

Not “just” a coincidence: Frontal-striatal interactions in working memory and interval timing

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The frontal cortex and basal ganglia play central roles in working memory and in the ability to time brief intervals. We outline recent theoretical and empirical work to suggest that working memory and interval timing rely not only on the same anatomic structures, but also on the same neural representation of a specific stimulus. Specifically, cortical neurons may fire in an oscillatory fashion to form representations of stimuli, and the striatum (a basal ganglia structure) may detect those patterns of cortical firing that occur co-incident to important events. Information about stimulus identity can be extracted from which cortical neurons are involved in the representation, and information about duration can be extracted from their relative phase. The principles derived from these biologically based models also fit well with a family of behaviourally based models that emphasise the importance of time in many working memory phenomena.

Working memory involves the storage and manipulation of information over brief time periods, typically in the seconds to minutes range. Interestingly, working memory relies on the same prefrontal cortex (PFC) and basal ganglia brain structures as those involved in interval timing, or the ability to perceive and make judgements about durations in the same seconds to minutes range (see reviews by Gibbon, Malapani, Dale, & Gallistel, 1997; MacDonald & Meck, 2003; Matell, Meck, & Nicolelis, 2003a, 2003b; Meck, 1996, 2003; Meck & Benson, 2002; Middleton & Strick,

2000; Rao, Mayer, & Harrington, 2001; Smith & Jonides, 1999). On the one hand, PFC and basal ganglia involvement in both working memory and interval timing might simply reflect a general contribution of these regions to cognition, perhaps through some ubiquitous element such as attention. Alternatively, this common neural substrate may reflect a deeper, more functional link.

Recent behavioural work favours the latter possibility. For example, accurate production of a brief time interval (e.g., 2 s) is increasingly distorted by increasing the size of the search set in

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a concurrently performed Sternberg working memory task, but is not altered by changing the set size in a visual search task with minimal working memory requirements (Fortin, Rousseau, Bourque, & Kirouac, 1993). Interference effects between working memory and interval timing appear robust across different durations and timing procedures (e.g., Fortin & Couture, 2002), and may be specific to processing, rather than storage, aspects of working memory (see review by Fortin, 1999).

The importance of temporal information in working memory has been given extensive consideration by some behaviourally based models including SIMPLE (Scale Invariant Memory, Perception, and Learning; Brown, Neath, & Chater, 2002) and OSCAR (OSCillator-based Associative Recall; Brown, Preece, & Hulme, 2000). SIMPLE emphasises the role that Weber's law plays in the ability to distinguish items that differ along some dimension (e.g., weight, size, or frequency) and assumes that the important dimension for memory is often time. (See Burgess & Hitch, 1999, and Howard & Kahana, 2002, for alternative ideas about the role of time in memory.) OSCAR is a variant of SIMPLE that is specifically concerned with memory and that implements the Weberian properties of time via a series of oscillating representations with hierarchically arranged periodicities. According to these models, items are arranged in memory along two dimensions: featural similarity and temporal similarity. The closer two items are within those dimensions, the more confusable they will be.

Models such as OSCAR characterise working memory representations as hierarchically organised and oscillatory over time. These characteristics allow them to account for a wide range of working memory phenomena. For example, in list learning, the list provides one level of representation, and individual items are temporally organised within it (i.e., associated with different oscillatory states of the list structure). When learning multiple lists, patterns of interference can occur such that a current list item is confused with a previous-list item in the same relative position. According to OSCAR, this occurs because the two interchanged items are very similar—and thus confusable—in terms of their position within their respective lists. Brown and colleagues (Brown & Chater, 2001; Brown & Vousden, 1998) draw an analogy to a clockface, with list information represented by the hour hand and position information represented by the minute hand: A 3:30

meeting is more confusable with a 4:30 meeting than with a meeting at 4:15.

In the serial recall of a single list, primacy and recency effects (the memory advantage for the first and last items in the list compared to intermediate items) may occur because the first and last items in the list have only one temporally adjacent item (the one immediately following or preceding), whereas other items have two adjacent—and thus confusable—neighbours. Importantly, Brown et al. (2000, 2002) note that within-list organisation is temporal, not ordinal: If items within the list are presented with variable interstimulus intervals, those items that are more temporally (not ordinally) distant from others will be better recalled (Neath & Crowder, 1990). This finding strongly implicates time as an important context for working memory.

How is the relationship between time and working memory reflected in the brain? To address this question, we summarise the general principles of two recent, separate biologically based working memory and interval timing models, and search for common ground between them. The working memory model (Frank, Loughry, & O'Reilly, 2001) is primarily concerned with identity, or item, information, as represented by the activation of different subsets of cortical neurons. The interval-timing model (Matell & Meck, 2000, 2004; Matell et al., 2003b) is primarily concerned with temporal and order information, as represented by the oscillatory state of neuronal firing over time. Both models emphasise the important role of the striatum, a basal ganglia structure, in detecting and reacting to those patterns of cortical firing that occur coincident to relevant stimulus events.

Our analysis suggests that this “coincidence detection” function of the striatum constitutes a fundamental connection between working memory and interval timing. To preview, working memory and interval timing may rely not only on the same gross neural structures, but also on the same neural representations of a particular stimulus event. Information about stimulus identity may be contained in the specific cortical neurons that fire in response to stimulus presentation. These neurons are presumed to fire in an oscillatory fashion, with duration information contained in their relative phase. Spiny neurons in the striatum may integrate inputs from the cortical neurons to allow the processing of important information about stimulus identity (which neurons are firing) and

duration (the state of those neurons at important times).

The mechanisms by which the same frontal-striatal interactions may support both working memory and interval timing are discussed in more detail below. First, to provide the necessary background, we outline the brain structures involved and their proposed functions in separate models of working memory and interval timing.

FRONTAL CORTEX AND BASAL GANGLIA IN MODELS OF WORKING MEMORY

For working memory, we start with a model recently proposed by Frank et al. (2001). The basic principles of this model are similar to and build upon other concepts of frontal cortex and basal ganglia function in working memory (e.g., Beiser & Houk, 1998; Wise, Murray, & Gerfen, 1996). It differs from previous work by emphasising specific roles for these structures, such that the “frontal cortex uses continuously firing activations to encode information over time in working memory (or, on a shorter time scale, to execute motor actions), and the basal ganglia fires only at very select times to trigger the updating of working memory states (or initiate motor actions) in the frontal cortex” (Frank et al., 2001, p. 146).

A diagram of the brain structures involved in working memory and interval timing is presented in Figure 1. Presentation of a stimulus activates its representation in prefrontal cortex (PFC) in addition to its representations in more primary areas, e.g., visual or auditory cortex. Recurrent excitation among the initially activated neurons may be sufficient to maintain this representation if there is no competition, but this passive maintenance quickly decays with the presentation of other stimulus inputs (Frank et al., 2001). Active maintenance in the face of competition requires the establishment of specific thalamocortical loops: Thalamic neurons fire upon Layer 4 PFC neurons, which in turn act upon PFC neurons in other layers to change their firing properties so that current representations are maintained at a level that is resistant to new inputs. By this characterisation, the primary role of the PFC is to maintain stimulus representations.

In contrast, the proposed role of the basal ganglia is to modulate the maintenance functions of the PFC—to turn them on or off. Under passive maintenance conditions, the globus pallidus

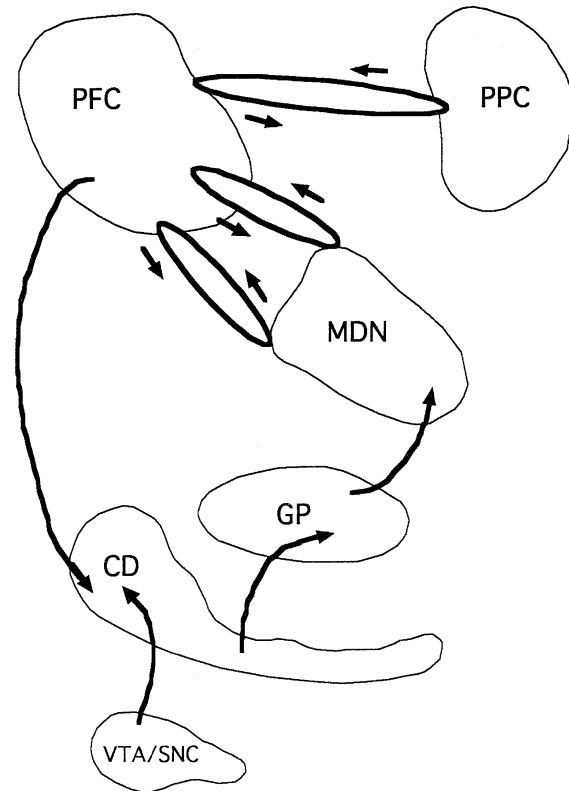


Figure 1. Illustration of frontal-striatal pathways connecting cortical and basal ganglia structures involved in working memory and interval timing. Excitatory glutaminergic circuits connect the dorsolateral prefrontal cortex (PFC) with the medial dorsal nucleus of the thalamus (MDN) and also with the posterior parietal cortex (PPC), forming multiple parallel loops. Excitatory glutaminergic pathways project from the PFC to the head of the caudate nucleus (CD) which sends inhibitory GABAergic projections to the internal segment of the globus pallidus (GP), which in turn sends inhibitory GABAergic projections to the MDN. Dopaminergic inputs to the CD originate from the ventral tegmental area and the substantia nigra pars compacta (VTA/SNC).

tonically inhibits the thalamus, preventing the establishment of thalamocortical loops. As noted above, under these conditions the frontal representations are easily overwritten upon presentation of new stimulus input. When a stimulus requires active maintenance, striatal neurons fire to inhibit neurons in the globus pallidus. This disinhibits thalamic neurons and allows establishment of the thalamocortical loops required for active maintenance.

An important feature of the updating function performed by the basal ganglia is that it must be selective. That is, there must be a way of determining when to update a representation, and furthermore a way of updating some

representations while maintaining others. For example, when learning a list, one must maintain the representation of the list structure while updating the representation of the current item. The importance of selective updating is even more apparent in complex tasks such as reading: For fluid comprehension, one must maintain a representation of the main idea of a paragraph or narrative, while continuously updating subordinate representations at the level of a sentence or word.

The organisation of connections between the PFC and basal ganglia facilitate this selective updating. First, striatal neurons are ideally situated for registering specific changes in neuronal activity that determine which representations should be maintained versus updated. They receive rich projections from the PFC, other cortical areas, and the thalamus. Each striatal spiny neuron has between 10,000 and 30,000 dendritic spines, each of which may receive input from a different cortical or thalamic neuron (Groves, Garcia-Munoz, Linder, Manley, Martone, & Young, 1995). The spiny neurons themselves have a very low rate of baseline firing, and require a large amount of simultaneous input to be activated. These properties make striatal neurons ideal for detecting and firing to very specific conjunctions of cortical inputs, while ignoring those that are irrelevant.

Second, Frank et al. (2001) note that the projections from the basal ganglia and thalamus to the PFC are much more sparse than those from the PFC to the striatum. They suggest that the projections to the PFC operate on selective regions to signal which representations should be updated or maintained, whereas the neurons within those regions are responsible for the details of those representations. They further suggest that the PFC may be hierarchically organised, with higher-order task representations located more anteriorly than lower-order stimulus-specific representations (see also O'Reilly, Noelle, Braver, & Cohen, 2002). Such an organisation would facilitate the selective updating and maintenance of different levels of representation.

The Frank et al. (2001) model thus provides an account of working memory phenomena that is consistent with current knowledge about the operations of the brain structures involved and the connections between them. A central tenet of this model is the separation between the proposed functions of the PFC versus the basal ganglia: PFC regions are thought to be responsible for main-

taining representations, whereas the basal ganglia's role is to control whether those maintenance functions are turned on or off.

We next turn to a discussion of the striatal beat-frequency (SBF) model of interval timing, which shares many features with the Frank et al. (2001) model of working memory. Both depend on a cortical-striatal-thalamic-cortical pathway wherein cortical and thalamic neurons are responsible for stimulus representations, and striatal spiny neurons detect important conjunctions in those representations. Where the working memory model is primarily concerned with stimulus identity as represented by which cortical neurons are active, the SBF model is primarily concerned with stimulus duration and sequencing as represented by the relative state of those neurons over time.

FRONTAL CORTEX AND BASAL GANGLIA IN MODELS OF INTERVAL TIMING

The ability to "get the timing right" is critical for the successful performance of many simple and complex behaviours. A predator must accurately synchronise its movements with those of its prey in order to intercept it, whereas a human might return to the microwave just before it beeps to indicate that the popcorn's done. Research on interval timing is concerned with the ability to perceive and make judgements about durations in the seconds to minutes range.

Like the Frank et al. (2001) working memory model, the SBF model of interval timing focuses on "coincidence detection" by striatal neurons (Matell & Meck, 2000, 2004; Matell et al., 2003a, 2003b). Specifically, the SBF model assumes that the cortical neurons that input to the striatum fire in an oscillatory fashion, and that different inputs have different oscillatory periods (ranging between approximately 5–15 Hz). At the onset of a stimulus, the cortical neurons involved in its representation fire simultaneously, and then continue to fire according to their individual oscillatory rates throughout its presentation. The different periodicities (oscillation rates) of the cortical neurons cause the composition of cortical activity to vary as a function of time from stimulus onset. Because this cortical state is continuously integrated by the striatal neurons, an association can be made between specific durations and specific cortical states as illustrated in Figure 2.

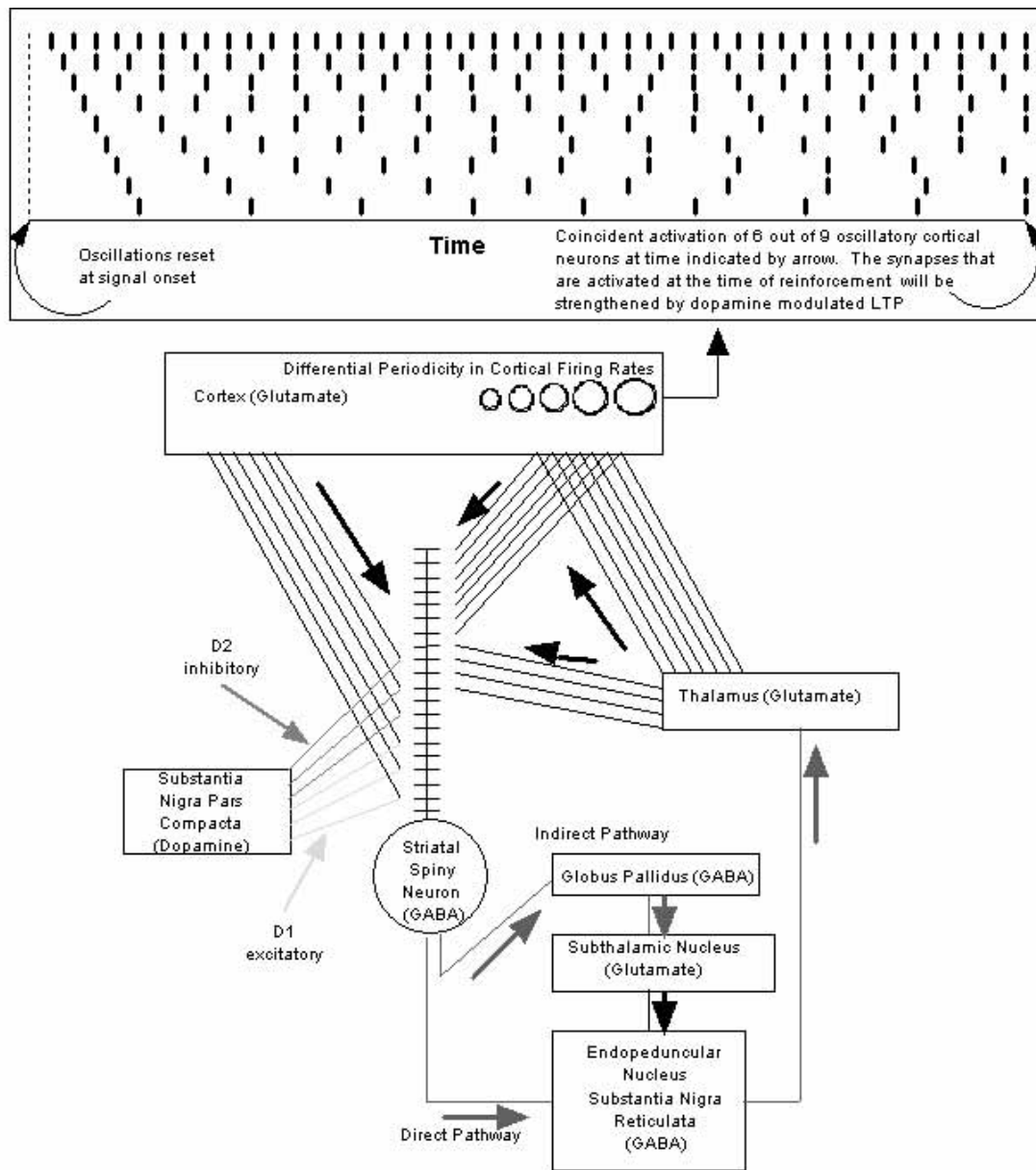


Figure 2. The major components of the striatal beat-frequency (SBF) model. Activity in the cortex is synchronised by onset of a relevant stimulus, after which the cortical activity resumes with a variety of oscillatory periods. The coincident activity of a subset of these cortical neurons is detected by striatal spiny neurons that are trained via long-term potentiation/depression (LTP/LTD)-type mechanisms and signify the end of the trained duration. The output of these neurons is integrated by the basal ganglia output nuclei (globus pallidus, subthalamic nucleus, entopeduncular nucleus, substantia nigra pars reticulata) and relayed to the thalamus for behavioural expression. The thalamic activity can also dynamically modulate cortical and striatal activity via multiple open and closed loops, increasing the model's flexibility to neurological insult. The excitatory and inhibitory neurotransmitters associated with each pathway (e.g., dopamine, GABA, and glutamate) are indicated in the diagram.

The SBF model is an important advance because of its realism at both a behavioural and physiological level. Previous models either provided a good description of timing behaviours but contained components that were inconsistent with the properties of the brain structures involved, or

were neurobiologically feasible but made inaccurate behavioural predictions (cf. Gibbon, Church, & Meck, 1984; Miall, 1989). In contrast, the computational version of the SBF model is constructed such that its mechanisms are consistent with research on the neural regions thought to be

involved in timing, and its output is consistent with physiological recordings and behavioural results from interval timing experiments. Indeed, recent data have shown that striatal neurons fire in a peak-shaped manner centred at a criterion time, following the predictions of the SBF model (Matell et al., 2003a, 2003b).

Critically, the SBF model reproduces the scalar property, a strict form of Weber's law by which the standard deviations of time estimates increase proportionally to the timed duration. Preservation of this scalar property is critical for experimental manipulations thought to have an influence on the timing system *per se*; deviations are considered diagnostic of influences on other systems that influence behaviour (e.g., Gibbon et al., 1997). In SBF, the scalar property occurs because of variability in the thresholds of striatal neurons and because cortical activity is assumed to be oscillatory, such that firing patterns at the harmonics (i.e., 1/2, 2/3, etc.) of the target duration are similar but not identical to those occurring at the target. The production of Weber's law via a system of oscillators as described by SBF is very similar to the assumptions made by working memory models such as OSCAR.

INTEGRATING MODELS OF WORKING MEMORY AND INTERVAL TIMING

Our analysis suggests an integration of these models of working memory and interval timing. Feature or item information as described by working memory models such as OSCAR might be instantiated by the *identity* of which subsets of cortical neurons fire to represent a stimulus, as in neurobiological models of working memory including that of Frank et al. (2001). Temporal or order information, also part of working memory and OSCAR, could be represented by the oscillatory *state* of those neurons over time, as described by the SBF model. On the neuronal level, working memory and interval timing may be intimately linked: Both depend on the patterns of cortical activity that occur in response to stimulus events, and on striatal neurons' detection of and response to those patterns.

Such an integration may help advance our understanding of both working memory and interval timing. For example, in its current state, the Frank et al. (2001) model might have difficulty explaining patterns of interference or temporal

confusability such as those demonstrated by Neath and Crowder (1990). This difficulty could be solved by incorporating hierarchical oscillations as described by OSCAR and SBF. Likewise, recent simulations (Matell, 2002) suggest that identity information may be required to separate the "wheat from the chaff" in terms of which cortical inputs are relevant to a to-be-timed stimulus. This information could be especially important when dividing attention between timing and another task, as in the papers reviewed by Fortin (1999), or when timing multiple events (e.g., Olton, Wenk, Church, & Meck, 1988; Pang & McAuley, 2003; Pang, Yoder, & Olton, 2001).

In OSCAR, items are thought to become more confusable as they recede in time. The variability of individual oscillators as described by the SBF model may provide a mechanism for this effect: Over time, this variability causes oscillators to fall increasingly out of sync with each other, thus making it less likely that they will fire in the exact coincident pattern that the striatal neurons associate with a particular temporal state. It is important to note that only state, not identity, information becomes increasingly noisy and confusable: It is the synchronisation, not the individual probability of firing, of the cortical neurons that declines over time. This idea of preserved identity information is echoed in the Frank et al. (2001) model's passive maintenance mechanism and SIMPLE's and OSCAR's emphasis on interference as the primary mechanism of forgetting (Brown et al., 2002).

The correspondence between these three models is not complete. They often offer complementary—or even competing—hypotheses for the potential mechanisms behind behaviour. For example, Frank et al. (2001) offer a different explanation for sequencing than would be used by OSCAR or SBF. OSCAR takes a retrospective approach to time, whereas SBF focuses on prospective timing. SIMPLE and OSCAR assume a preservation of mechanism across many domains and time scales that cannot be literally true at a neurobiological level (i.e., there are clear separations in the brain systems for working versus long-term memory), although it is possible that certain principles of organisation have been preserved across different systems as they have co-evolved (cf. Ramachandran, 1990).

Despite these caveats, the convergence across these models is striking. For example, the flow of information through thalamocortical loops during active maintenance as described by Frank et al.

(2001) could clearly provide an oscillatory pattern like the one assumed by SBF. ERP and other neurological recording data from related fields, including working memory, suggest that cortical neurons often show oscillatory activity (e.g., Nicolelis, Baccala, Lin, & Chapin, 1995; Raghavachari et al., 2001; Varela, Lachaux, Rodriguez, & Martinerie, 2001). Of particular relevance for the relation between the Frank et al. and SBF models, recent intracranial recordings show a “reset” of cortical and hippocampal oscillations in response to stimulus events during a working memory task, with topographically distinct sets of neurons resetting in response to different types of stimuli (Rizzuto et al., 2003).

CONCLUSIONS

This paper outlines a recent and remarkable convergence of ideas across three separate fields: a neurobiologically based model of working memory (Frank et al., 2001), a neurobiologically based model of interval timing (Matell & Meck, 2000; Matell et al., 2003b; Meck, 2003), and a family of behavioural models of memory and perception (Brown et al., 2002). The core of this convergence is the idea that cognitive and neural representations contain information about both identity (encoded by which cortical neurons are involved in a representation) and temporality (encoded by the oscillatory state of those neurons over time). From a neurobiological standpoint, another key feature is that striatal spiny neurons are responsible for detecting and triggering responses to the specific conjunctions of identity and state information that are associated with important events.

Rather than attempting to be comprehensive, this review has selectively highlighted points of contact between recent models of working memory and interval timing. These models complement each other in a way that suggests that working memory and timing are intricately linked at both neuronal and phenomenological levels. Our hope is that the similarities emphasised here will spark further connections between the fields of working memory and interval timing. Understanding how a stimulus is perceived and remembered may help our understanding of the perception and memory of its duration. Likewise, research on memory may benefit from understanding how we perceive time, its fundamental context.

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