience of the self in the past is integral to future-oriented perspective taking, then evidence of forward-looking mental time travel in non-human species strengthens the case for true episodic memory in non-human animals. Unfortunately, the research on episodic-like memory is unable to measure the subjective experience of these species, leaving a large gap in our understanding.

We can ask the question: Do primates show future planning as a basis of episodically-acquired information? Evidence suggests that primates may be able to keep or remember the location of an object for future use as a tool based on single-trial learning of that object's location (Mulcahy & Call, 2006; Osvath & Osvath, 2008; for a different interpretation, see Suddendorf, Corballis, & Collier-Baker, 2009). Moreover, research suggests that chimpanzees store items for future actions (i.e. hiding items to throw at zoo visitors, Osvath & Karvonen, 2012). In non-primate species, scrub jays (*Aphelocoma californica*) plan for future food needs (Correia, Dickinson, & Clayton, 2007; Raby, Alexis, Dickinson, & Clayton, 2007). Thus, there is evidence that some animals plan for the future on the basis of past learning. Therefore, Klein's assertion that episodic memory is a byproduct of future planning appears promising when considered from the perspective of comparative psychology.

2. Functional social memory

Klein's view is that mental time travel prepares individuals for future planning in ways that would not be possible without mental time travel. Planning now for events in the future is one application, but surely not the only one. We assert here that autonoesis or mental time travel may serve vital social functions in humans and other species that live in complex social networks. Research touting an explicitly functional (and evolutionary) perspective on human social memory is not new (e.g. Nelson, 1993). In fact, the functional importance of social memory likely leads to different adaptations of memory across the lifespan (see Bjorklund & Sellers, 2013; Sellers & Bjorklund, 2014). Two lines of research can be brought to bear on this functional perspective on social memory, memory for faces and memory for cheaters.

Human face memory illustrates the social requirements of a functional naturally selected memory system. Relative to other stimuli, human beings are tuned to learn and remember faces (Schwartz, 2013). Specific neural systems have evolved in humans (and other primates) for learning new faces and the recognition of old ones. Neuroimaging evidence shows specialized neurological processing of faces in humans (Johnston & Edmonds, 2009; Kanwisher & Dilks, 2013; McCarthy, Puce, Gore, & Allison, 1997). Face-specific recognition deficits (i.e. acquired and developmental prosopagnosia) exist in a small number of individuals (Duchaine & Nakayama, 2005). Faces appear to be a domain-specific class of stimuli that prompt enhanced attention and recognition in comparison to other classes of stimuli (McBain, Norton, & Chen, 2009). It is likely that social evolutionary pressures crafted the human mind to specialize in face-related cognitions because of the importance of social functioning to our species. We need to be able to recognize kin and foes and learn to which of these categories new faces belong. In fact, social pressures are often cited as an important factor in hominid brain evolution and phylogenetic encephalization (Dunbar, 1998, 2010; Joffe, 1997).

A host of variables highlight the role that ancestral function may play in face memory. For example, source memory for the context associated with the faces of cheaters is greater than for non-cheaters (Buchner, Bell, Mehl, & Musch, 2009) specifically when associated with a negative valence (Bell & Buchner, 2010). High-status faces are recognized more frequently than low-status faces (Ratcliff, Hugenburg, Shriver, & Bernstein, 2011). In addition, greater need to belong and social exclusion prompt greater memory for own-group faces (Bavel, Swencionis, O'Connor, & Cunningham, 2012). Thus, faces are preferentially remembered in a manner consistent with social functional needs for the future. Of course, cheaters, high-status individuals, and faces encountered during social exclusion are likely to be relevant in the future. This is consistent with Klein's thesis, although it is a stretch to call recognizing familiar faces future-oriented planning.

3. Memory accuracy

This brings us back to Klein's questioning the necessity of memory accuracy for adaptive function. He suggests that studying accuracy tells us little about the function of memory. We agree with the view that benefit trumps accuracy (Sellers & Bjorklund, 2014), but, in many cases, remembered information can only be a successful guide to the future if it reflects lessons well-learned. Because the past does predict the future, remembering the past allows us to accurately predict the future, consistent with Klein's view concerning the function of episodic memory. As mentioned above, cheaters and their contexts are more accurately recognized. Although prehistoric humans may not have had court systems, recalling who had stolen food or abetted an enemy group would have been useful information in planning to deal with this person in the future. If the wrong person is recalled as having stolen food, there are consequences both nutritional and social. Today, we want witnesses to crimes to be accurate in their testimony for similar reasons (Schacter & Loftus, 2013). Memory for survival-relevant places also illustrates the importance of accuracy. If one learns and later can recall where to find water during times of drought, the person can plan appropriate travel routes when water is scarce again. In both of these examples, context plays an

important role in encoding, as a person may be a friend in one context, but a rival in another. Similarly, if locations are dangerous, they ought to be avoided unless going there is unavoidable. Even infants show dependence on context for memory and reproduction of past actions (Rovee-Collier, Schechter, Shyi, & Shields, 1992) suggesting that contextual cues may serve a functional role in infant memory by guiding appropriate memory retrieval (Bjorklund & Sellers, 2013). Thus, a traditional principle of memory, encoding specificity, follows both from the need for accuracy and the ability to anticipate future events (Thompson & Tulving, 1970).

Thus, our specific examples of functional social memory support the idea that accuracy is important. Mis-remembering the cheater's identity, location, or infraction renders the memory unusable. If the past did not have to be remembered accurately, there would be no use for memory at all. Thus, in almost all memory situations, accurate retrieval is what makes a memory system functional to aid the individual now and in the future. Although we agree that memory may be *for* the future, we also assert in order for projection of the future to be successful, accurate memory of the past is required.

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