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Review

Fellow travellers: Working memory and mental time travel in rodents

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ABSTRACT

The impairment of mental time travel is a severe cognitive symptom in patients with brain lesions and a number of neuropsychiatric disorders. Whether animals are also able to mentally travel in time both forward and backward is still a matter of debate. In this regard, we have proposed a continuum of mental time travel abilities across different animal species, with humans being the species with the ability to perform most sophisticated forms of mental time travel. In this review and perspective article, we delineate a novel approach to understand the evolution, characteristics and function of human and animal mental time travel. Furthermore, we propose a novel approach to measure mental time travel in rodents in a comprehensive manner using a test battery composed of well-validated and easy applicable tests.

Contents

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1. Background

1.1. What is mental time travel

Mental time travel into the past (also known as episodic memory) or future (also referred to as episodic future thinking) is the most sophisticated cognitive function to have evolved in humans [1–7]. This remarkable capacity enables the reconstruction of past events (episodic memory), the anticipation of future events (episodic future thinking) and the construction of imagined scenarios. Suddendorf and Corballis [4] have compared mental time travel to a "time theater" where our self is the main actor in old (reconstructed past events), scheduled (anticipated events) or new plays (imaginary future scenarios) [8]. Mental time travel serves a wide range of important functions, including the formation of our identity (extracting knowledge about our self from reconstructed past events), decision-making, problem solving, goal-directed behavior, planning, anticipation of future events and the preparation for future needs [9].

1.2. What are the prerequisites of mental time travel?

In order to reconstruct past events or to construct imaginary future scenarios in a most accurate and authentic way, two major elements are required. The first one would be a certain level of consciousness or autonoetic awareness, that is, the awareness of the own existence in time, the "self", and the ability to project this self into the past, present and future [10–13]. The second critical element of mental time travel is the requirement of a sufficiently high working memory capacity and processing power in order to reconstruct past events and to construct imagined future scenarios as detailed as possible [9]. Working memory is indispensable for the reconstruction of past events because, the core information of past events has to be maintained in working memory, while gaps in the fragmentarily event memory have to be filled with knowledge from semantic memory to end up with a reasonably faithful event reconstruction. The demand in working memory capacity and processing power is even higher if past events are used for the preparation for similar events in the future, e.g. the simulation or the playing through of alternative options for action as well as the calculation or prediction of their most likely consequences [9,14–16]. Consequently, aging-related impairments in episodic memory formation and mental time travel into the future are correlated with age-related impairments in working memory capacity [17,18].

1.3. The evolution of mental time travel

Cognitive neuroscientists and neuroanatomists have aimed for decades to understand human cognition by dissection and comparison of animal and human brains. Here we wish to emphasize the fact that very different brains e.g. those of insects, birds or mice that have different anatomical and neurophysiological organizations can perform surprisingly similar cognitive operations. Therefore, one can conclude that there is more than one solution to construct a brain that can perform certain cognitive operations. The comparison of these different brains as such might not help much to understand how higher human cognition has evolved. It would be perhaps more promising to dissect the cognitive architecture of different species to see how higher cognitive functions have evolved in humans.

It is not clear at which stage of human anthology mental time travel emerged. However, it is very likely that it appeared gradually in terms of both range of coverage (how far mental time travel extended retro- and anterograde) and sophistication (richness in detail and whether they were used for self-contemplation, prediction and planning) and reached its most advanced form in the modern human [3,4,7,9,19–26]. If one compares the presence of mental time travel across animal species, it is evident that mental time travel, at least in very basic forms, exists in animals with very different types of brains, including nonhuman primates [27,28], birds [29–31], zebrafish [32], cuttlefish [33], bees [34], dogs [35] and rodents [36–41]. Thus, even very different types of brains are capable of at least very rudimentary forms of mental time travel. Therefore, the emergence or presence of mental time travel cannot be directly linked to mammalian brain development and processes such as cephalization [45]. It is also unclear how the development of language and the conservation of knowledge via language facilitated the refinement of mental time travel [42–44]. In a recent theoretical paper we proposed that the range of coverage and sophistication of mental time travel should be critically dependent on working memory capacity, respectively, processing power. Therefore, the evolution of mental time travel in different species should be correlated with the evolution of working memory capacity and processing power [9].

1.4. The mental time travel platform

A theoretical framework to model and study the interplay between working memory capacity/processing power and mental time travel in humans and animals, is provided by the extended multi-component model of working memory [9]. The multi-component model of working memory by Alan Baddely [46–48] was complemented by an additional component, the 'mental time travel platform' and its subsystems – the 'experience reconstruction and scenario simulation systems' (Fig. 1). This extended model integrates the cognitive operations associated with mental time travel into a well-validated model of cognitive and working memory function.

2. Present challenges

2.1. Neuropsychiatric disorders and mental time travel

Cognitive impairment (including impairments in mental time travel) is a cardinal behavioral symptom in patients with brain lesions and neuropsychiatric disorders [49–59] and is a major obstacle to the active participation of patients in work and social life. Patients with mental time travel impairment are generally in need of intensive care and have a bad prognosis. Treatment approaches should mainly focus on the amelioration of behavioral symptoms, including cognitive impairment. Therefore it is of utmost importance to develop valid animal models of retro- and proactive mental time travel that can be utilized to develop better pharmacological treatments and therapeutical interventions [50,60]. In this review we will propose a mental time travel test battery for mice and rats that can be used for research in the field of translational psychiatry.

2.2. Mouse models of mental time travel

In the last two decades a number of mouse models for mental time travel into the past have been developed that are based on the novelty-preference paradigm [38,61]. These tests either focused on the demonstration of memory for the temporal order of events [62,63], the context-dependent learning of event sequences [64], or an integrated memory (episodic-like memory) for what happened, where and when [39,40,65–67]. The latter approach has been successfully used to map cortico-hippocampal circuits critically involved in episodic memory [68–70].

Although the measurement of mental time travel into the past is now well established in the mouse and rat (see Binder et al. [38] for a comprehensive review), it is still controversial as to whether

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