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Computational models of interval timing

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In recent years great progress has been made in the computational modeling of interval timing. A wide range of models capturing different aspects of interval timing now exist. These models can be seen as constituting four, sometimes overlapping, general classes of models: pacemaker–accumulator models, multiple–oscillator models, memory–trace models, and drift–diffusion (or random-process) models. We suggest that computational models should be judged based on their performance on a number of criteria — namely, the scalar property, their ability to reproduce retrospective and prospective timing effects, and their sensitivity to attentional and neurochemical manipulations. Future challenges will involve building integrated models and sharing model code to allow direct comparisons against a battery of empirical data.

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Although there are numerous ways in which computational models of interval timing can be classified, we have chosen to group these models into four major, although sometimes overlapping, classes: firstly, pacemaker–accumulator models (PA models), secondly, multiple–oscillator-coincidence detection models (also sometimes called timestamp models), thirdly, memory or neural process models and, finally, fourthly random-process (or drift–diffusion) models. For alternative classification schemes, see, for example [1,2••].

In what follows we will suggest that computational models of interval timing be judged on the basis of the following criteria: *the scalar property*, *prospective and retrospective timing*, and *the effects of attention and neuropharmacological manipulations*.

Extensive empirical evidence [3–6] suggests that time-estimation errors in interval timing grow approximately linearly with the size of the estimate. Known as the *scalar property* of time estimation, this fact sets a hard constraint on the nature of the underlying processes involved in time estimation [7]. This effect has been widely replicated in humans, pigeons, and rodents (see [8–10]. Similar behavioral responses to time scales can even be found in rate-dependent habituation in *C. elegans* [11]. Even though the scalar property has not been found to hold under all conditions [12], modeling it has proved to be a significant challenge for a number of existing models of interval-time judgments [7,13]. In a recent paper, Hass and Hermann [7] use information theoretic arguments to show how the scalar property places several important restrictions on the nature of any interval timing mechanism. Crucially, they argue that, in order to display scalar error profiles, the neural process underlying time perception must be based on a measure of growing variance in the system.

Secondly, it has been established that the perceived passage of time by human adults differs according to whether they are forewarned that they will need to make a timing judgment, and are, therefore, actively attending to its passage (*prospective* time estimation), or whether they are required to make an unexpected, after-the-fact judgment of the passage of time (*retrospective* time estimation). Models should be judged on how well they account for both of these regimes.

And thirdly, there are various systematic effects on the lengths of estimates caused by levels of attention [14] and neurochemistry, such as endogenous levels of dopamine or the effects of dopaminergic drugs [15–17].

We avoided the criterion of 'neurobiological plausibility' because it is notoriously difficult to pin down exactly what is meant by this expression. So, for example, how realistic do computational neurons have to be before the model that uses them can be said to be biologically plausible?

Pacemaker–accumulator models

The pacemaker–accumulator models (PAM) [18,19•] have had a great influence on the way that experiments on timing are conceived and interpreted. Many of the recent models of timing still utilize the pacemaker and accumulator processes described by Treisman [20]. These models currently constitute the most popular computational approaches to interval timing. In the pacemaker–accumulator model, the arrival of a stimulus starts a clock which generates pulses that are counted by an accumulator. Time judgments are then made by a comparison of what is stored in the accumulator and what is stored in memory. Gibbon's Scalar Expectancy Theory

Table 1

Summary of computational models of interval timing.

Reference	Model type/Name	What keeps the time?	What tells the time?	Scalar property?	Neurochemical or attention effects?	Prospective or retrospective?	Comment
[18]	Pacemaker–accumulator: Scalar Expectancy Theory (SET)	Poisson process pacemaker and error free accumulator	Comparing estimates to those retrieved from memory.	Via memory comparison not via clock	No	Prospective	The first Pacemaker model to address the Scalar property.
[21]	Pacemaker–accumulator	Poisson pacemaker	Unreliable/stochastic multistage accumulator	Under special circumstances	No	Prospective	An unreliable counter mechanism can give rise to scalar property under very narrow circumstances.
[19•,62]	Pacemaker–accumulator	Pacemaker with geometrically increasing tick length and Gaussian noise	Accumulator built into larger ACT-R model.	Via implausible pacemaker assumptions	Attention effects	Prospective	A classical PAM embedded in an ACT-R framework models attention effects as a result of resource competition.
[63]	Pacemaker–accumulator	Constant rate pacemaker	ACT-R model with time stored in working memory	No	Some attention effects	Prospective	Simplistic PAM model built in ACT-R.
[22]	Pacemaker–accumulator	Poisson pacemaker	Accumulator and memory	Via ad hoc Gaussian error mechanism	No	Prospective	Notable for allowing direct quantitative test of SET by implementing it in Framsticks simulation environment.
[23]	Multiple–oscillator: beat frequency	Set of cortical oscillators of different phase	Time measured by selecting subset that will be in phase at correct interval	No	No	Prospective	Original multiple–oscillator model.
[25••]	Multiple–oscillator: striatal Beat Frequency (SBF)	Set of cortical oscillators of different phases	Coincidence detectors based on striatal spiny neurons	Only under assumption of globally correlated phase variations	Several neurochemical effects	Prospective	A modern oscillator model that takes good account of neuroscience evidence.
[26••,27]	Multiple–oscillator: SBF with realistic noisy neurons	Set of cortical oscillators with different phases and uncorrelated noise	Neural network 'coincidence detector'	Yes	Yes–numerous pharmacological effects.	Prospective	A nice reinvention of SBF where scalar property emerges naturally from network noise.
[11,34]	Memory decay: multiple time scales (MTS)	Chain of decaying activations	Reading off absolute level of decay	By assuming fixed Gaussian error threshold	No	Prospective	First memory decay model was actually model of habituation in *C. elegans*. Only models prospective timing because requires dedicated mechanism.
[36••]	Memory decay: Gaussian Activation Model (GAMIT)	Spreading cortical activation from event to be timed and rate of change of activation.	Comparison of activation to learned reference curve	Yes	Cognitive load effects via attentional resource competition	Both	Retrospective case a single estimate is made at end of interval. In prospective case multiple estimates during interval contribute.

Table 1 (*Continued*)

Reference	Model type/Name	What keeps the time?	What tells the time?	Scalar property?	Neurochemical or attention effects?	Prospective or retrospective?	Comment
[37]	Memory decay: GAMIT-Net	Spreading cortical activation	Neural network learns to estimate time	Yes	Attention effects via resource competition	Both	Neural network version of GAMIT model.
[35•,53]	Memory decay: temporal context model (TCM)	Set of leaky integrators that stores stimulus event plus 'context' from previous events	Feedforward connections permit reconstruction of sequences of events	Due to choice of reconstruction algorithm	No	Both	Adapts model of serial memory performance to more general task of interval timing. Estimation method is relatively complex approximate inverse Laplace Transform.
[64•]	Memory decay: coupled leaky integrators	Decay in activation in a two neuron systems acts like a simple oscillator.	Network has wait or respond states.	No	No	Prospective	A very simple neural system model animal learning data. Noise plays important role in stabilizing network behavior.
[38]	Climbing activation	Firing rate adaptation in inhibitory neurons leads to increasing activity in excitatory neurons.	When active population crosses fixed threshold. Changes to adaptation rate change interval	Yes	No	Prospective	Detailed neural model inspired by recordings from macaque inferotemporal cortex.
[65]	Climbing activation: Dual klepsydra model	Leaky integrator	Comparing one integrator to another	No	No	Prospective	Unclear why integrator values cannot be accessed directly.
[42•,43]	Climbing activation: evolved, embodied neural net model.	An evolved continuous time recurrent neural network	Networks seemed to work via climbing activation.	No	No	Prospective	Evolved neural network with standard leaky-integrator neurons tells time without clock-like control a robot in a simulated environment.
[45]	Random process: population of bistable units	Population of independent bistable units transitioning from off to on	When number of ON neurons crosses threshold	Yes	No	Prospective	Different intervals measured by different global transition probabilities. Not clear how this would be implemented.
[46,47••]	Random process: drift–diffusion model of interval timing & decision making	Random walk by competing random inhibitory and excitatory processes.	When total crosses particular threshold.	Yes	No	Prospective	An probabilistic model than accounts for decision making and interval production in same framework.
[66]	Contextual change	Estimates derived from amount of activity, number of actions and ACT-R system time.	ACT-R model	No	Some attention effects	Retrospective	Underspecified mechanism but embedding model in ACT-R framework allowed testing of attention effects.

(SET) model emphasized the importance of reproducing the property of scale invariance observed in interval timing [3,18]. Scalar error in this model arises not from the clock itself but rather from noise in the comparison process. Several variants on this original pacemaker–accumulator design have been produced. For example, Killeen and Taylor [21] use a different approach to the scalar property by using a noisy accumulator process rather than a noisy comparator (Table 1).

Recent models have taken the pacemaker–accumulator process and incorporated it into a larger cognitive system. For example, Taatgen *et al.* [19•] place a timekeeping module in the context of a general ACT-R architecture to capture the effects of attention and resource competition on interval timing. This model incorporates an attentional gate which modulates the rate of pulse accumulation hence leading to changes in the perception of intervals. Another example is Komosinski and Kups [22] who build a classical PAM in a neural simulator environment to model time-judgment errors in successively presented time intervals.

One difficulty with these models is that errors in sequential processes grow too slowly (as the square root of length of the interval). Any timer based on direct accumulation of ticks would be too accurate. In order to account for the scalar property of time, pacemaker–accumulator models have to introduce a secondary source of multiplicative error in the comparison process [7].

Multiple–oscillator models

Multiple–oscillator models [23,24] refer to models of interval timing in which intervals are represented as a set of activities of several oscillators. An early form of the model was developed by Miall [23]. In this model, referred to as the beat frequency (BF) model, timing is carried out by the activation of several oscillators, each of which oscillates at its own particular frequency. The arrival of a stimulus resets the oscillators so that they begin to fire together. The time elapsed since the arrival of the stimulus would then depend on the oscillatory phases of the entire set of oscillators. However the distribution of firing was not normally distributed, having a sharp peak at the target time and smaller peaks at the major harmonics of the fundamental interval. In addition, the width of the peak was not proportional to the length of the interval. For this reason, and because the model did not contain any noise, it was unable to account for the property of scalar invariance.

The Striatal Beat-Frequency (SBF) model tried to address these problems [25••]. They modified the BF to induce the scalar property. The SBF model took into account experimental findings that interval timing was not exclusively the result of activity in the basal ganglia but also of activity in a thalamo-cortico-striatal circuit. In this model, oscillations are generated by cortical neurons and timing is indicated by the coincidental activation of spiny neurons in the striatum of the basal ganglia by the cortical oscillators. Oscillator speeds and neuronal firing thresholds were adjusted on a trial by trail basis in order to reproduce the Gaussian shaped response profiles seen in timing experiments that use the peak procedure experimental method and thereby produce scalar invariance. However, these adjustments had to be globally coherent, otherwise the coincidence-detections mechanisms would not operate appropriately. This tends to make the SBF model oversensitive to small amounts of noise.

Improvements to the SBF model have been made by [26••,27]. This model retained the separation of cortical and striatal roles used in the SBF models. The neurons in the new models however, were far more realistic. The simpler neuronal models were replaced by more detailed Morris–Lecar neurons and neural activity was now the result of the dynamics in several ionic channels. This model succeeded in replicating several experimental findings on the effects of dopamine and cholinergic agents on timekeeping. In a more generalized version of the model in which a perceptron replaced the striatum and its coincidence detection, scalar errors were an emergent property of the network without the need for global coherence [26••]. The SBF model has also been extended to include a unified account of duration-based and beat-based timing mechanisms [28,29].

Memory-based models

A third class of models relies on memory decay and falling (or rising) neural activation. These neural processes are relatively well understood and provide evidence that timing and memory use the same cognitive resources [30], recruiting neurons in the dorso-lateral prefrontal cortex [31–33]. Once again, the scalar property does not always arise from these models in a straightforward manner. For example, the Multiple Time Scales model (MTS, [11,34]) relies on a series of leaky integrators with power law decay and these integrators must be carefully linked to approximate the required logarithmic decay function. The Temporal Context Model (TCM, [35•]) relies on many leaky integrators and far more complex dynamics than the MTS model.

Computational memory models have been introduced which take into account not only the amount of activation decay of a memory trace but also the rate at which activation decays (GAMIT: [36••,37]). In this model, there is a mechanism of attentional-resource sharing that allows GAMIT to model both retrospective and prospective timing.

By contrast with these falling activation-trace models, Reutimann *et al.* [38] use a single climbing neuronal trace that attains a threshold at the expected end of an interval.

This model [38] is built on a single mechanism using well-understood principles of synaptic plasticity and the decision rule is built into the model itself. Single cell recordings in the inferotemporal cortex of monkeys have, in fact, found neurons with the appropriate time-dependent firing rates [39,40]. This interpretation of climbing activation remains controversial, however, see [41].

An interesting recent addition to this class is [42•,43], in which neural networks with standard leaky-integrator neurons were evolved to control a robot in a simulated environment in order to perform a temporal comparison task. When network activity was examined timing appeared to be due to a climbing activation mechanism.

Random process models

Models discussed so far have been broadly deterministic or based on probabilistic processes (e.g. counting random ticks) that produce time estimates that have less than scalar error. The models in this section are based on probabilistic processes with linear or greater than linear error. The simplest approach [44] replaces a single Poisson process with a group of 100 independent Poisson process and a leaky integrate-and-fire neuron that fires and resets every time it crosses a threshold. With a fixed threshold this model underestimates intervals but improves with the incorporation of a dynamic threshold that is inhibited by recent firings. However, the actual fit to empirical data remains poor. A better fit to data is obtained by [45] in which a timer starts by setting 50 bistable units to 'off'. Thereafter, each bistable unit transitions to 'on' independently with probability p (adjusted by learning) and the timer stops when a total of 40 units are active.

If excitatory and inhibitory processes both contribute to the same integrator then, unless the processes are precisely balanced, the resulting random walk will drift in one direction. Adjusting the balance adjusts the rate of drift allowing different intervals to be learned [46,47••]. The learning process is simpler than in [45] because it does not rely on fine tuning a group of probabilities. The approach has additional advantages that the same framework can model decision making and that it makes several quite precise predictions about skew and coefficients of variation of responses in temporal reproduction tasks.

Finally, it should be noted that in subsecond timing most successful models are random-process models, based on stochastically connected chains of noisy neurons [48,49•,50]. However, most authors do not think that these models can be extended to the multi-second domain of interval timing [51]. This inability to scale up to multi-second timing applies only to these random-process models. It remains an open question as to whether other classes of models can account for both subsecond and multi-second timing.

Difficulties with the models

As currently implemented pacemaker–accumulator and multiple–oscillator models rely on a dedicated timing mechanism which needs to be started when a particular event occurs. This is problematic for retrospective timing because all perceived events are potential candidates for retrospective time judgments and, therefore, each event would require a separate timer.

Staddon [52] suggested that memory–trace models could overcome this reset problem because all perceived events encoded by the cognitive system automatically result in representations that are governed by the same trace dynamics. However, most activation-trace models posit a specialist timing mechanism that is only recruited when timing is required (e.g. [34,38]) and models of this type can only address prospective timing. The Temporal Context Model (TCM) [35•] developed from a model of episodic memory, can potentially perform both retrospective and prospective timing. To the best of our knowledge, TCM is the first attempt to use features of memory directly as a mechanism for interval timing. GAMIT [36••] has similar motivations but is much simpler than TCM.

Our estimates of time passing can also be affected by whether or not we are actively attending to the passage of time and by cognitive load. Block *et al.* [14] found that high cognitive load *increases* retrospective time estimates and *decreases* prospective time estimates. Modeling this surprising effect is a challenge for all existing models of interval timing. French *et al.* [36••] suggest an attentional resource-sharing mechanism that allows prospective and retrospective timing to be accounted for in a single model. Moreover, this model, GAMIT [36••], is currently the only computational model to account for this interaction.

Most models simply do not consider attentional effects on interval time perception [34,38,53]. One simple proposal is that attention might modulate clock speed directly [25••]. If decreased attention to timing causes the organism's internal clock to beat slower, then it will tend to underestimate the length of intervals. This idea is developed further in the time-sharing model [54]. Working memory, timing and attention all depend on dopaminergic pathways [32,55,56]. The changes observed in interval timing estimates following pharmacological interventions that modulate clock speed [16,57] have been modeled by letting dopamine levels affect oscillator frequency (e.g. [26••,27,58]). Nevertheless, none of these models can account for the *increase* in retrospective estimates under high cognitive load.

Far fewer models attempt to explain retrospective timing, in part because retrospective timing does not have an equivalent in animal behavior. A common theme behind all approaches to retrospective timing is that intervals are estimated by reconstructing a sequence of remembered events. Cognitive load could affect this by changing the memorability or numerosity of events [59,60].

Future challenges

In conclusion, computational models of interval timing have come a long way but are still faced with many challenges. Besides the difficulties already discussed, a genuinely mature model needs to:

- fit individual not just group data
- give a coherent account of relationship between retrospective and prospective timing,
- apply to the full range of timing tasks and their associated attentional and pharmacological modulations,
- explain commonalities and differences between animal and human time perception.

We have argued elsewhere [61] that modelers need to make their code available and user accessible so that their models can be directly compared and developed. The current variety of modeling approaches is a strength. Bringing the successes of these varied models into a comprehensive framework is the long term goal for the field.

Conflicts of interest

Nothing declared.

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