

DOSSIER

Situating *mental time travel* in the broad context of temporal cognition: A neural systems approach

Situando o conceito de *viagem mental no tempo* no amplo contexto da cognição temporal: uma abordagem de sistemas neurais

Fabiana Mesquita Carvalho¹

ABSTRACT

Mental time travel (MTT) is the ability of remembering personal past events or thinking about possible personal future happenings. This mental property is possible due to our capacity to be aware of subjective time, which enables us to experience the flow of time, to conceive non-present times, and to process time as a dimension of real world phenomena. Temporal cognition encompasses the mental functions which rely on temporal information enabling the experience of the temporal flow and the processing of the temporal dimension of external phenomena. Given the broad range of our time experiences and, hence, the broad scope of our temporal cognition, it is expected that certain kinds of temporal information can be of particular importance when we mentally transport ourselves to events in the past or future, whereas others could be unrelated to this mental property. The present paper seeks to situate the process of MTT within human temporal cognition. This will be done by identifying the commonalities and differences in the neural correlates of MTT and those of the three main subjective time processing systems, namely metric timing, ordinal timing and autobiographical timing.

Keywords: mental time travel, time perception, temporal cognition.

RESUMO

Viagem mental no tempo (VMT) diz respeito à habilidade de se lembrar de eventos pessoais do passado ou pensar sobre possíveis acontecimentos pessoais futuros. Essa propriedade mental é possível devido a nossa capacidade de estar ciente do tempo subjetivo, o que nos permite ter a experiência do fluxo do tempo, conceber tempos não presentes e processar 'tempo' como uma dimensão de fenômenos do mundo real. Dada a vasta gama das nossas experiências temporais e, portanto, o amplo escopo da nossa cognição temporal, é de se esperar que alguns tipos de informação temporal sejam de particular importância quando nos transportamos mentalmente para eventos no passado ou futuro, enquanto que outros

¹ Universidade de São Paulo. Av. Professor Luciano Gualberto, 403, 05508-900, São Paulo, SP, Brasil. E-mail: bibimesq@yahoo.com.br

podem ser irrelevantes para essa propriedade mental. O presente artigo busca situar o processo de VMT dentro da cognição temporal humana. Isto será feito identificando-se convergências e divergências dos correlatos neurais da VMT com aqueles dos três principais sistemas neurais de processamento temporal, a saber, temporização métrica, temporização ordinal e temporização autobiográfica.

Palavras-chave: viagem mental no tempo, percepção temporal, cognição temporal.

Introduction²

Mental time travel (MTT) is a psychological concept coined by Endel Tulving (1993) from his own formulation of the nature of episodic memory. Since the late nineties, it has received considerable attention in the cognitive psychology literature and has been further investigated and developed (Suddendorf and Corballis, 1997). MTT refers to the ability to mentally reconstruct personal past events and mentally construct possible future events. Thus, it is directed towards personal non-present times and it is only possible due to our capacity to process time as a dimension of real world phenomena (Szpunar, 2011). Several authors agree that the phenomenal aspect of MTT goes beyond the mere content of the recollection or future thinking in question (i.e., the what, where and when tied to the event). It is said that the phenomenal aspect that accompanies the content requires chronesthesia and auto-noetic awareness³. Another concept tangled to that of MTT is the concept of episodic memory, which refers to conscious recollection of specific episodes in one's personal past. Indeed, it could be assumed that when MTT is directed toward the past it is termed episodic memory (Suddendorf *et al.*, 2009).

As it is a general mental faculty which depends upon subjective time perception, one might wonder to what extent and by which means MTT is related to the broader concept of temporal cognition. Temporal cognition encompasses the mental functions which rely on temporal information enabling the experience of the temporal flow and the processing of the temporal dimension of external phenomena (Maniadas and Trahanias, 2011; Matthews and Meck, 2016). It includes subjective time perception (e.g., judgements about temporal order and duration) as well as memory processes (e.g., working memory and episodic memory). Although psychological and neurobiological studies have made considerable progress in elucidating the role of episodic memory and prospective thought in MTT, the contribution of time per-

ception itself to MTT still remains elusive. This is in part due to the fact that time perception has often been investigated and discussed in relative isolation from the mnemonic aspects of temporal cognition (Matthews and Meck, 2016).

The present article aims at addressing the question of which kind of temporal information is of particular importance when we mentally transport ourselves to events in the past or future in order to situate MTT within the broader theoretical framework of human temporal cognition. This will be done by identifying the commonalities and differences in the neural correlates of MTT and those of the three main subjective time processing systems: (i) the processing of temporal order in past and future events, which is the event-sequencing aspect of time perception, (ii) the processing of interval timing of events, which is the aspect of duration estimation of time perception, and (iii) the processing of the temporal dimension of episodic memories, which includes the encoding of temporal context information as well as the encoding of the passage of time. The article is structured as follows. First, the neurobiological substrates of temporal order and interval timing, which are part of the so-called "perception of time" literature, will be reviewed. Then, the neural correlates of episodic memory will be presented, followed by the discussion of neuroimaging studies on self-related memory, imagination and MTT. Finally, I will compare the neural bases of MTT and episodic memory with those of perception of time. Elucidating the type of temporal information MTT is dependent on is crucial to understand how MTT is related to temporal cognition.

Perception of time of external events: Definition of terms and neurobiological substrates

Although we all have a sense of time, our bodies are not equipped with a sensory system for detecting time in the

² Abbreviations used in this article: BG = Basal ganglia, DMN = Default mode network, MTT = Mental time travel, SMA = Supplementary motor area, TPJ = Temporal parietal junction.

³ Chronesthesia could be understood as the cognitive capacity to be aware of one's subjective time, i.e., a subjective sense of past, present and future times. Thus, chronesthesia is a broader mental function which would be the basis – or the medium, as Tulving and Kim (2007) put it – that makes personal past recollection and future prospection possible. Auto-noetic awareness is the subjective conscious experience of an event – hence, it describes not the general awareness of subjective time but the awareness of one's existence in this subjective time.

same way we detect light and sound – i.e., time is not a type of material object of the world for which there are specifically dedicated sense organs, receptors and sensory cortices. Yet the perception of the passage of time by the experiencing subject is as obvious as the colour of an object or the timbre of a sound. How is temporal information represented in the subject's brain?

First of all, it is important to make clear that “temporal processing” is not a monolithic concept. It comprises several characteristics of timing that can be functionally⁴ dismantled. Studies on perception of time consider a more general distinction between duration estimation (how long an event lasts, or when an event is likely to occur), which involves analysis of elapsed time and requires a *metrical* representation of time, and temporal order judgement (order of successive events in a series), which requires an *ordinal* representation of time (Ivry and Spencer, 2004; Coull *et al.*, 2011). It is also important to note that these studies employ supra-second time intervals, that is, intervals spanning a few seconds. This means that the temporal processing mechanisms of interest rely on conscious encoding of duration, which require cognitive control (as opposed to sub-second intervals which are embedded in automatic sensory processes and action plans⁵).

Within metrical timing, two functional distinctions have been made. The first is a distinction between “explicit” and “implicit” timing, whereas the second is a distinction between “perceptual” and “motor” timing. These functional concepts are defined as follows. Explicit timing refers to overt estimations of duration required from subjects during a temporal task (the task's goal is to estimate elapsed time). Being asked to estimate for how long the red traffic light stayed on is an example of explicit timing. Contrarily, implicit timing regards the implicit engagement of timing mechanisms in a task which has an inherent temporal structure (the task's goal is non-temporal, but temporal expectation is induced by temporal elements such as speed or rhythm). For instance, crossing a busy streets requires an implicit interval estimation (expectation) given by the position and speed of vehicles. Both explicit and implicit timing tasks may require subjects to either provide a perceptual judgement or to perform a motor act, which have been referred to as “perceptual timing” and “motor timing”, respectively.

Still regarding metrical timing, neuroimaging studies of explicit duration estimation have revealed a core⁶ corticostriatal network composed of the basal ganglia (BG), the

supplementary motor area (SMA), and the right-lateralized inferior frontal cortex. Studies of implicit timing (or temporal expectation) have also implicated a core network constituted by the BG and the SMA, together with the cerebellum, and the left-lateralized premotor and parietal cortices (Coull *et al.*, 2011). The BG and the SMA participate in both types of metrical timing, independently whether perceptual or motor responses were given. These two brain regions have been associated with distinct stages of the pacemaker–accumulator model (Buhusi and Meck, 2005). According to the model, the pacemaker BG participates in the encoding phase of long-term memory of duration (i.e., creation of our “offline” reference of duration) whereas the SMA is involved in keeping the elapsing time of a current stimulus in short-term memory (accumulation) and comparing this “online” duration with the “offline” reference of duration.

In addition to metrical timing, the other component of perception of time is ordinal timing. Being able to judge whether two events are simultaneous or successive is crucial to the moment-to-moment interpretation of the sensory world. Neuroimaging studies have pointed towards a core brain region involved in judgments of the temporal order of two stimuli, irrespective of the sensory modality: the right-lateralized temporal parietal junction (TPJ). The demonstration of the role of the right inferior parietal lobe (which is part of the TPJ) in judgments of temporal order has been so robust that this region has been considered the “when” pathway of the visual system (in addition to the well-known “where” and “what” pathways) (Battelli *et al.*, 2007).

It is clear that metric and ordinal timing engage different brain regions, or two distinct functional systems. Nonetheless these brain regions have also been described as the neural components of either of two major networks, namely the salience network and the motor control network. The salience network is active whenever worldly stimulation demands awareness. Amongst the myriad of sensory information we are constantly bombarded with, only a tiny part is actually relevant for our goals and interests. The salience network is involved in selecting what matters in a given context. It is composed of frontal and parietal cortices which exert top-down modulation of attention and working memory. Regarding the motor control network, it is engaged not only by actions *per se*, action planning or action emulation, but also by prediction of the unfolding of external events, both biological and non-biological (Schubotz, 2007). We live in a dynamic

⁴ By functional I mean mapped using functional neuroimaging techniques (e.g., PET, fMRI, ERP). Such techniques allow researchers to investigate the set of brain regions which robustly correlate with certain mental functions delivered via a perceptual or cognitive task. The set of brain regions can be referred to as functional system (e.g., the functional system of attentional control).

⁵ Different types of perception and behaviour implicate different ranges of time intervals. The estimation of the duration of a few hundreds of milliseconds (i.e., sub-second) is called “automatic timing” and is crucial for motor control in automated motor sequences (e.g., walking on the street, speech perception and production). Estimating the duration of over a few seconds (i.e., supra-second) is called “cognitively controlled timing”. It requires attention and working memory and is necessary for conscious time estimation and decision making.

⁶ By “core” network I mean regions that are recruited by different types of motor and perceptual tasks, and irrespective of the sensory modality in which stimuli were presented. Thus, core network would refer to a context-independent, supramodal representation of duration (in explicit timing) and of temporal expectation (in implicit timing).

world, and anticipating future states of relevant events is important to grasp the causal relationship between the dynamic behaviour of our body and the environment, as well as their consequences. The salience and the motor control networks work together since selecting what matters in a given context involves capturing its dynamic aspects.

Thus, the core timing network utterly overlaps the salience network and the motor control network. What does this embedment suggest? It could be interpreted by considering “timing” (i.e., subjective time perception) an essential component of human cognition which underlies mental functions such as attention, working memory and anticipation of external events. In other words, processing of temporal information could be seen as a central subcomponent of these mental functions. In fact, empirically speaking, the concept of timing cannot be easily untangled from the concepts of attention and working memory (Coull *et al.*, 2011). This conceptual interdependence suggests that “timing” is not an inaccessible foundational component: At the same time that “timing” underlies certain mental functions, it is also modulated by these very functions. This makes it quite challenging to accept “timing” as an encapsulated neurobiological mechanism. Rather, given the empirical evidence, it is more tenable to conceive or approach the questions on where and how “timing” is represented in the brain in relation to mental functions (i.e., attention and working memory) to which it seems to be deeply bound up with. In other words, trying to escape conceptual circularity on the search for the neurobiological mechanisms of time perception is a thorny task.

The concept of episodic memory and its neurobiological substrates

The intuition that the concept of memory is rather broad and does not correspond to only a single mental faculty is an old one. Experimental inquiry by cognitive neuroscience, complementary to philosophical questioning and psychological explorations, has been crucial in understanding the neural aspect of memory systems. The modern experimental approach has begun with the famous patient H.M. (Henry Gustav Molaison), who in 1953, and at the age of 27, underwent a bilateral medial temporal lobectomy due to epilepsy. The successful surgery made him an anterograde amnesic patient, but despite his amnesia he could still learn new motor skills with practice, as well as maintain and manipulate information for a few minutes (i.e., hold a conversation). These observations showed that memory was not a unitary construct. First, it could be understood in terms of accessibility of temporary and permanent information to the subject. These two types of memory are called short- and long-term memory, respectively, and they involve separate neural mechanisms and are independently processed. Second, long-term memory includes motor (non-declarative or implicit) and cognitive (declarative or explicit) forms of memory. Later, affective

mnemonic properties, usually acquired as subtle associations, were included as another form of non-declarative memory. The declarative form of long-term memory is also called autobiographical memory, since it concerns recollections of specific personal events and facts. In the 1970s, Tulving (1972) suggested that autobiographical memory should be separated into episodic (particular *events* or *episodes* about the self) and semantic (*facts* about the self and the world) systems.

Since then, autobiographical memory has been conceptualized and empirically approached in terms of, on one hand, recalling personal semantic information linked to feelings of familiarity and of, on the other hand, recalling personal episodic information which requires re-experiencing or re-constructing unique past events. Indeed, functional neuroimaging and lesion studies have strongly suggested that the neural basis of the declarative self can be fractionated into two functionally independent systems. One system involves lateral cortical regions in the frontal (inferior frontal gyrus), parietal (inferior parietal lobe), and temporal (superior temporal gyrus, anterior temporal lobe) lobes as well as medial frontal (medial prefrontal cortex), parietal (precuneus), and temporal cortices (fusiform gyrus) (Binder and Desai, 2011). It supports semantic knowledge of facts about one's own life and personal identity, and is associated with noetic awareness (i.e., a sense of simply “knowing” without contextual – including temporal – details). The content of semantic memory is usually abstracted from actual experience and is therefore said to be conceptual (i.e., generalized). The other system is composed of the hippocampus and surrounding medial cortices such as the entorhinal and parahippocampal cortices – the so-called medial temporal lobe, and also the medial prefrontal cortex and the precuneus (Moscovitch *et al.*, 2016). It enables recollection of personal episodes, including information specific to the time and place of acquisition, and is associated with auto-noetic awareness. Thus, this ability goes beyond simply knowing “what” happened, “where” it happened and “when” it happened – the so-called *www* criteria (Suddendorf *et al.*, 2009). It requires a subjective sense of time and of the self as the one who experienced the episode and possesses the memory. The agent's personal relation with the specific episodic context (a context which includes the *www* criteria) is central for the mental capacity for reconstructing and reliving that episode.

As suggested by the neuroimaging data, the content of episodic memory depends heavily on retrieval of semantic knowledge. Recalling, for instance, having a glass of wine during dinner last night requires retrieving the concepts of glass, wine and dinner. The semantic knowledge plays a role in encoding semantically meaningful events in episodic memory. Therefore, it is not surprising that the two memory systems described above are highly interconnected. There are strong reciprocal connections between the hippocampus in the episodic network and the precuneus as well as the lateral and anterior temporal cortices in the semantic network.

Having brought forth the conceptual and neurobiological relations between semantic and episodic memory, it is

clear that, although both memory systems are fundamental parts of the declarative self, only episodic memory is associated with auto-noetic awareness. Thus, there must be something about the hippocampus and associated cortices regarding tracking personal time which makes up the sense of a continuous self⁷ that is part of the totality of the phenomenal experience. This would allow the phenomenal recollection during mental re-enactment of previous personal episodes. In fact, a key role for the hippocampus has been shown both in temporal organization of episodic memories (i.e., the dating of memories) and in remembering sequential organization of events within memories.

Regarding the labelling of “when” episodes occurred, studies have demonstrated that the hippocampal CA1 neurons are central in the retrieval of both remote and recent episodes (Bartsch *et al.*, 2011), and that the distinction between memories that are widely separated in time is given by the hippocampal activity patterns of CA1 neurons (Eichenbaum *et al.*, 2014, p. 275). These studies indicate that shifts in the spatiotemporal firing patterns of CA1 neurons are associated with evolving temporal context representation, with gradual changes in the neural representation of the hippocampal CA1 neural population over many days. Thus, it seems that these changes in the firing patterns of CA1 neurons represent the temporal labels of the temporally organized episodic memories. The retrieval of an episodic memory and its re-consolidation with a new memory trace goes beyond the CA1 neurons – it depends on the entrainment of a dynamically distributed hippocampal-cortical network (Moscovitch *et al.*, 2016). On the other hand, the preservation of the sequential order of events within episodes, including spatial and temporal contextual details, depends upon the stability of the activity patterns of hippocampal CA3 neurons (Davachi and DuBrow, 2015). More stable firing patterns – compared to the dynamic CA1 patterns discussed above – support the enduring feature of context-mediated episodic sequence. These findings indicate that both hippocampal subregions are critical in representing temporal information (involving ordered stimuli) across multiple timescales. While CA1 neurons show a gradually changing firing pattern across multiple days and are important in establishing the temporal gap between distant episodes, the stable response of CA3 neurons is critical in bridging events much closer in time and that supposedly belong together. In other words, CA1 represents how long ago an episode took place (“feeling of remoteness”) whereas CA3 represents the semantic cohesiveness of retrieved memories (“feeling of

rightness”). Thus, the hippocampus is central for the event-sequencing aspect of time, in both short and long timescales. This is important not only for the reconstruction of episodic memory, but also for the construction and organization of future planning – which will be discussed in the next section.

Neural correlates of MTT and self-referential cognition

MTT is the ability of an agent to mentally reconstruct past events as well as construct possible future events that involves the self. When it is directed toward the past it is called episodic memory (see the previous section); when it points toward the future it has been called future planning or future thinking and it concerns thinking about a hypothetical personal future event which can be flexibly used to plan future actions (Suddendorf *et al.*, 2009). In recent years, the field of cognitive neuroscience has prolifically produced studies investigating the neural underpinnings of this mental phenomenon – particularly examining the relation between re-experiencing one’s personal past and pre-experiencing an event by moving one’s self forward in time.

Neuroimaging research has revealed remarkable similarities between remembering the past and imagining or simulating the future. Also, counterfactual thinking seems to activate the same pattern of brain regions but with more pronounced activity (in both strength and extension) in some particular areas. These studies, thus, suggest a common core brain network underlying episodic memory, imagination, and counterfactual thinking (Schacter *et al.*, 2012; Van Hoeck *et al.*, 2013), which includes the medial frontal, parietal and temporal lobes (including the hippocampus) together with lateral parietal and temporal areas (overlapping the TPJ – see the section “Perception of time of external events”). These regions overlap substantially with the so-called default mode network (DMN)⁸. Activity in the DMN has been observed whenever the participant is put in a passive test condition with no requirements of broadly monitoring the external environment (i.e., watchfulness). The DMN seems to maintain unfocused external attention while engaging internally cognitive processes (i.e., external sentinel and internal mentation). Several studies have observed that task contexts that encouraged or allowed for stimulus-independent thoughts (i.e., mind-wandering or day-dreaming) are associated with increased activity in the DMN. However, these internal mentations include not only remem-

⁷ I take for granted that a neurotypical human adult subject has a sense of self extended in time (or continuous self), since it is impossible to conceive a neurotypical subject not extended in time (the very concept of “subject” must involve “continuation in time”). However, discussing how the representation of the self as an entity extended in time emerges or is built up is not the focus of the present article – it is a debated philosophical topic with several conflicting theories. For a neurocognitive approach, please see Gallagher (2000).

⁸ The discovery of the DMN was entirely accidental since no early neuroimaging studies were explicitly designed to examine unconstrained mental states. The DMN was identified when researchers decided to analyse the data by looking for significant increase of activation during the control (passive) condition compared to the experimental (goal-directed task) condition. Activity of a specific set of brain regions increased during undirected mentation rest conditions compared to virtually all cognitive tasks. This set of regions was labelled as the “default mode network” (for a review, see Buckner *et al.*, 2008).

bering the past and imagining the future, but also taking the perspective of others and engaging in spatial navigation in the present time. Thus, virtually the same brain regions subserve the mental transportation of one's self to events in the past or future and the imagination of self-referential situations which do not require this temporal displacement. These findings have complicated the hypothesis of mental time travel as an ability underpinned by an independent cognitive mechanism (Buckner and Carroll, 2007). It is more likely that the construct of mental time travel can be further reduced to several dissociable and more basic cognitive processes.

The aforementioned conceptual intricacy present in studies of timing (section "Perception of time of external events") is also present in studies of MTT, which poses experimental challenges in controlling for confounds of more basic processes that are part of the MTT ability. The process of MTT comprises the DMN to some extent. It is known that the DMN underlies internal mental exploration within the "self" dimension, i.e., thoughts that are self-relevant or self-referential. Thus, it is acceptable to say that MTT is a self-reflexive mental process. On the other hand, it still remains unclear what aspects of the DMN – or MTT function – reflect the conscious awareness of the existence of one's self in subjective time (i.e., the *temporal* component) as opposed to the constructive features of events of the declarative self (i.e., the *narrative* component) (Schacter *et al.*, 2012). Several studies on self-referential imagination tasks favour a non-temporal perspective of cognitive processes such as episodic memory, prospection, theory of mind, and spatial navigation. They defend that these processes are primarily narrative or constructive, that is, they rely upon the ability to retrieve disparate elements from a number of sources and bind details into coherent self-narratives rather than mentally travel through time (Eacott and Easton, 2012), eliminating the need for a concept of mental time travel. Contrarily, studies with careful experimental designs targeting precisely processes of interest have tapped into specific contributions of temporal and atemporal factors in MTT. These studies strongly indicate differences in neural representations between temporal and atemporal imagined scenarios (Nyberg *et al.*, 2010) – within the DMN areas, the middle frontal cortex showed greater activity in the non-present time (past and future) conditions compared to the present time condition.

Despite the great experimental challenge in isolating the cognitive processes associated with temporal factors from non-temporal cognitive activities and in balancing the cognitive load of the temporal and atemporal conditions, neuroimaging studies have started to uncover the neural substrate involved in imagery structured in time. But there is still a long way to be explored.

How does MTT relate to other temporal systems in the brain?

Modest contributions of neuroimaging studies of MTT relate the ability to mentally project oneself to non-present

times to the DMN, which is recruited during remembering the past and imagining the future. These findings in healthy adults are supported by two other types of studies. First, it has been observed that brain lesions and neurodegenerative diseases which disrupt certain types of activity in the DMN also impair only the auto-noetic component of self-reference tasks. For instance, Rosenbaum *et al.* (2007) report that amnesic individuals who cannot transport themselves into past or future personal episodes (i.e., are limited to a life about their immediate environment) could nevertheless take the perspective of others by imagining what others might be thinking. Second, developmental studies have reported a relationship between memory and imagination, MTT and the functional architecture of the default-mode network in the developing brain (Østby *et al.*, 2012). Thus, although we cannot make absolute claims about the neural correlates of auto-noetic awareness during MTT, there is sufficient scientific evidence to allow the inference that it possibly has to do with the DMN.

So, considering that the DMN somehow underlies the subjective sense of time during MTT tasks, how would it be associated to the neural substrates of the also called "subjective time" in tasks of duration estimation and order judgements? In other words, how and to what extent are the internal (projective "travel") and the external (watching) subjective time systems related?

The medial temporal lobe – which includes the hippocampus – is part of the DMN. The hippocampus is strongly connected to the striatum, which is one of the nuclei in the BG (see section "Perception of time of external events"). The striatum is one of the main components of the corticostriatal network which underlies metric timing, i.e., the explicit and implicit interval timing. Hippocampal lesions result in increased dopaminergic transmission in the striatum, which leads to long-term alterations in the accuracy and precision of estimating the duration of intervals (in the seconds-to-minutes range) (Meck, 2005). Therefore, patients with hippocampal amnesia, in addition to impaired episodic memory and future imagining, also underestimate retrospective durations and underproduce prospective durations. Conversely, the disruption of striatal dopaminergic circuits also impairs the hippocampal function of constructing non-present time episodes. Parkinson's disease patients, which have low dopamine in the nigrostriatal pathway, exhibit an impaired ability in imagining future events, but have no difficulties in imagining atemporal scenarios (de Vito *et al.*, 2012). Other studies have reported that schizophrenic patients, who have dopaminergic hyperfunction in the mesolimbic pathway (which includes the striatum), experience a distorted sense of continuity of self across time. They show pronounced difficulties in recalling events from their personal past and in generating events that might happen to them in the future (D'Argembeau *et al.*, 2008).

These results strongly suggest a connection between the functional systems supporting internal subjective time awareness and external subjective time perception. The per-

ception of the passage of time seems to be dependent on a balanced dopaminergic transmission between the striatum on the one hand, which is part of the metric timing network, and the hippocampus on the other hand, which is part of the DMN.

Conclusion

Neuroimaging evidence described in the present article points towards more than one subjective timing network. The two major “timekeeping” systems described in the literature are those related to the perception of time of external events and the internal mentation of projecting ourselves through time. It has been suggested that the former is underpinned by a network of brain regions that are part of the salience network and the motor network. There is evidence that the latter is supported by the default mode network. In addition, the former could be seen as the timing mechanism for processing “the now” (by which the subject perceives events happening in the present moment), and the latter could be seen as the timing mechanism which allows the subject to engage in past and future episodes (processing the non-present moments). Also, the structuring in our minds of our subjective feeling of the passage of time seems to involve the integration of these two main systems, particularly via connections between the basal ganglia (striatum) and the hippocampus. Neuroimaging and neuropsychological data suggest that the dynamic coupling between the externally- and internally-oriented temporal attention supports temporal cognition across a broad range of stimulus contexts and temporal scales.

However, in neuropsychology, the concepts of working memory and attention cannot be defined (and, thus, assessed) without resorting to the concept of timing, which in turn cannot be understood without making reference to the concepts of attention and working memory. This conceptual circularity causes timing to both underpin and be underpinned by attention and working memory. Thus, attention and working memory are not simply confounding factors, as authors put it. For that, they would have to be task-related but non-temporal processes, which seems not to be the case since they belong in the very definition of “timing”. Similarly (but to a lesser extent), the neuropsychological concept of subjective time is intertwined with that of self-reference. Conceptual confusion leads to incoherent experimental premises, dampening clarity in experimental design and data interpretation.

Given the extent of recent interest in MTT in cognitive neuroscience, it would be important to investigate the logical relations among key concepts. This is a philosophical task that should be conducted in cooperation with the field of neuroscience. Understanding the neural structures and dynamics involved in temporal mental processes – including the complex construct of MTT – demands ingenious experimental designs that cannot be achieved without conceptual and categorical clarity.

References

- BARTSCH, T.; DOHRING, J.; ROHR, A.; JANSEN, O.; DEUSCHL, G. 2011. CA1 Neurons in the Human Hippocampus are Critical for Autobiographical Memory, Mental Time Travel, and Autonoetic Consciousness. *Proceedings of the National Academy of Sciences of the United States of America*, **108**(42):17562-17567.
<https://doi.org/10.1073/pnas.1110266108>
- BATTELLI, L.; PASCUAL-LEONE, A.; CAVANAGH, P. 2007. The “When” Pathway of the Right Parietal Lobe. *Trends in Cognitive Sciences*, **11**(5):204-210.
<https://doi.org/10.1016/j.tics.2007.03.001>
- BINDER, J.; DESAI, R. 2011. The Neurobiology of Semantic Memory. *Trends in Cognitive Sciences*, **15**(11):527-536.
<https://doi.org/10.1016/j.tics.2011.10.001>
- BUCKNER, R.L.; CARROLL, D.C. 2007. Self-projection and the Brain. *Trends in Cognitive Sciences*, **11**(2):49-57.
<https://doi.org/10.1016/j.tics.2006.11.004>
- BUCKNER, R.L.; ANDREWS-HANNA, J.R.; SCHACTER, D.L. 2008. The Brain’s Default Network: Anatomy, Function, and Relevance to Disease. *Annals of the New York Academy of Sciences*, **1124**(1):1-38.
<https://doi.org/10.1196/annals.1440.011>
- BUHUSI, C.V.; MECK, W.H. 2005. What Makes Us Tick? Functional and Neural Mechanisms of Interval Timing. *Nature Reviews Neuroscience*, **6**(9):755-765.
<https://doi.org/10.1038/nrn1764>
- COULL, J.T.; CHENG, R.K.; MECK, W.H. 2011. Neuroanatomical and Neurochemical Substrates of Timing. *Neuropsychopharmacology*, **36**(8):3-25.
<https://doi.org/10.1038/npp.2010.113>
- D’ARGEMBEAU, A.; RAFFARD, S.; VAN DER LINDEN, M. 2008. Remembering the Past and Imagining the Future in Schizophrenia. *Journal of Abnormal Psychology*, **117**(1):247-251.
<https://doi.org/10.1037/0021-843X.117.1.247>
- DAVACHI, L.; DuBROW, S. 2015. How the Hippocampus Preserves Order: The Role of Prediction and Context. *Trends in Cognitive Sciences*, **19**(2):92-99.
<https://doi.org/10.1016/j.tics.2014.12.004>
- DE VITO, S.; GAMBOZ, N.; BRANDIMONTE, M.A.; BARONE, P.; AMBONI, M.; DELLA SALA, S. 2012. Future Thinking in Parkinson’s Disease: An Executive Function? *Neuropsychologia*, **50**(7):1494-1501.
<https://doi.org/10.1016/j.neuropsychologia.2012.03.001>
- EACOTT, M.J.; EASTON, A. 2012. Remembering the Past and Thinking about the Future: Is It really about Time? *Learning and Motivation*, **43**(4):200-208.
<https://doi.org/10.1016/j.lmot.2012.05.012>
- EICHENBAUM, H.; MacDONALD, C.J.; KRAUS, B.J. 2014. Time and the Hippocampus. In: D. DERDIKMAN; J.J. KNIERIM (eds.), *Space, Time and Memory in the Hippocampal Formation*. Heidelberg, Springer, p. 273-301.
https://doi.org/10.1007/978-3-7091-1292-2_11
- GALLAGHER, S. 2000. Philosophical Conceptions of the Self: Implications for Cognitive Science. *Trends in Cognitive Science*, **4**(1):14-21.
[https://doi.org/10.1016/S1364-6613\(99\)01417-5](https://doi.org/10.1016/S1364-6613(99)01417-5)
- IVRY, R.B.; SPENCER, R.M. 2004. The Neural Representation of Time. *Current Opinion in Neurology*, **14**(2):225-232.
<https://doi.org/10.1016/j.conb.2004.03.013>

- MANIADAKIS, M.; TRAHANIAS, P. 2011. Temporal Cognition: A Key Ingredient of Intelligent Systems. *Frontiers in Neurobotics*, **5**:2. <https://doi.org/10.3389/fnbot.2011.00002>
- MATTHEWS, W.J.; MECK, W.H. 2016. Temporal Cognition: Connecting Subjective Duration to Perception, Attention, and Memory. *Psychological Bulletin*, **142**(8):865-907. <https://doi.org/10.1037/bul0000045>
- MECK, W.H. 2005. Neuropsychology of Timing and Time Perception. *Brain and Cognition*, **58**(1):1-8. <https://doi.org/10.1016/j.bandc.2004.09.004>
- MOSCOVITCH, M.; CABEZA, R.; WINOCUR, G.; NADEL, L. 2016. Episodic Memory and beyond: The Hippocampus and Neocortex in Transformation. *Annual Review of Psychology*, **67**:105-134. <https://doi.org/10.1146/annurev-psych-113011-143733>
- NYBERG, L.; KIM, A.S.; HABIB, R.; LEVINE, B.; TULVING, E. 2010. Consciousness of Subjective Time in the Brain. *Proceedings of the National Academy of Sciences of the United States of America*, **107**(51):22356-22359. <https://doi.org/10.1073/pnas.1016823108>
- ØSTBY, Y.; WALHOVD, K.B.; TAMNES, C.K.; GRYDELAND, H.; WESTLYE, L.T.; FJELL, A.M. 2012. Mental Time Travel and Default-mode Network Functional Connectivity in the Developing Brain. *Proceedings of the National Academy of Sciences of the United States of America*, **109**(42):16800-16804. <https://doi.org/10.1073/pnas.1210627109>
- ROSENBAUM, R.S.; STUSS, D.T.; LEVINE, B.; TULVING, E. 2007. Theory of Mind Is Independent of Episodic Memory. *Science*, **318**(5854):1257. <https://doi.org/10.1126/science.1148763>
- SCHACTER, D.L.; ADDIS, D.R.; HASSABIS, D.; MARTIN, V.C.; SPRENG, R.N.; SZPUNAR, K.K. 2012. The Future of Memory: Remembering, Imagining, and the Brain. *Neuron*, **76**(4):677-694. <https://doi.org/10.1016/j.neuron.2012.11.001>
- SCHUBOTZ, R.I. 2007. Prediction of External Events with Our Motor System: Towards a New Framework. *Trends in Cognitive Sciences*, **11**(5):211-218. <https://doi.org/10.1016/j.tics.2007.02.006>
- SUDDENDORF, T.; ADDIS, D.R.; CORBALLIS, M.C. 2009. Mental Time Travel and the Shaping of the Human Mind. *Philosophical Transactions of the Royal Society B*, **364**(1521):1317-1324. <https://doi.org/10.1098/rstb.2008.0301>
- SUDDENDORF, T.; CORBALLIS, M.C. 1997. Mental Time Travel and the Evolution of the Human Mind. *Genetic Social and General Psychology Monographs*, **123**(2):133-167.
- SZPUNAR, K.K. 2011. On Subjective Time. *Cortex*, **47**(3):409-411. <https://doi.org/10.1016/j.cortex.2010.07.008>
- TULVING, E. 1972. Episodic and Semantic Memory. In: E. TULVING; W. DONALDSON (eds.), *Organization of Memory*. New York, Academic Press, p. 382-402. <https://doi.org/10.1111/1467-8721.ep10770899>
- TULVING, E. 1993. What Is Episodic Memory? *Current Directions in Psychological Science*, **2**(3):67-70. <https://doi.org/10.1017/S0140525X07002208>
- TULVING, E.; KIM, A. 2007. The Medium and the Message of Mental Time Travel. *Behavioral and Brain Sciences*, **30**(3):334-335. <https://doi.org/10.1093/scan/nss031>
- VAN HOECK, N.; MA, N.; AMPE, L.; BAETENS, K.; VANDERKERCKHOVE, M.; VAN OVERWALLE, F. 2013. Counterfactual Thinking: An fMRI Study on Changing the Past for a Better Future. *Social Cognitive and Affective Neuroscience*, **8**(5):556-564.

Submitted on October 20, 2017

Accepted on January 16, 2018