

# The persistence of memory: how the brain encodes time in memory

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Time and memory are inextricably linked, but it is far from clear how event durations and temporal sequences are encoded in memory. In this review, we focus on resource allocation models of working memory which suggest that memory resources can be flexibly distributed amongst several items such that the precision of working memory decreases with the number of items to be encoded. This type of model is consistent with human performance in working memory tasks based on visual, auditory as well as temporal stimulus patterns. At the neural-network level, we focus on excitatory–inhibitory oscillatory processes that are able to encode both interval timing and working memory in a coupled excitatory–inhibitory network. This modification of the striatal beat-frequency model of interval timing shows how memories for multiple time intervals are represented by neural oscillations and can also be used to explain the mechanisms of resource allocation in working memory.

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## Introduction

Time is an integral aspect of action, perception, and cognition [1,2,3•,4]. However, the neural mechanisms that encode and store intervals of time in memory for the perception of sensory stimulus patterns and production of complex sensorimotor output are not fully understood [5–7]. Here, we describe recent behavioral, computational, neuroimaging, and physiological findings that shed new light on the neurobiological bases of

temporal memory. Specifically, we focus on resource allocation models of working memory which suggest that memory resources can be flexibly distributed amongst several items such that the precision of working memory decreases with the number of items to be encoded. These models are consistent with human performance in working memory tasks based on visual, auditory as well as temporal stimulus patterns [8]. At the neural network level, we focus on an excitatory–inhibitory oscillation (EIO) model that encodes both interval timing and working memory in a coupled excitatory–inhibitory network [9•]. This model shows how the memories for multiple time intervals are represented by neural oscillations and also explains the mechanisms of resource allocation in working memory. We review the results from these experimental studies and generalize how these findings might be integrated in order to obtain a neurobiologically-plausible code for incorporating temporal information in working memory [10].

## Models of working memory

Working memory is traditionally defined as a cognitive capacity for transiently storing, processing, and manipulating information [11]. Although the notion of working memory extends naturally for sensory information like visual or auditory signals, it is not clear how it applies to temporal information, even though conceptually, time and memory are closely interlinked. Classical models of working memory propose a fixed number of discrete memory ‘slots’ where only a limited number of items can be represented in memory with a fixed resolution [12,13]. However, these models based on change-detection paradigms have been recently challenged by new models that suggest working memory is a limited resource that is dynamically shared between all sensory items to be stored in memory [14–16]. Furthermore, this memory resource is flexible and can be modulated by cognitive factors like selective attention and task demands where each item is stored with either a fixed [14,17] or variable resolution [15]. These models suggest that memory recall is a continuous rather than a binary measure and characterized in terms of ‘precision’ (computed as the inverse of the standard deviation of error responses) that might be equal or variable across all items [16]. Several experimental studies have demonstrated these novel hypotheses to be consistent with visual [14–20] and auditory working memory performance [21–23]. In light of these recent findings, the current consensus is that working memory might be best viewed as a limited resource that is flexibly

allocated across all items to be stored in memory [8,24,25,26\*].

### Resource models of temporal memory

Recent work has examined the resource model of working memory in the context of interval timing behavior [27\*]. Participants were presented a sequence of clicks, where the temporal jitter between clicks was parametrically varied from 5% to 50% across four distinct levels of jitter. At the offset of the sequence, a visual probe displayed the interval number whose duration participants were required to reproduce. The start of the reproduction interval was cued by another click and participants had to respond at a point in time that corresponded to their memory of the probed interval duration. The difference between the actual and the reproduced duration was quantified to obtain the error distribution and the precision of temporal memory recall. An outline of this timing task is provided in Figure 1.

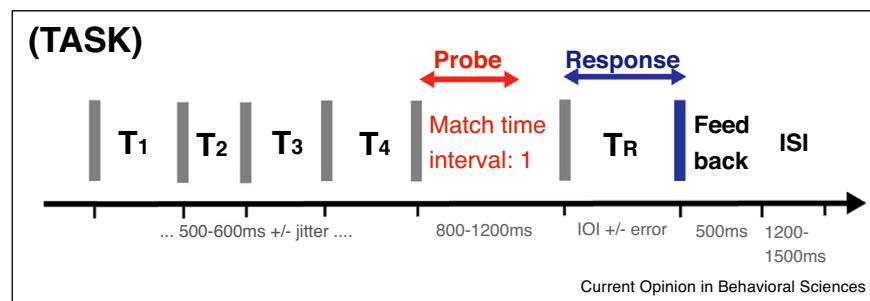
In two separate experiments, the time intervals between the clicks were either in the sub-second (500–600 ms) or supra-second range (1.0–1.2 s). In both experiments, working memory for the probed interval declined in irregular sequences with higher levels of jitter. This result demonstrated for the first time that temporal memory depends on the temporal structure of the sequences containing those intervals, a finding that cannot be concluded from binary judgment of the duration of single time intervals. The effect was stronger for sub-second compared to supra-second intervals, and primacy and recency effects of memory recall were also observed for the sub-second, but not the supra-second sequences of intervals. Furthermore, the precision values for the sub-second versus the supra-second intervals were approximately in the ratio 1:2, demonstrating a trend consistent with the scalar property of interval timing [28–31,32\*].

Another experiment in the same study introduced a variable number of clicks in the sequences to simulate variable working memory load (1–4 items). The precision of temporal memory decayed nonlinearly with increasing number of intervals in the sequence, consistent with the predictions of the resource allocation models of working memory [8]. These results were recently replicated in another set of behavioral experiments [32].

### Neural mechanisms of temporal memory

A key question that follows from these behavioral experiments concerns the underlying neuronal substrates of temporal memory. Dedicated models of interval timing suggest that time is encoded in distributed subcortical and cortical networks [6,10,33–35]. However, the neural substrates of temporal memory have received considerably less attention. Initial studies focused on memory-based comparison of the absolute duration of a target interval versus a single reference interval. Rao and colleagues [36] used event-related functional magnetic resonance imaging (fMRI) and observed early activity in the basal ganglia associated with encoding time intervals and late activation in the cerebellum. Early cortical activation was observed in the right inferior parietal cortex and bilateral premotor cortex associated with attention and maintenance of intervals whilst late activation in the right dorsolateral prefrontal cortex emerged during the actual comparison of time intervals. In a similar rapid event-related fMRI study, Coull and colleagues [37] found the left putamen to be active during encoding the stimulus duration into working memory and the putamen response was also predictive of timing performance whilst retrieval and comparison of stimulus durations engaged the right superior temporal gyrus. These results, however, are limited as they only account for encoding single time intervals in working memory.

**Figure 1**



Temporal memory task [adapted from 38\*]. Listeners are presented a sequence of time intervals separated by clicks. A visual message is used to display the probe interval to be remembered and reproduced at the offset of the last click in the sequence. After a variable delay period, listeners hear another click which signifies the start of the interval to be reproduced by pressing a button when they think that duration equal to the probed interval has elapsed. Feedback measured as the difference between the duration of the reproduced and the probed interval is presented after each trial.

Teki and Griffiths [38<sup>\*</sup>] used fMRI to examine the substrates of temporal memory that vary according to the temporal structure and number of items in the sequences based on their previous behavioral task [27<sup>\*</sup>]. In two orthogonal conditions, the temporal jitter in sequences was parametrically varied (5–50% jitter) for a fixed number of intervals (4), and the number of intervals in the sequence was modulated (1–4 intervals) for a fixed jitter level (20–25%).

Blood-oxygen-level-dependent (BOLD) responses associated with the recall of the probed interval were observed in the cerebellum as a function of increasing jitter and the striatum (left putamen and caudate nucleus) as a function of decreasing jitter respectively. This result is consistent with previously reported dissociation of perceptual timing responses in the cerebellum and striatum according to the temporal context of the sequences: cerebellum is more active during perception of time intervals in an irregular context whilst the striatum is more active for regular, beat-based sequences [39]. These results suggest that mnemonic precision of temporal memory recall also shows the same contextual pattern of responses in these two core sub-cortical timing networks [6,35,40]. Furthermore, activity in bilateral inferior parietal cortex and the caudate nucleus increased as a function of increasing number of time intervals (or working memory load), in accord with previous findings [36,37].

### Neural models of temporal memory

Although neuroimaging studies can shed light on the underlying neuronal substrates, the precise mechanism by which time is encoded in working memory is not yet understood. Gu *et al.* [9<sup>\*</sup>] recently proposed a coupled excitatory-inhibitory oscillation mechanism in order to integrate the striatal beat frequency (SBF) model of interval timing [41<sup>\*</sup>,42,43] with oscillatory models of working memory [44]. This hybrid EIO model is based on the assumption that information for both interval timing and working memory is represented in the same network with oscillatory interactions between excitatory and inhibitory inputs. According to the EIO model, interval timing and working memory differ in terms of which dimension of the neural oscillations is utilized for the extraction of item, temporal order or duration information. Specifically, the model suggests that duration information can be extracted from theta oscillations entrained in the delta rhythm while item information in working memory can be extracted from gamma oscillations entrained in the theta rhythm respectively. Moreover, this proposal is supported by recent electrophysiological studies [45,46<sup>\*</sup>,47].

The EIO model primarily accounts for duration information that is not defined by specific movements or a continuous predictable pattern of stimulus presentations,

but a cognitively controlled measurement of supra-second durations. However, other ranges of duration including sub-second are reported to involve beta and/or gamma rhythms, especially when specific movements or predictable patterns are involved [48–50]. In this case, the EIO model can be extended to explain the representation of sub-second, rhythmic duration using beta oscillations entrained in delta/slower rhythm. In addition, the EIO model readily explains the basic features of resource allocation (e.g., reduced precision with increasing number of intervals) when maintaining multiple intervals in working memory.

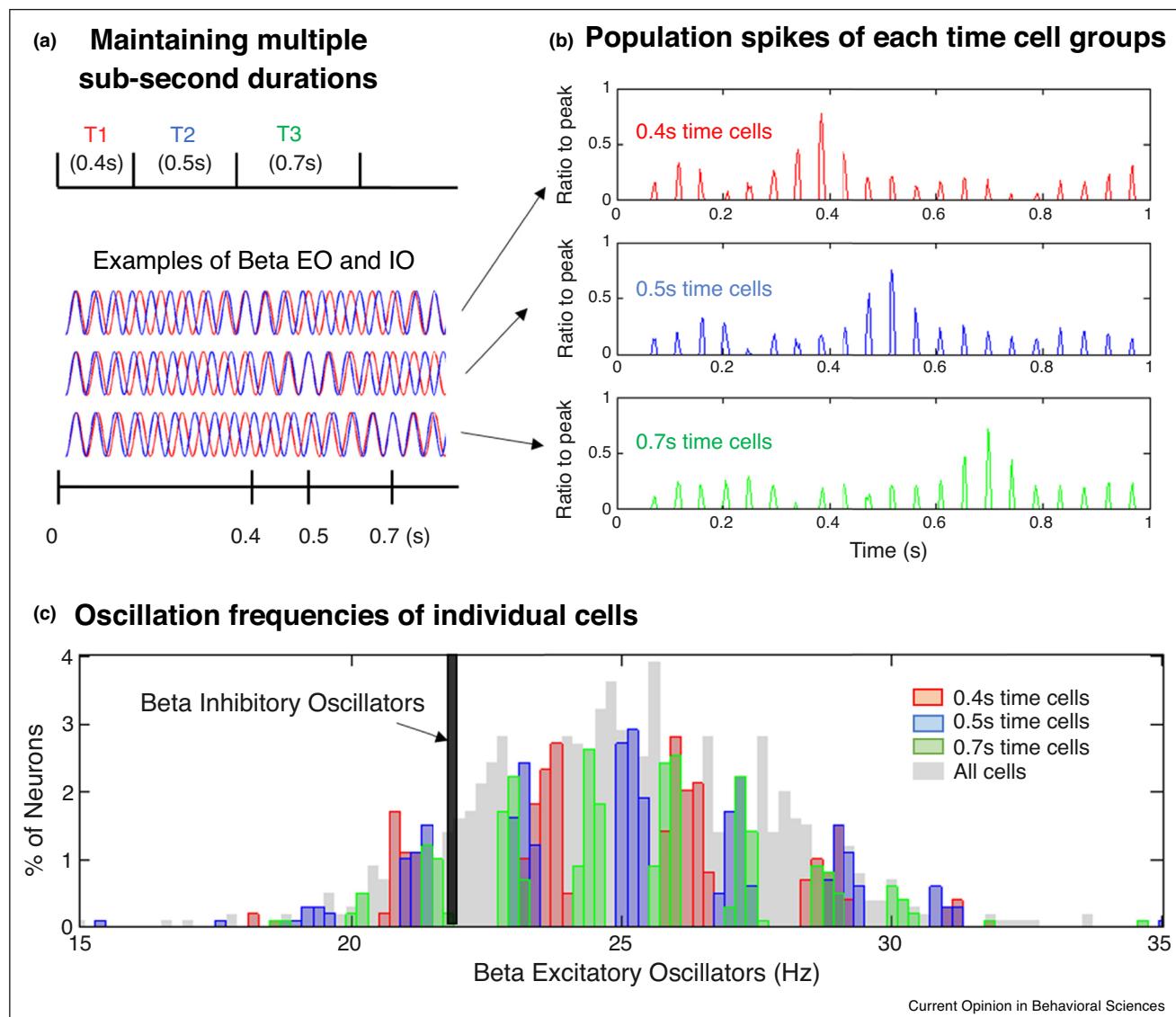
The EIO model assumes that a triggering event will perturb the neural network such that the frequency of excitatory oscillation (EO) inputs varies across neurons while inhibitory oscillation (IO) inputs are relatively synchronized within a local neuronal network (Figure 2a). With sound onset to be timed, EO and IO will oscillate in beta rhythms and the summation of EO and IO inputs in each neuron will produce an interference pattern of beta entrained in delta or a slower rhythm. Variation in EO frequencies produces the variation of the envelope delta frequencies, thus the peak firing rate of each neuron varies in time. The coincident pattern of a group of neurons encodes duration information, for example, the group of cells that have a peak activity at 0.4 s form a triggering event that can represent the 0.4-s duration (Figure 2b). Different groups of cells are used to represent different durations, however, there will be overlapping cells among different time cell groups (Figure 2c). These overlapping time cells reduce the precision of temporal memory when multiple durations have to be maintained simultaneously, consistent with the resource allocation models of working memory.

Multiple brain areas such as cortico-striatal circuits, hippocampus, and cerebellum have been suggested to mediate interval timing [51<sup>\*</sup>,52–54]. The characteristics of time intervals such as the duration range or regularity of intervals have been associated with the involvement of specific brain areas. The network properties of those brain areas are different from each other, therefore different patterns of neural oscillations will be optimally represented by each brain area. The oscillatory property of a neural network is likely to be the determining factor for which brain area is the best place to represent certain characteristics of an interval of time.

### Integration of hippocampal time cells

The hippocampus is largely involved in relational memory and encodes information based upon almost any salient features of a task, evidenced by the vast changes in its information processing as a function of context [55]. The capacity to support relational memory makes the hippocampus an ideal brain structure for temporal integration [56,57], as temporal connections are implicitly

Figure 2



Excitatory-inhibitory oscillation model of interval timing and working memory. **(a)** Multiple sub-second durations can be maintained by multiple interference patterns produced by excitatory oscillators (EO, blue) and inhibitory oscillators (IO, red). A triggering event (e.g., click sound) can drive various frequencies of EOs in beta frequency range across a cell population (desynchronized) with relatively synchronized IOs. The EO and IO inputs produce beta rhythms entrained in delta or a slower frequency, and this pattern can be maintained during sub-second durations. **(b)** The coincident firing pattern of a relevant neuronal group encodes the duration information for a time interval. For example, the 0.4-s time cells are a neuronal group showing a firing peak around 0.4 s and their population firing produces beta rhythm whose power peaks at 0.4 s. Similarly, other groups of time cells represent different durations. **(c)** A distribution of beta EO frequencies for simulated neurons. The EO frequency of individual neurons determines the duration that they can represent. Increasing the number of durations to encode will produce overlaps between the cell groups, and this overlap will undermine the precision of temporal memory. This prediction is consistent with the results of Teki et al. [38\*] showing that time is embedded in the memory code.

made between events. These implicit connections can be made in many contextual frames so it is essential to identify the most parsimonious reference point (e.g., temporal or spatial). The temporal reference frame in hippocampal ‘time cells’ was first identified in the CA1 pyramidal layer of rats by MacDonald and colleagues [58]. Their findings provided support for the proposal that

hippocampal ‘time cells’ signal both temporal and spatial information on a continuum. This was based on the observation that when the duration of a delay period was suddenly changed, largely new sequential patterns of activity emerged. Thus, just as ‘place cells’ remap to represent different spatial contexts, these ‘time cells’ adjusted (what the authors referred to as ‘retimed’) in

order to represent a different temporal context. Consequently, these hippocampal neurons are referred to as ‘time cells’ because they share many of the same general properties of ‘place cells’, but are instead correlated with the temporal domain.

The temporal coding properties of hippocampal CA1 cells are thought to arise from either changing cortical states, strengthening of chain-like connectivity causing sequential activation, or a combination of the two [59]. Computational modeling may provide an additional tool to understand how CA1 cells acquire their ability to time [60–62]. For example, one model has shown that the firing rate and phase of ‘time cells’ relative to theta oscillations can approximate physical time on a single trial basis [63]. Recent evidence also points to a role of CA2 in timing behavior given that activity within this region is more time dependent compared to other CA subfields. One hypothesis is that CA2 provides temporal information to CA1 whereas CA3 sends spatial information [64]. Entorhinal ‘grid cells’ are also probably a source of temporal information for these ‘time cells’ [65]. It is important to note that some of the timing properties of CA1 may arise from many complex anatomical connections. For example, CA1 pyramidal neurons are excellent at integrating information across spatiotemporal gradients. With approximately 30 000 synapses to manage, the pyramidal neurons use hyperpolarization-activated cyclic nucleotide-gated channels to synchronize synaptic inputs across time and distance in relation to the soma so that each input carries equal weight [66]. In this respect, there is an interesting similarity between the ‘oscillatory interference’ models of grid cell firing and the currently proposed EIO model of timing [67,68].

By contrast to the studies of hippocampal involvement in prospective timing [69], none of the behavioral tasks used to evaluate hippocampal ‘time cells’ require that specific durations be timed in order to earn reward. It is therefore likely that hippocampal ‘time cells’ are used to construct a temporal framework for memories using retrospective timing rather than being used to time specific durations [56]. This greatly reduces attentional demands as retrospective timing creates a sense of time for events that were not explicitly timed. This retrospective framework is consistent with the vast literature showing the hippocampus is crucial for sequence learning and retrieval. BOLD fMRI studies have been used to show that hippocampal activation patterns during retrieval carry information about when objects occur in learned sequences, even without being instructed to pay attention to the temporal structure of sequences [70].

## Conclusions

As suggested above, information derived from and maintained by interval timing and working memory can be conveyed through different ranges of brain oscillations

involving theta entrained in delta and gamma entrained in theta, respectively. The functional role of neural oscillations is unlikely to be limited to interval timing and working memory, but can also be applied to most of other psychological functions via different frequency ranges of oscillations conveying different dimensional information [71–77]. Gamma oscillations, for example, have been proposed to be responsible for the ‘binding’ of features into a coherent cognitive unit [78,79] and the ultrafast oscillations, which are also known as ripples (150–250 Hz), represent replay of previously experienced firing patterns in a temporally compressed manner and has been shown to be vital for memory transfer and consolidation [80–82]. Moreover, increasing evidence supports the importance of infra-slow fluctuations (<0.1 Hz) in cognition as well as in brain signals [76]. The variance in cognitive performance fluctuates over tens to hundreds of seconds and has largely been considered ‘noise’; however, the variance of cognition/behavior has shown to increase with time scales, showing 1/f-type power distribution rather than just a random (white noise) distribution in the temporal sequence of errors [83–85]. This suggests that the temporal variance of cognition originates from a common mechanism that coordinates time and memory across a wide range of memory processes that are modulated by competitive cuing, temporal precision, and oscillator-based encoding of duration [86–98].

## Conflict of interest statement

Nothing declared.

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