2014

Animal Memory: Rats Bind Event Details into Episodic Memories

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Recommended Citation
Beran, Michael J. Animal Memory: Rats Bind Event Details into Episodic Memories.Current Biology , Volume 24 , Issue 24 , R1159 - R1160. doi: http://dx.doi.org/10.1016/j.cub.2014.11.019

Dispatches

Animal Memory: Rats Bind Event Details into Episodic Memories

A recent study shows that rats remember multiple details of an event in a way that suggests those details are bound into episodic memories that the rats use when faced with a foraging task.

Michael J. Beran

Humans have their own personal past, and typically can opt to 'relive' that past by remembering specific episodes, ranging from a short time interval ago ("what did I have for breakfast?") to long ones ("what was it like the first time I rode my bicycle?"). In these instances of remembering, the features of the event being remembered are intricately bound, in the sense that the 'who', 'what', 'when', 'where', and even 'why' information within the memory feels interwoven. This 'episodic memory' system allows us to relive our personal past in a way that gives rise to a feeling of continuity of experience, and that also allows us to re-experience the feelings that came along with the bound features of the past event [1,2]. Such a system is seen as distinct from semantic memory stores that contain factual information, but without the personal qualities of episodic memories. A new study [3] reported in this issue of *Current Biology* assesses whether rats may have episodic memories, using multiple events experienced in succession to determine what rats remember about each event.

There is an ongoing debate about whether nonhuman species show evidence of such episodic memories, with numerous species having been tested (for example [4–9]). There is no controversy over whether animals have memories, or how specific those memories can be, or what kinds of things can be remembered. In many cases, animals even can provide some or all of the 'who', 'what', 'when' and 'where' information from a previously experienced event [10–15]. What has been controversial is the degree to which animals exhibit the bound, specific and contextual memories that humans have, and whether those memories also contain the experience of an event being relived, as they do for humans [16,17]. It is this last component that makes episodic memory research contentious in comparative cognition research, because there may be no way to show that this 'autonoetic' component of episodic memory occurs in animals [2,18]. This issue can be minimized, however, by focusing on the nature of the remembered information itself, without worrying about whether the animal has the experience of remembering it.

In the newest attempt to assess episodic memory in animals, Crystal and Smith [3] have taken this approach by documenting what objective information rats can remember about events they experienced. They have shown that rats encode what foods were hidden in different radial arm mazes, and where they were hidden, while also remembering context cues that were important for knowing how to forage when the rats returned to each maze at a later time. These results afford the opportunity for progress in understanding how animals might remember their experiences, and the development of potential animal models of various forms of human memory (including episodic memory), as well as of forms of memory impairment and loss.

Crystal and Smith [3] presented rats with a radial arm maze in which some arms contained highly preferred chocolate at their endpoints and some ended with less preferred chow pellets. Rats sometimes found the chocolate on their own by running down the arm of the maze, whereas other times the rats were placed at the chocolate by the experimenter, and it was this aspect of a trial that was critical to assessing what the rats remembered. These different means of discovering the chocolate indicated whether or not chocolate would again be at the same location in that maze on the next visit. The rule was that "if you find chocolate on your own in this location, it will be here again next time, but if the experimenter places you at the chocolate, this location will be empty next time." And, further complicating the rats' experiences was the use of two rooms in some conditions, where sometimes the initially baited chocolate locations were the same in both rooms but the means of finding the chocolate differed (i.e., in one room the rat was placed in one arm with chocolate but ran to the other arm, whereas in the other room the manner of finding chocolate was reversed for those same locations in the maze). This required the rats to pay attention to and remember what room they were in, whether they found the chocolate on their own or with help, and where the chocolate was when they found it. All of these individual units of information were informative as to whether the rats should go back to specific arms of the maze where chocolate had been, or whether they should avoid those arms. (The low preference chow was always in different arms on the second visit compared to the first, and the rats typically switched arms for chow pellets and did not revisit the original chow locations.)

What is critical about this study [3] is the use of the two rooms with some overlapping features but also some unique features in each of the memories the rats formed when in the rooms. When only one room is used in this kind of test, rats could learn where chocolate would be on the next visit without need of remembering all aspects of the event as a bound set. When a rat went into successive rooms, however, it had to use the cues in the room as part of its memory of whether it was placed next to the chocolate or found chocolate on its own in that room, and thereby could anticipate whether chocolate would replenish in specific locations or would not. Because the authors increased the memory load, there were multiple overlapping features of each event that could only be used accurately during future maze visits if the rats

remembered that each event occurred in a distinct room.

Crystal and Smith [3] argue that keeping separate in memory multiple episodes that share similar components is a central feature of bound memory representations. If the rats instead had just remembered each of the unbound aspects of each event, then performance would have suffered because the two events shared some of these aspects. Rats would have struggled to find the preferred chocolates in the correct locations when revisiting the mazes. But the authors found that rats were likely to go to maze arms that held chocolate, taking into account which room they were in, and how they had found chocolate in that room previously. This suggests that they remembered each experience (in each room) as an event with multiple, bound features.

Whether these results indicate that the rats' bound memories meet everyone's definition of episodic memory (for example [1,2,16,17]) should not be the main issue. Perhaps they do not, but that makes these results no less important. Questions about whether animals do or do not show 'mental time travel' [16–18] sometimes can distract us from the equally important (and perhaps more immediately pressing) goal of establishing just how accurate and flexible the memories of animals can be when those memories are needed to generate intelligent behaviors (or, for those studying prospective cognition, just what kinds of anticipatory behaviors we can find in nonhuman animals). Certainly, consideration of whether these kinds of experiences have the qualities that are critical for human mental time travel will highlight aspects of the nature of animal consciousness, and can offer insights into the evolution of human cognitive abilities and consciousness. But there is at least equal importance in comparative cognitive science in documenting where and why success and failure occur in memory tasks, and how bound the components are for personal memories of the past, along with how episodic memories may serve an adaptive function in future oriented behaviors such as prospective memory and planning [19,20]. Crystal and Smith [3] have provided compelling new data in this debate, showing that the binding of features is likely a widespread aspect of animal memory and one that is potentially of high translational value in terms of understanding some of the fundamental aspects of human memory.

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http://dx.doi.org/10.1016/j.cub.2014.11.019

Sensory Biology: Echolocation from Click to Call, Mouth to Wing

Echolocators use echoes of sounds they produce, clicks or calls, to detect objects. Usually, these signals originate from the head. New work reveals that three species of bats use their wings to generate echolocation signals.

M. Brock Fenton[1] and John M. Ratcliffe[2]

Donald R. Griffin [1] coined the term 'echolocation' to describe the use of echoes of self-generated acoustic signals for orientation, as seen in bats and some blind people. However, not all bats echolocate. The list of echolocating animals also includes toothed whales, some shrews and tenrecs, as well as oilbirds and some swiftlets [2]. Most bats produce their echolocation signals in their voice boxes (larynges) [3] but at least two species of Old World fruit bats, (Pteropodidae) *Rousettus aegyptiacus* (Figure 1) and *Rousettus leschenaulti*), use tongue clicks as echolocation signals [2]. Some blind people also use tongue clicks as echolocation signals [4]. But the arsenal of bats for producing echolocation signals is even broader than we had realized. In this issue of *Current Biology*, Arjan Boonman, Sara Bumrungsri and Yossi Yovel [5] show that some bats