

Dedicated and intrinsic models of time perception

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Two general frameworks have been articulated to describe how the passage of time is perceived. One emphasizes that the judgment of the duration of a stimulus depends on the operation of dedicated neural mechanisms specialized for representing the temporal relationships between events. Alternatively, the representation of duration could be ubiquitous, arising from the intrinsic dynamics of nondedicated neural mechanisms. In such models, duration might be encoded directly through the amount of activation of sensory processes or as spatial patterns of activity in a network of neurons. Although intrinsic models are neurally plausible, we highlight several issues that must be addressed before we dispense with models of duration perception that are based on dedicated processes.

Perceiving the passage of time

Cognition is dynamic, with our perceptions, actions and comprehension of the world unfolding over time. A generation ago, research on timing was limited, emphasizing the study of behaviors marked by temporal regularities [1]. More recently, a renaissance has taken hold in the study of time perception, with researchers addressing a broad range of temporal phenomena. Behavioral studies have revealed a host of puzzling effects in which our perception of time is far from veridical [2]. Neuroscientists have described how activity in single neurons varies with time and how this might relate to psychophysical judgments [3–5]. Theorists have asked how the dynamics of neural networks might encode temporal patterns in a reliable manner [6–11].

As has long been noted by philosophers and psychologists, we lack a sensory system devoted to the sense of time. Nonetheless, many percepts, and our actions in response to these percepts, are acutely dependent on the precise representation of time. Of course the terms ‘time’ and ‘temporal processing’ encompass a broad range of phenomena, including simultaneity, temporal order and the perception of duration. In this review we focus on the last of these, addressing how the nervous system encodes information concerning the duration of events in the range of hundreds of milliseconds, the units of time that are especially relevant for immediate perception and the actions we produce in relation to these events. In particular we focus on a fundamental question that has defined much of the recent discussion: is our perception of the passage of time the consequence of dedicated, clock-like neural

mechanisms? Or is duration coded in an accessible manner as an intrinsic and ubiquitous property of neural activity?

Dedicated models of temporal processing

Dedicated models of time perception are, at their core, modular. As vision scientists speak of dedicated mechanisms for color or motion perception, modular models of time perception entail some sort of specialized mechanism that represents the temporal relationship between events. The pacemaker-counter model is one example of a modular system [12]. These two components define a clock with an interval specified by the accumulation of inputs from a pacemaker. Spectral models of timing constitute a second example of a modular process. The phasic interactions of a bank of oscillators [8,13] or the exploitation of differential activity patterns in a set of delay lines [14,15] can define different intervals. In dedicated models these representations are viewed as specializations, unique to particular neural structures, that provide a functional chronotopy that is recruited across diverse task domains.

One motivation for dedicated models comes from the observation that our sense of the passage of time appears to transcend the sensory modality of a stimulus. We can compare the duration of a tone to a light (although not as well as we assume [16–18]) or metrically reproduce the duration of a visual stimulus with a keypress. Such interactions are less apparent in other perceptual domains; for example, only rare individuals describe the color of a tone. The facile manner with which we compare time across different modalities suggests some sort of internal clock.

Behavioral data provide additional motivation. Individual differences in temporal acuity correlate between perception and action [19]. Measures of variability or dispersion are proportional to mean duration, and when the tasks are appropriately matched this ratio is similar for perception and action [20]. Based on the assumption that this property arises from signal-dependent noise in a common system, these results point towards a dedicated system for timing.

A neural instantiation of a dedicated model is the cerebellar timing hypothesis [21]. Patients with cerebellar pathology are impaired on a range of tasks that require precise timing, including perceptual tasks such as judging the duration of brief tones [22,23] or categorizing speech sounds that vary in the duration of a silent period [24]. The timing hypothesis also provides a principled basis for specifying the cerebellar contribution to sensorimotor learning: this structure would be essential when learning

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requires the representation of the temporal relationship between events, as in eyeblink conditioning. Consistent with a modular perspective, the cerebellar timing hypothesis is based on the assumption that the cerebellum has a unique representational capability and is accessed whenever a particular task requires precise timing.

Similar arguments have been developed for other neural regions that might serve as dedicated timing systems [25]. These include the basal ganglia [26,27], supplementary motor area [28,29] and prefrontal cortex, especially in the right hemisphere [30,31]. For the most part, converging evidence has been offered in support of all of these candidate regions. Patients with lesions encompassing a particular region might be impaired in judging the duration of an auditory stimulus yet show no problems in judging other acoustic features [30]. Correspondingly, an area might be activated in an imaging study when the task requires attending to the duration of the stimulus in comparison to a nontemporal attribute [28]. These dissociations, whether from lesions, pharmacological manipulations or neuroimaging, favor dedicated mechanisms for temporal processing (Figure 1a).

Although dissociations across task domains have been obtained readily, considerable debate continues on the question of whether temporal-processing deficits are uniquely associated with damage to a particular neural structure. For example, patients with cerebellar degeneration, Parkinson's disease or prefrontal lesions all show a similar perceptual dissociation between duration and pitch [32]. The neuroimaging literature presents a similarly murky picture [32]. Not only have highly divergent patterns of activation been observed across studies but also substantive task differences amplify the problem [32,33]. Given the required investment, replication studies are rare in the imaging literature.

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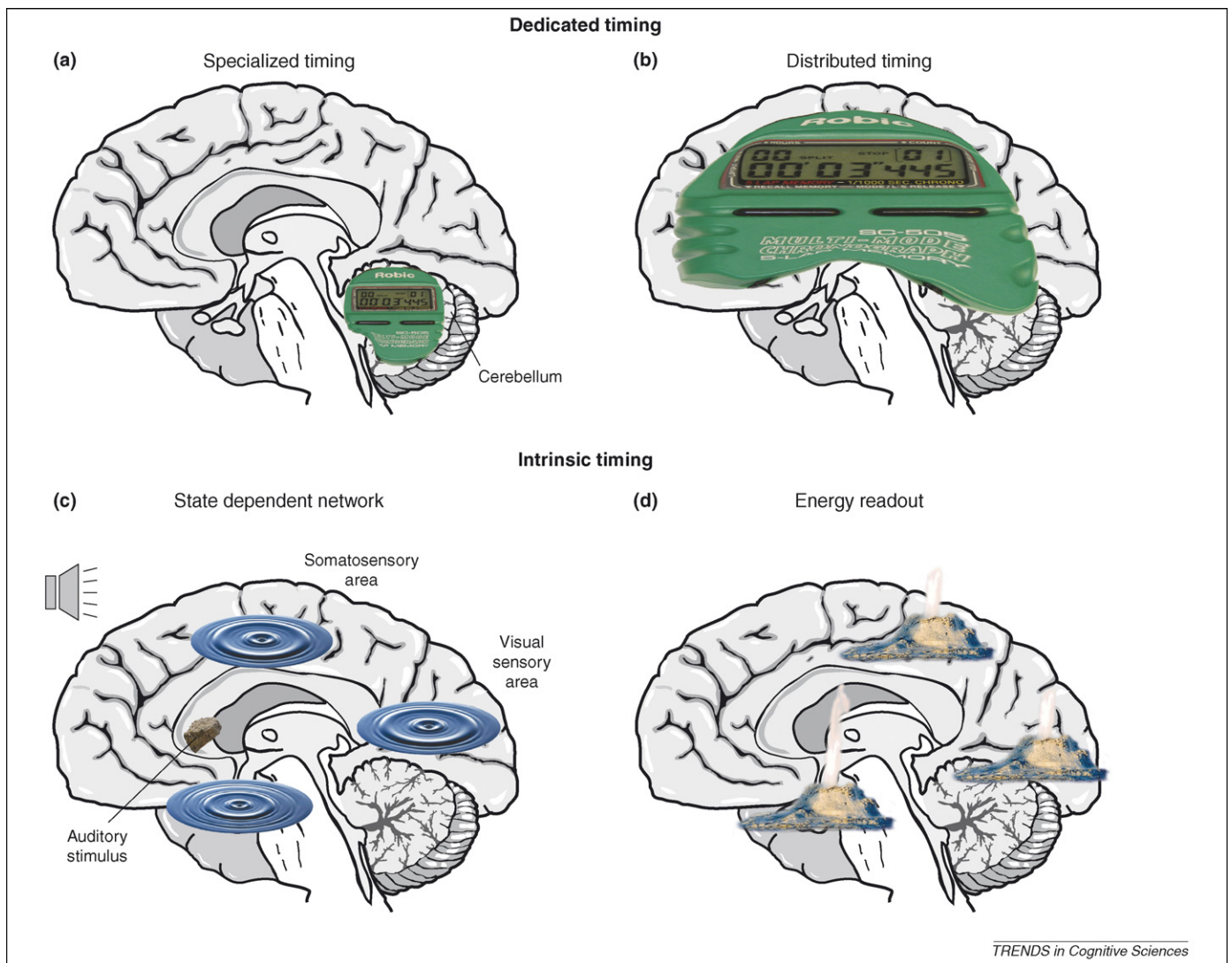


Figure 1. Neural models for temporal representation. The top two panels depict two dedicated models. **(a)** A neural structure might be specialized to represent temporal information. The example shows the cerebellum as a dedicated system, although some models postulate a specialized role for the basal ganglia, supplementary motor area or right prefrontal cortex. **(b)** A dedicated system could involve activity across a distributed network of neural regions. The bottom two panels depict two models for modality-specific intrinsic timing. **(c)** In a state-dependent network, temporal patterns are represented as spatial patterns of activity across a neural network. **(d)** In an energy readout model, elapsed time corresponds to the amount of neural activity.

areas might provide more general functions (e.g. working memory to store temporal information). Pathology in any node of this network would disrupt performance on timing tasks.

Intrinsic models of temporal processing

A spate of recent studies has promoted a more generic view of timing, which we will refer to as ‘intrinsic models’. Intrinsic models offer a radically different perspective on the perception of time. These models assume that there is no specialized brain system for representing temporal information, asserting that time is inherent in neural dynamics (Figure 1c,d). In one class of models, this property might be limited to neural regions that are capable of sustaining their activity in the absence of sensory input [3,10]. For example, in delayed response tasks duration can be encoded in the ramped activity of neurons that provide a working memory representation of the stimulus or the time until the response [36].

Alternatively, timing might be ubiquitous and arise as part of modality-specific processing [37,38]. Thus, perceiving the duration of a visual event would depend on the dynamics of neurons in visual regions of the brain whereas the same duration of an auditory event would depend on similar operations in auditory regions. This idea contrasts with how modality-specific effects are conceptualized in dedicated models. For example, in our cerebellar model the duration of a tone is assumed to be represented in different cerebellar subregions than the representation of the duration of a light [15]. Nonetheless, both representations depend on a specialized cerebellar computation.

In a provocative paper titled ‘Timing in the Absence of Clocks’, Karmarkar and Buonomano [7] develop a neural network composed of excitatory and inhibitory neurons that exhibit a range of synaptic time constants and short-term plasticity mechanisms. This network is capable of representing different durations as unique spatial patterns of activity, even without any explicit mechanism that provides a linear metric of time. Judging the duration of a stimulus requires learning to recognize these spatial patterns.

An essential feature of this model is that temporal representation is context dependent. This property not only implies modality specificity but also that, even within a modality, the representation of a particular interval will be state dependent. Thus, the network’s representation of the duration of a tone is related not only to activity occurring during the presentation of the tone but also to the state of the network at the onset of the tone. Consistent with this state dependency, perceptual acuity for duration is much poorer when the target interval is presented in a variable context compared to a fixed context [7]. Interestingly, this effect is limited to judgments involving relatively short intervals (e.g. 100 ms). Context manipulations had no effect on intervals of 1 s, consistent with the idea that the physiological processes underlying state-dependent networks are of limited temporal extent [39] (see Box 1).

A different mechanism for intrinsic timing is based on the idea that duration could be encoded in the magnitude of neural activity, in which the passage of time is gauged by

Box 1. Different ranges, different mechanisms?

Time perception studies use intervals that extend from a 100 ms to tens of seconds or minutes. Does the requisite set of neural mechanisms change across this range? One important division is made between short intervals that range up to 1–2 s and longer intervals [35,66]. Within dedicated models of timing, the system can directly encode short intervals [15]. By contrast, longer intervals require the recruitment of attentional and working-memory processes. Repeated output of a timing mechanism might be used [23] or time perception could be indirect, the result of an inferential process [67].

Although evidence for such a division is compelling, the interpretation of time-perception studies frequently has favored a singular model across a large range of intervals. For example, clock-counter models have proved extremely useful in accounting for behavior. Nonetheless, it is unlikely that a single mechanism could operate at these different time scales. A pacemaker used to judge an interval of 40 s is unlikely to have the resolution to judge a 100 ms interval. The strength of these models is in their heuristic value: by specifying multiple components the model provides quantitative predictions to test how particular variables influence performance.

State-dependent networks suggest that an additional division is required. The physiological mechanisms that drive such networks are useful for differentiating patterns of a few hundred milliseconds. Beyond this range, time-dependent neural properties provide inadequate resolution [68,69]. By inference, intervals of a half-second or longer require additional processes. This division was anticipated at the end of the 19th century by Munsterberg, who suggested that short intervals might be directly perceived by sensory mechanisms [17].

To date only a few studies have examined whether distinct mechanisms underlie the perception of short intervals. Secondary tasks [17,70] or pharmacological manipulations [71] affect judgments of 1 s intervals while having little or no effect on intervals of around 100 ms. Secondary tasks that affect judgments of 1 s have little effect on intervals of 100 ms [17,70]. Temporal acuity normalized to mean duration is relatively constant for intervals between 200 ms to 2 s but becomes considerably poorer for intervals shorter than this range [7,72]. In preliminary work we (R.B. Ivry, *et al.*, unpublished) failed to find context effects in a replication of Karmarkar and Buonomano [7] when the base interval was increased to 300 ms.

It is possible that the distinction between intrinsic and dedicated mechanisms for duration perception will map onto temporal range, with the former applicable to relatively short intervals (e.g. a few hundred milliseconds) and the latter to longer intervals. Nonetheless, at present, variants of both classes of models have been applied to tasks spanning up to a few seconds. Thus, we focus in this review on outlining issues that allow for a comparison between these models when applied to a common set of phenomena.

some form of energy readout [40]. Consider a task in which participants view a stream of digits, each presented for a duration of around 500 ms [41]. If the same digit is presented repeatedly, the initial stimulus is perceived as longer in duration (or conversely, the perceived duration of subsequent stimuli is shortened). A similar effect is found when a set of digits are presented in their standard ordinal position (e.g. 1 2 3 4): the ‘1’ is perceived as longer than the ‘2’, ‘3’ and ‘4’. However, if the order is scrambled (e.g. 1 4 3 2), there is no distortion of duration. Each digit cannot be anticipated and, thus, receives a similar degree of neural processing. Drawing on an intriguing parallel to the repetition suppression effect observed by functional magnetic resonance imaging (fMRI) [41], Pariyadath and Eagleman suggest that ‘the conditions that lead to a suppressed neural response are the same as those that lead to a reduction in perceived duration’ (p. 5). By extension,

events that capture attention produce an increase in neural activity [41,42] and, as would be predicted by an energy readout model, are perceived as longer in duration [43–45]. As with a state-dependent network [7] the perception of time is not attributed to mechanisms specialized for temporal processing but, rather, is based on generic and modality-specific features of neural activity.

Evaluating the evidence for modality specificity in intrinsic timing

Some of the most compelling evidence for intrinsic timing comes from physiological studies that emphasize local representations that are, at least implicitly, modality specific. In one study neurons in the lateral inferior parietal region LIP were recorded during a visual duration discrimination task [5]. Two lights, the first of a fixed duration (e.g. 316 ms) and the second a variable duration, were presented at fixation. The animal judged the relative duration of the second by making a saccade to one of two peripheral targets. Strikingly, perceptual judgments were well predicted by the activity of individual neurons. When the target for ‘shorter’ judgments fell within the neuron’s response field, it would exhibit high firing rates at the onset of the second light. If the stimulus persisted, this response dropped off. When the target for ‘longer’ judgments fell within the response field of the neuron, the firing rate increased over time, eventually surpassing that of neurons with response fields tuned to the ‘shorter’ target.

This parallel between behavior and single-unit activity has been seen with other visual attributes. For example, psychophysical performance on motion perception tasks can be predicted from the activity of neurons in area MT (middle temporal, also known as area V5) [46,47]. By analogy, Shadlen and colleagues suggest that LIP neurons code the time of behaviorally relevant visual events. However, the authors acknowledge that activity in these eye-movement-related neurons might be driven by an upstream (dedicated) system for temporal processing [4].

A recent transcranial magnetic stimulation (TMS) study provides converging evidence in favor of modality-specific timing [48]. When judging the duration of a visual display, an increase in the difference threshold was observed on trials in which repetitive TMS was applied over V5/MT. Consistent with a modality-specific assumption, no change in performance was found when subjects judged the duration of a tone. Similarly, modality specificity was observed in an fMRI study when people were asked to tap a simple rhythm, initially specified by either a visual or auditory metronome [49]. In the visual condition only, activity remained high in area V5/MT after the metronome was terminated. One might suppose that, in terms of a state-dependent network, a persistent modality-specific pattern continues to provide a reference to time each response even in the absence of further sensory stimulation.

A further challenge to dedicated models comes from studies showing modality-specific distortions of perceived time. Morrone and colleagues reported a dramatic illusion in which time is compressed [50]. Just before the onset of a saccade to a peripheral target, a pair of bars was flashed

with an onset asynchrony of 100 ms. Participants compared the duration of this interval to a variable one that was presented a few seconds later. Under these conditions, participants reported the stimuli to be of similar duration when the variable interval was around 50 ms long. This temporal compression was not seen if the initial interval was presented well before the saccade nor was it evident if auditory clicks were used to define the pre- and postsaccadic intervals. In subsequent work, similar compressive effects were spatially specific for intervals of a half-second [38].

Although evidence of modality and task specificity provides strong support for intrinsic timing, several crucial issues must be addressed as these models mature. For example, why would individual differences in producing consistent rhythms be selectively correlated with acuity in judging the duration (as opposed to the pitch) of a tone if these tasks engage distinct mechanisms? One might suppose that there are individual differences in noise properties associated with the time constants of neural activity. However, this would not account for the deficits observed after relatively focal brain lesions on a range of tasks that require precise timing [21]. Dedicated models offer a parsimonious way to computationally link disparate tasks.

Intrinsic models in their current form have difficulty accounting for crossmodal transfer. It is unclear how training on an auditory duration discrimination task would facilitate performance for judging the duration of a visual stimulus. Surprisingly, the empirical record on temporal transfer is rather thin. Humans [51] and rats [52] both show transfer between timing of visual and auditory signals. However, this work involves intervals of many seconds. Only a few studies have looked at transfer in the subsecond range, and these have not provided ideal tests for assessing intrinsic models. Meegan *et al.* [53] reported that, after extended training in judging the duration of a 300 ms tone, people were more consistent in producing a 300 ms interval compared with a 500 ms interval: an interval-specific transfer effect. Notably, participants were prevented from hearing sounds generated by their movements during production; thus, one cannot argue that they were reproducing sounds matched to their training. An intrinsic-based account of this form of transfer probably would require postulating that the movements were guided by an auditory temporal model. The auditory modality might have some special status compared to other senses with respect to the encoding of temporal information [54]; nonetheless, arguments of this sort are problematic for current versions of intrinsic models.

Moreover, intrinsic models that emphasize temporal encoding in early sensory areas could not fully account for transfer within a modality. Westheimer [18] gave participants extended training on a visual duration discrimination task, using a standard interval of 500 ms. During training the stimulus was always presented in the left visual field and acuity improved by ~60%. Perfect transfer was observed when the stimulus was presented in the right visual field. It is hard to reconcile this finding with the notion that activity in retinotopically organized areas provides the representation for temporal judgments.

The role of nontemporal factors on perceived duration

Performance on time-perception tasks entails several component processes, many of which are not specific to time. These include attention, working memory and long-term or reference memory [55]. To date few studies of intrinsic timing have asked which of these processes are affected by training. Perceptual studies of generalization have reported that benefits are interval specific [56,57], similar to the results observed by Meegen *et al.* [53]. Although this would rule out training effects related to processes of attention or working memory, it cannot be assumed that training has strengthened interval-specific timing elements or specific patterns in state-dependent networks. Consider a model in which there are patterns (or clock-like units) that correspond to 80 ms, 100 ms, 120 ms and so on. When given repeated training over this range, one might suppose that the strength of these patterns is enhanced. Alternatively, decision processes might become more reliant on neurons that recently provided relevant information, although the actual patterns remain unchanged. With either mechanism, improvement would be limited to the trained interval.

More generally, some of the behavioral effects attributed to intrinsic mechanisms probably are related to processes not directly involved in representing temporal information (see Box 2). As noted above, activity in LIP neurons that is predictive of psychophysical performance might reflect intrinsic dynamics that measure time or reflect fluctuations in decision and/or response preparation processes [4,58], with the perceptual analysis of duration occurring upstream. A transfer test would provide an important tool here. Suppose after extended training the monkey was presented with identical stimuli but now required to respond by using his fingers to press keys to indicate stimulus duration, rather than respond with an

eye movement. If timing and the benefits of training were restricted to activity in LIP neurons, little transfer would be expected because LIP is involved mainly in preparing the saccades. Although not tested, this seems highly unlikely. We assume that humans would show immediate transfer.

The nature of decision processes is also important for understanding how judgments of perceived duration might be influenced by task-irrelevant information. A 100 ms interval is more likely to be judged as 'long' when it is preceded by a long foreperiod compared to when it is preceded by a short foreperiod [59]. It is likely that the duration of the foreperiod is implicitly coded, providing a form of a congruency effect or introducing a response bias. Such biasing effects also can come from nontemporal information given congruencies that exist between axes of seemingly orthogonal dimensions (Figure 2a). Although 'small' and 'large' typically refer to space, these concepts map onto 'short' and 'long', respectively, in the temporal domain. This congruency can introduce biases that masquerade as distortions of time [60]. For example, when presented with a visual stimulus composed of an array of dots, people are more likely to report the duration as 'long' when the array contains more dots, larger dots or brighter dots. Even more abstract, for two stimuli of the same duration, the digit '7' is perceived as longer than the digit '1'.

At the earlier side of the processing stream, some temporal distortions are probable due to sensory or attentional effects in registering the onset or offset of a stimulus (Figure 2b). The observation that visual stimuli are perceived as shorter than auditory stimuli [61,62] might result from differences in the temporal resolution of the auditory and visual pathways. Similarly, attention and expectancies might influence the response to the onset and offset of a stimulus. Attended objects might reach a recognition threshold faster than unattended objects [44,63,64], which would result in an increase in perceived duration [44]. In contrast to the extended percept of attended objects, expected events might be perceived as shorter than unexpected objects because their hold on attention is reduced, leading to premature termination of stimulus processing.

A variant of these access effects also might account for the temporal compression illusion described above [50]. Compression occurs when a saccade target appears just before the first flash marking the start of the 100 ms interval. The abrupt onset of the saccade target might capture visual attention, delaying the recognition of the initial flash and, thus, result in a temporally shortened percept. Even when such masking-like effects are eliminated, compressive effects could be due, at least in part, to attentional effects. The spatial specificity observed in Burr *et al.* [38] occurs under conditions in which attention is biased away from the location of the standard stimulus (i.e. inhibition of return [65]). This would delay the recognition of this stimulus relative to other locations, resulting in an illusory compression of time.

Future directions

Following a modular paradigm, neuropsychological research generally has promoted models in which time is represented by dedicated neural systems. An appealing

Box 2. Outstanding questions

- Does training people on time-perception tasks in one modality transfer to other modalities? Are transfer benefits specific to judgments of time or do they reflect reductions in other sources of variability, such as those related to sensory detection or decision processes? Transfer designs also would be ideal for neurophysiological studies of time perception. For example, are the ramping functions evident in neural activity related to encoding the passage of time or preparation of specific responses? Could intermodal transfer be related to crossmodal projections between primary sensory areas [73], or would it depend on activity in association regions of cortex?
- In studies of patients with neurological disorders, deficits in temporal representation generally are manifest as increases in variability. By contrast, recent psychophysical studies have focused on manipulations that distort perceived duration, in other words, a change in the mean. How do changes in mean occur in intrinsic models of temporal processing, and what are the consequences of these changes on measures of variability? More generally, are temporal distortions the result of changes in the mechanisms used to represent temporal information, or do they reflect the influence of nontemporal processes on performance (see Figure 2)?
- What kinds of neural mechanisms can extend the temporal range for intrinsic models, or will these models be limited to the perception of very short intervals, similar to that proposed by Karmarkar and Buonomano [7]?

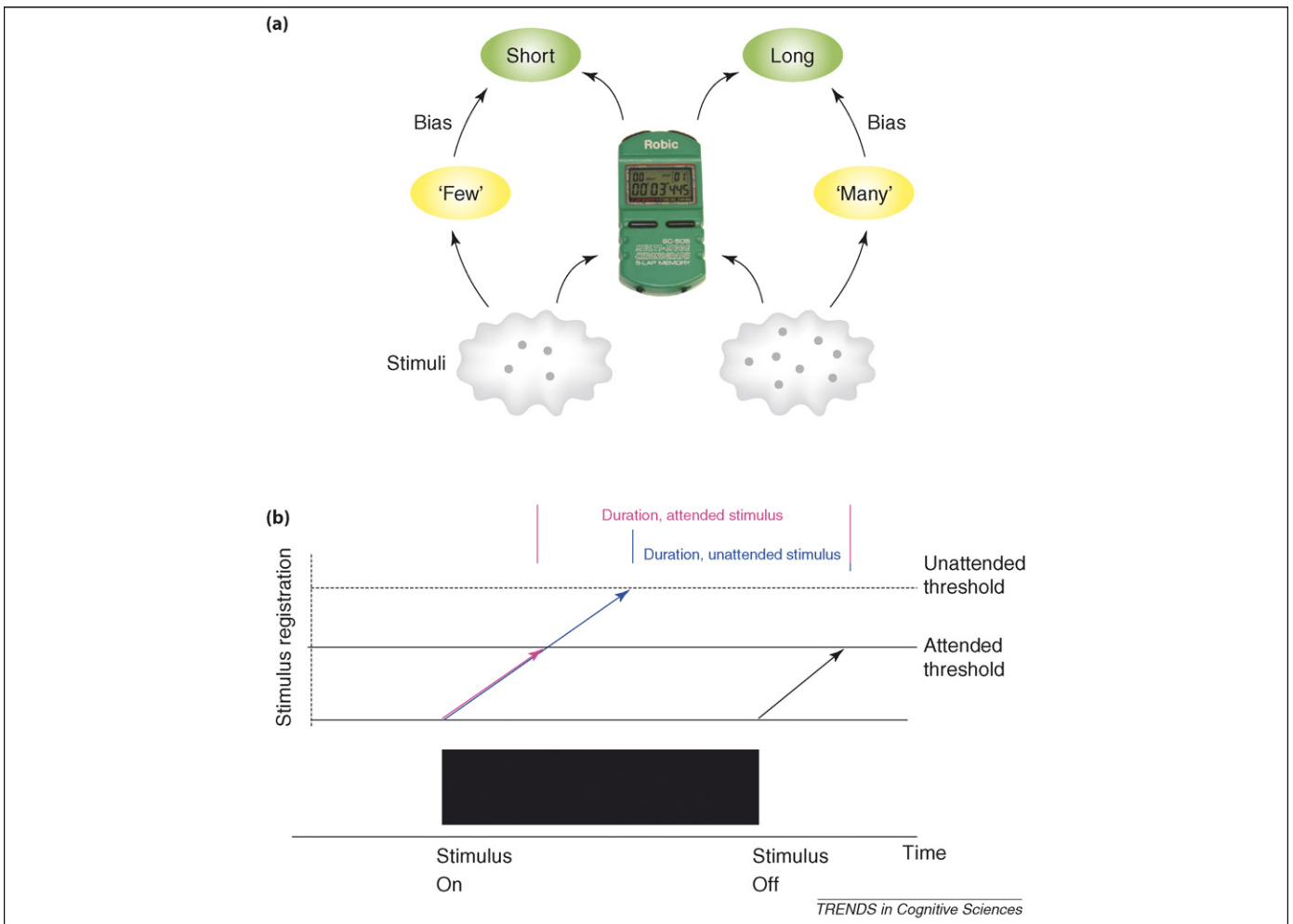


Figure 2. Nontemporal processes influence on the passage of time. **(a)** Decision processes in a time-perception task can be biased by nontemporal factors. For a stimulus presented for a fixed duration, a visual display composed of many dots is perceived as longer than a display composed of few dots. This illusion could result from the incidental activation of the overlap of spatial and temporal concepts. The spatial concepts 'few' and 'many' map onto 'short' and 'long', respectively. **(b)** Processes involved in detecting the onset and offset of a stimulus will influence perceived time. The registration threshold for an attended object is lower than for an unattended object. Assuming attention is then directed to the stimulus, the threshold for registering the offset will be the same for both stimuli, resulting in a longer perceived duration for the attended object. Similarly, faster detection times for the onset of an auditory stimulus might help explain why auditory stimuli are perceived as longer than visual stimuli. These nontemporal effects are relevant independent of whether temporal processing is dependent on dedicated or intrinsic mechanisms.

feature of these models is that they account for supramodal features of time perception and provide a principled basis for linking temporal processing in action, perception and cognition. By contrast, recent physiological and computational studies have highlighted how temporal information is reflected in the intrinsic dynamics of neural activity. This work complements behavioral studies showing distortions and disruptions of time perception that appear at odds with dedicated models.

Nonetheless, there remains much to be done in linking these behavioral and physiological signatures to a computational architecture of temporal representation. Intrinsic models need to account for some of the phenomena that provided the initial impetus for dedicated models; for example, these models need to account for commonalities, both in terms of behavior and neural systems, observed across disparate tasks requiring precise timing. Moreover, many of the effects now taken as evidence in favor of intrinsic mechanisms might, in actuality, be demonstrations of how nontemporal information can influence performance on temporal perception tasks. An important

point to guide future research in this arena is that temporal and nontemporal mechanisms need not be married. Processes related to sensory registration, attention and decision making remain relevant, regardless of whether temporal representation is dependent on a dedicated process such as a pacemaker or tapped delay line or an intrinsic process such as the firing rate of sensory neurons or the spatial pattern across a state-dependent network.

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