Mental time travel: a case for evolutionary continuity

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In humans, hippocampal activity responds to the imagining of past or future events. In rats, hippocampal activity is tied to particular locations in a maze, occurs after the animal has been in the maze, and sometimes corresponds to locations the animal did not actually visit. This suggests that mental time travel has neurophysiological underpinnings that go far back in evolution, and may not be, as some (including myself) have claimed, unique to humans.

A distinction is commonly drawn between episodic memory, which is memory for specific personal events, and semantic memory, which is general knowledge about the world. Endel Tulving, who was the first to draw this distinction, has long argued that only humans are capable of episodic memory. He also recognized that episodic memory is adaptive in the planning of future episodes and provided a subjective sense of time [1]. This has led to the extended notion of ‘mental time travel’, implying that we can mentally travel backward or forward in time, imagining possible future events, as well as re-experiencing past ones. I am among those who have claimed that this, too, is a uniquely human capacity [2], but I now question whether this is so.

A number of behavioral studies have purported to show that some nonhuman animals can act on the basis of specific information from past events or with respect to possible events in the future, suggesting that they are capable of mental time travel. For example, scrub jays can choose to retrieve food items on the basis of both where and when they were cached, suggestive of episodic memory, and, if watched by another bird while caching food, they later privately cache it elsewhere, suggesting anticipation of future theft [3]. Chimpanzees also appear capable of selecting tools appropriate to future activity [4].

These and other behavioral studies proclaiming mental time travel in nonhuman species have been criticized, by myself and others, for failing to meet the criteria for episodic memory or episodic foresight, or for not ruling out simpler explanations [5,6]. However, perhaps the main ingredient missing from these studies is the subjective one – or what Tulving called ‘autoneosis’. It is this issue that has prompted some to use the term ‘episodic-like’ rather than episodic when referring to examples from nonhuman species. Indeed, one might ask whether we can ever know what, or even whether, an animal is actually thinking.

A partial answer, however, may lie in recordings of brain activity. Researchers have identified a widespread network in the brain, known as the ‘default mode network’, which is involved in autonomous mental activity, including mental time travel [7]. This network has been identified in humans, as well as in rats [8]. A critical region in the network is the hippocampus, which is active in humans both when they recall past episodes and imagine future ones [9], raising the possibility that hippocampal activity might indicate subjective experience not only in humans, but also in nonhuman species. Some support for this comes from recent studies of hippocampal activity in the rat.

Individual cells in the rat hippocampus discharge when the animal is in particular locations in an environment, such as a maze, suggesting that the hippocampus is involved in the construction and activation of cognitive maps of the environment [10]. This activity occurs while the animal is exploring a maze, but is also observed in sharp-wave ripples (SWRs), sometime after the animal has actually been in the maze, either during slow-wave sleep [11] or when the animal is awake but immobile [12]. Further, the paths indicated by the replay activity need not correspond to the actual paths taken in the maze. Sometimes, the replayed path is the reverse of the one actually taken [13] or it corresponds to paths the animal did not actually take [14], which might suggest anticipation of future excursions in the maze (Figure 1).

This activity has been interpreted to reflect consolidation of a cognitive map that includes regions beyond those the animal actually explored. The cognitive map is, therefore, extended beyond actual experience, allowing more flexible navigation in the future. Given the role of hippocampal activity in human mental time travel, however, it may not be unreasonable to suppose that SWR activity in the rat brain is more than a process of consolidation, but that it also represents ongoing mental processes. It has been suggested that such processes might involve the possible linking of past, present, and future in the guidance of behavior [15]; they might also be considered tantamount to mental time travel. Regardless of whether or not a rat can be said to be mentally reliving a past experience or imagining a future one during SWRs, it seems highly likely from an evolutionary perspective that this activity is homologous to that involved in mental time travel in humans.

How might mental time travel in humans differ from that in the rat? The most obvious answer lies in complexity. Humans imagine much more than locations – our imagined episodes are populated with people, things, places, actions, giving rise to unlimited possible combinations. One measure

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of this may be language, which may indeed be uniquely adapted to communicating the nonpresent, including the outcomes of our mental time travels. The uniqueness of language, however, may lie more in the imperative to share the contents of thought than in the thoughts themselves. With respect to memory and mental time travel, at least, it may be salutary to remember Darwin’s comment that ‘The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind.’

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References

Figure 1. In this example, the rat makes a counterclockwise circuit of the left side of the maze (dotted circle). Later replays are either forward (ABCD), backward (EFGH), or on the opposite side (JKLMN).