

The representation of temporal information in perception and motor control

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The representation of temporal information can be examined from both a neurological and a computational perspective. Recent evidence suggests that two subcortical structures, the cerebellum and basal ganglia, play a critical role in the timing of both movement and perception. At a computational level, models of an internal clock have been developed in which timing is based on either endogenous oscillatory processes or distributed interval-based representations derived from relatively slow physiological processes.

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Abbreviations

CS	conditioned stimulus
PET	positron emission tomography
rCBF	regional cerebral blood flow
US	unconditioned stimulus

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Introduction

The fourth dimension of our world, time, has tended to be the forgotten stepchild in many theories of perception and motor control. Yet, actions and events take place over time. This review will focus on the neural and computational processes associated with the representation of temporal information.

Even though actions evolve over time, it is not mandatory to postulate that temporal information is represented or regulated in an explicit manner. Variation in the speed and duration of a reaching movement might be an emergent property of the rate at which muscle units are recruited. Therefore, temporal regularities in sequential actions may not reflect direct control processes, but may arise because of the complex dynamics of the neuromuscular system.

Nonetheless, many phenomena suggest the existence of an internal timing system in which temporal information is explicitly represented. For example, humans can readily discriminate the interval between two arbitrary events (e.g. two tones) that are separated by either 400 ms or 425 ms or show high sensitivity to perturbations in a stream of rhythmic events. Correlations between motor and perceptual timing [1•] also point toward a common mechanism, given that the peripheral constraints are quite different in these two domains.

Neural systems associated with temporal behavior

The intimate links between time perception and production have led researchers to wonder whether a common neural system is exploited in both domains. It is, of course, possible that there may not be a single specialized neural structure for timing. The representation of temporal information may be redundant in relatively independent systems or distributed across a set of neural structures.

The cerebellum

It has been hypothesized that the cerebellum operates as a specialized module for timing [2,3••]. The evidence in support of this hypothesis has been marshaled from studies involving a number of diverse tasks. First, patients with cerebellar lesions show inappropriate timing in the activation of agonist and antagonist muscles during rapid limb movements [4] and increased variability during repetitive finger tapping [5].

Second, patients with cerebellar lesions are impaired on perceptual tasks that require precise timing [6,7,8•]. Converging evidence for a role in perceptual timing comes from a PET study in which regional cerebral blood flow (rCBF) was measured while subjects listened to pairs of auditory intervals [9••]. Increased rCBF was observed bilaterally in the cerebellar hemispheres as well as in inferior vermis when subjects were required to compare the durations of the intervals compared to a control task in which the responses were not related to the perceptual events.

Third, the cerebellum has been shown to be the locus of learning in eyeblink conditioning, a Pavlovian paradigm in which the conditioned response is exquisitely timed to minimize the consequences of an aversive stimulus (reviewed in [10]). A series of studies with human subjects has confirmed the critical role of the cerebellum in eyeblink conditioning [11–13]. Glucose metabolism within the cerebellum has also been found to be greater after eyeblink conditioning [14•]. Associative processes are likely to occur at both nuclear and cortical cerebellar loci. However, while lesions of the deep nuclei may abolish the conditioned response, aspirations of the cerebellar cortex disrupt the timing of the response [15]. It appears that the cortex plays a critical role in shaping the temporal topography of the conditioned response.

The basal ganglia

The basal ganglia have also been suggested to be a key component in an internal timing system. Patients with Parkinson's disease become more variable on a repetitive

tapping task after skipping their normal levodopa medication [16••]. When analyzed with the two-process model of Wing and Kristofferson [17], the increased variability was attributed to both 'clock' and 'motor implementation' processes (see also [18]). Similar problems were observed in patients with Huntington's disease [19].

Patients with Parkinson's disease have also been reported to have abnormalities in their ability to estimate temporal intervals [20]. The patients tend to underestimate time, suggesting a slowing of an internal clock. Animal studies have also implicated dopaminergic pathways in the regulation of the speed of an internal clock [21••]. This work has generally involved much longer time intervals than those studied in the cerebellar research; for example, in the peak procedure, the animal is reinforced for the first response it produces after 30 s. After training under drug-free conditions, rats injected with dopamine agonists tended to respond earlier than expected whereas the reverse was observed in rats given dopamine antagonists [22]. More recently, it has been proposed that the basal ganglia function as a clock-counter system [21••]. In this view, dopaminergic neurons of the substantia nigra, especially those terminating on dopamine D2 receptors, operate as pacemaker units, with the pulses from these neurons being accumulated in the dorsal striatum.

Cortical structures

Lesions in cortical structures can also disrupt motor timing. Von Steinbuchel *et al.* [23] have reported a hemispheric asymmetry in the ability of patients with precentral lesions to reproduce temporal intervals. Right-hemisphere damage led to a consistent overestimation across a range of intervals from 1–5 s, whereas left-hemisphere damage was associated with underestimation. Patients with damage in either lateral premotor cortex or supplementary motor cortex have difficulty in producing rhythmic sequences [24].

Importantly, the patients in the latter study were unimpaired on perceptual tests of rhythm discrimination. The lack of a perceptual deficit following cortical lesions is in accord with other studies of patients with cortical damage [6,25]. Thus, it does not appear that time perception disturbances are a generic problem following neurological damage.

Component analysis of neural structures associated with internal timing

Information processing models of timing make clear that even simple tasks, such as duration discrimination or repetitive tapping, entail a number of component processes (e.g. [1•,26]). While cortical structures have not been linked to an internal clock, the frontal lobe appears to be essential for memory and attentional operations required in many timing tasks, especially those with long intervals [27,28•].

Defining the roles of the basal ganglia and cerebellum in timing remains a subject of debate. The tasks and measures used in these two literatures have tended to be quite different. Cerebellar research has focused on relatively short intervals, usually under 1 s, and the emphasis has been on variability. In contrast, intervals spanning many seconds characterize most of the basal ganglia research, and here the emphasis has been on clock rate (i.e. bias) rather than variability. Considerations of temporal range may provide an important clue for dissociating the functions of these two subcortical structures. Clarke *et al.* [29•] trained rats on two time-discrimination tasks, one in which the intervals were centered around 500 ms and the other in which the intervals were centered around 30 s. Cerebellar lesions led to a selective impairment on the short duration task.

On the other hand, the two systems may both contribute to temporal performance. Some researchers favor a view in which the representation of temporal information is distributed across the two systems [16••]. Alternatively, the basal ganglia and cerebellum may perform separable operations, and the similar performance deficits observed following lesions to either structure may reflect limitations in our current analytic tools. For example, the two-process model used to isolate 'clock' variability during repetitive tapping lumps the contributions from all processes upstream from the final motor commands [1•].

Characterizing an internal clock

The previous discussion has focused on the literature attempting to localize an internal timing system. Paralleling this search has been more theoretically oriented research aimed at describing how time is represented in the nervous system.

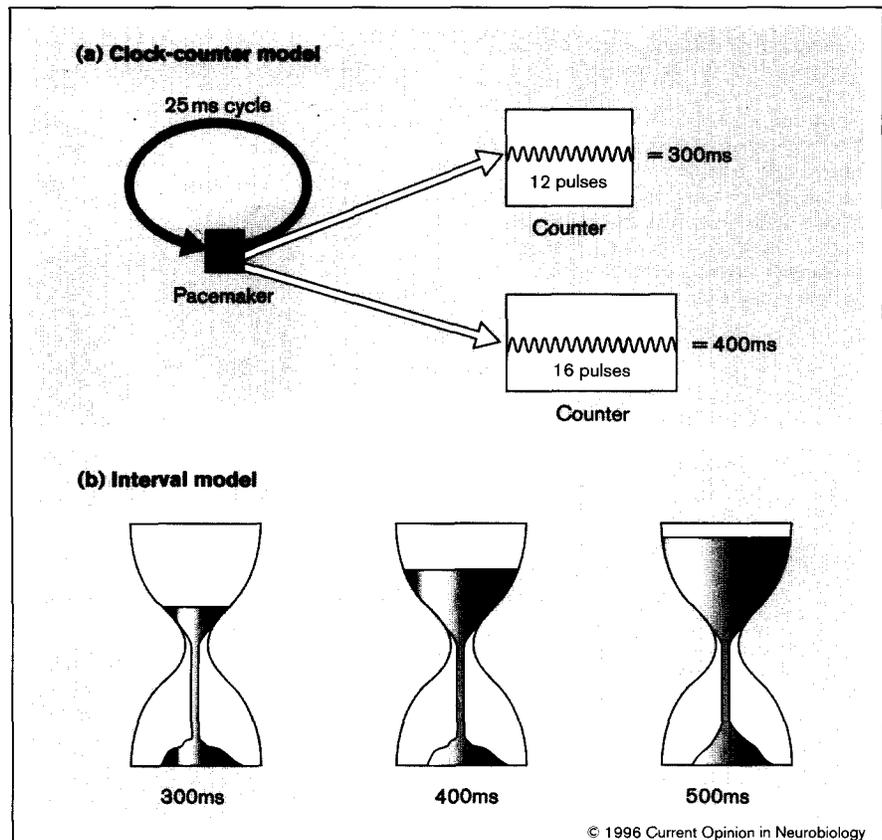
Oscillator models

Endogenous rhythms are observed at multiple levels of the nervous system, operating over many different time scales. Circadian rhythms, regulating metabolic and behavioral activity over 24-hour cycles have been associated with the superchiasmatic nucleus of the brainstem [30]. In motor control studies, researchers have elegantly described how central pattern generators, composed of small networks of spinal neurons, produce complex patterns of locomotion [31]. The existence of such periodic mechanisms motivated models of time perception and production centered on a putative central pacemaker.

One such model has been proposed by Treisman [32]. In this model, the temporal pacemaker is composed of two parts: an oscillator and a calibration unit. The oscillator produces an output at a constant frequency. The calibration unit re-scales this base frequency as a function of external influences and task demands. Together, this pacemaker provides flexible timing information. Using a series of interference tests in time production and perception experiments, estimates of the oscillatory frequency

Figure 1

Two mechanisms for representing temporal information. **(a)** Clock-counter models postulate a pacemaker that produces output to a counter. Longer intervals are represented by increases in the number of pacemaker outputs that accumulate in the counter. **(b)** Interval-based models assume that different intervals are represented by distinct elements, each corresponding to a specific duration.



have converged on a value of approximately 49 Hz [33,34]. This value is of interest given recent neurophysiological evidence suggesting that oscillatory brain activity near 40 Hz might serve as a mechanism for integrating activity across different neural regions [35,36,37•]. By allowing for flexibility in the calibration unit, pacemaker models can account for why the subunits of an action retain their proportional timing when that action is performed at different overall rates [38•,39•].

Distributed timing mechanisms

Pacemaker models assign the origin of temporal information to a single mechanism (Figure 1a). This need not mean that there is a single oscillator; a set of similarly entrained oscillators can provide reliability and robustness [21•]. Alternative timing models emphasize a distributed representation in which temporal information is encoded across a set of processors tuned with differential sensitivity functions. An analogy can be drawn here to the way cells in the visual cortex are tuned to edges at different orientations. The distribution of temporal information, however, may be functional rather than structural. To date, physiologists have not observed chronotopic maps in any brain area.

Neural network models have been used to explore the viability of distributed models of timing. Some of

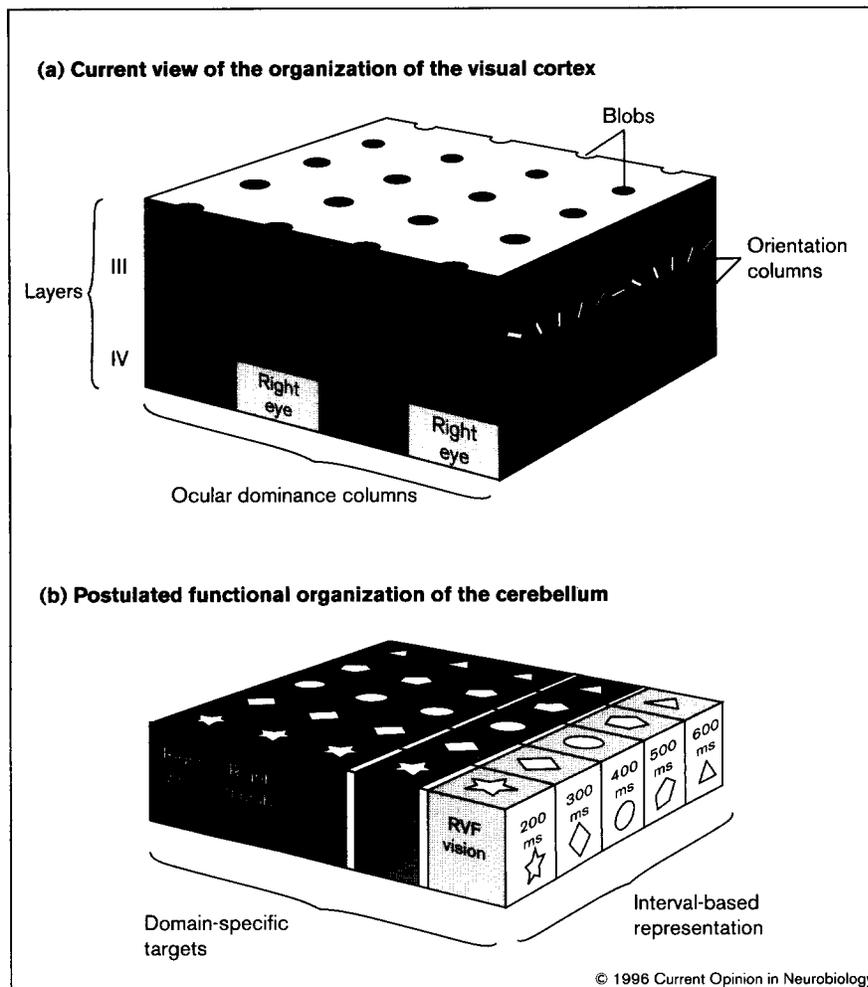
these models still retain the basic oscillatory idea, but envision either a series of harmonically related oscillators [40] or a population of oscillators distributed around a mean frequency [41]. By selecting combinations of these oscillators or exploiting beat frequencies (phase interactions) such networks can encode intervals over a range of durations.

An alternative metaphor for a timing mechanism is given by the hour-glass (see Figure 1b). While there is still periodicity at a microscopic level (e.g. the falling grains of sand), the system as a whole represents a particular interval. The representation of time may then be distributed across a set of such interval timers, each with a particular processing cycle. In such models, intervals of 300 ms and 400 ms are represented by distinct mechanisms (Figure 1b); in clock-counter models, short and long intervals are constructed from the same mechanisms, with the counter threshold increased in the latter case (Figure 1a).

Interval-based models have been used to explore how the cerebellar cortex might encode the precise timing between the conditioned stimulus (CS) and unconditioned stimulus (US) in eyeblink conditioning. In computer simulations, a population of different intervals can be created by incorporating neuronal processes that operate

Figure 2

Hypothesized functional architecture of how temporal information is represented in the cerebellum. (a) Analogous to the way in which orientation, spatial position, and input source are reflected in the organization of the visual cortex, (b) cerebellar neurons are hypothesized to be tuned to particular intervals (depicted as different symbols) and linked to specific input and/or output systems (depicted in different shades of gray). RVF, right visual field.



over relatively slow time scales. This may occur through a negative feedback loop involving granule and Golgi cells [42] or by varying the activation function of Purkinje cells via a second-messenger glutamate system [43•]. In both systems, learning centers on identifying the CS-related activity that is maximal near the time of arrival of the signal triggered by the US. Models such as these essentially transform temporal information into a spatial code [44••].

There are a variety of reasons favoring interval timing mechanisms over oscillatory mechanisms. First, they offer a principled reason why timing is most accurate over a limited range of durations [45] and why eyeblink conditioning is optimal over a narrow range of durations [46]: this constraint presumably reflects the range of intervals that the system is capable of representing. Second, they are well suited for allowing behavior to be maximally flexible. Time production and perception are not constrained by a fundamental frequency. For example, an animal could learn any arbitrary interval between the CS and US in eyeblink conditioning. Third, contrary to the predictions of oscillatory models, subjects are no better

on duration discrimination tasks when the comparison and test intervals are in phase with one another compared to when they are out of phase [1•,47].

Temporal coupling is a ubiquitous property of multi-effector movements (reviewed in [48]). Assuming that the timing of these movements is centrally controlled, temporal coupling would suggest either that the different limbs are governed by a single timing process [49] or that separate timing mechanisms become functionally coupled. Evidence from bimanual tapping studies favor the latter hypothesis [50••]. Within-hand variability was reduced when the two hands tapped together in comparison to when either hand tapped alone. The magnitude of the improvement suggests that two independent timing signals were generated, one for each hand, and that these signals were 'averaged' by a common output gate, ensuring interlimb coordination. In a related study [51], tapping variability was reduced in the ipsilesional hand in patients with unilateral cerebellar lesions during bimanual tapping. Rather than assume that timing was regulated by the intact half of the cerebellum, the multiple timer model assumes

that separate timing signals, one noisier than the other, are associated with the movements of each limb.

This model extends the notion of interval-based timing by proposing not only multiple timing mechanisms, but also that these mechanisms are linked to particular task domains (Figure 2). Thus, in bimanual tapping, different timing mechanisms must be accessed for each effector, even when the movements are performed in synchrony. According to this view, there would be a set of timing elements to regulate tapping at different rates with one limb, with this organization repeated for other limbs. Similarly, sensory input to the timing system would not need to access the identical units used in motor timing. Correlations across different temporal tasks need not reflect the operation of a single clock, but may reflect the fact that the timing system as a whole is associated with common noise properties.

Conclusions

This review has addressed two primary issues guiding current research on how the nervous system represents temporal information in perception and production. In the first half, the focus was on research seeking to identify neural structures associated with temporal processing. Both the cerebellum and basal ganglia have been hypothesized to play a critical role in internal timing. While these subcortical structures may form an integrated circuit with their respective roles yet to be defined, it is also possible that the cerebellum operates over a relatively short temporal window and that timing functions of the basal ganglia are utilized in tasks spanning longer durations. Dissociations between these two structures are likely to emerge from experiments using common tasks and measures.

The second half of this review explored different mechanisms that might form the basis for the representation of temporal information. The traditional view has been that temporal codes rely on endogenous oscillatory processes. Recent challenges to this idea come from network models in which time is distributed across a set of neural elements, with the different elements providing an interval-based representation. This distributed representation could be restricted to a single neural structure such as the cerebellum. In this view, the representation of time might be one defining property of the computational capability of that structure, although the exact elements recruited would be task-dependent. This hypothesis seems more biologically plausible in comparison to models postulating a single internal clock.

Acknowledgements

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