Dedicated Clock/Timing-Circuit Theories of Time Perception and Timed Performance

Hedderik van Rijn, Bon-Mi Gu, and Warren H. Meck

Abstract

Scalar Timing Theory (an information-processing version of Scalar Expectancy Theory) and its evolution into the neurobiologically plausible Striatal Beat-Frequency (SBF) theory of interval timing are reviewed. These pacemaker/accumulator or oscillation/coincidence detection models are then integrated with the Adaptive Control of Thought-Rational (ACT-R) cognitive architecture as dedicated timing modules that are able to make use of the memory and decision-making mechanisms contained in ACT-R. The different predictions made by the incorporation of these timing modules into ACT-R are discussed as well as the potential limitations. Novel implementations of the original SBF model that allow it to be incorporated into ACT-R in a more fundamental fashion than the earlier simulations of Scalar Timing Theory are also considered in conjunction with the proposed properties and neural correlates of the "internal clock".

Keywords

Interval timing • Scalar timing theory • Striatal beat-frequency theory • Adaptive control of thought-rational cognitive architecture

Introduction

There are abundant examples of behavioral processes engaged in by humans and other animals in which short-timescale temporal information plays an critical role, ranging from estimation of how long one can safely look away from the highway during driving [1], to the subtle role that pauses in a speech signal play in language-based communication [2], to the trap-line foraging of bumblebees and hummingbirds that is partly guided by their knowledge of how long it takes a flower to replenish its nectar after a previous visit [3–5]. In all these examples, interval timing enables the organism to improve its prediction about the onsets and offsets of impending

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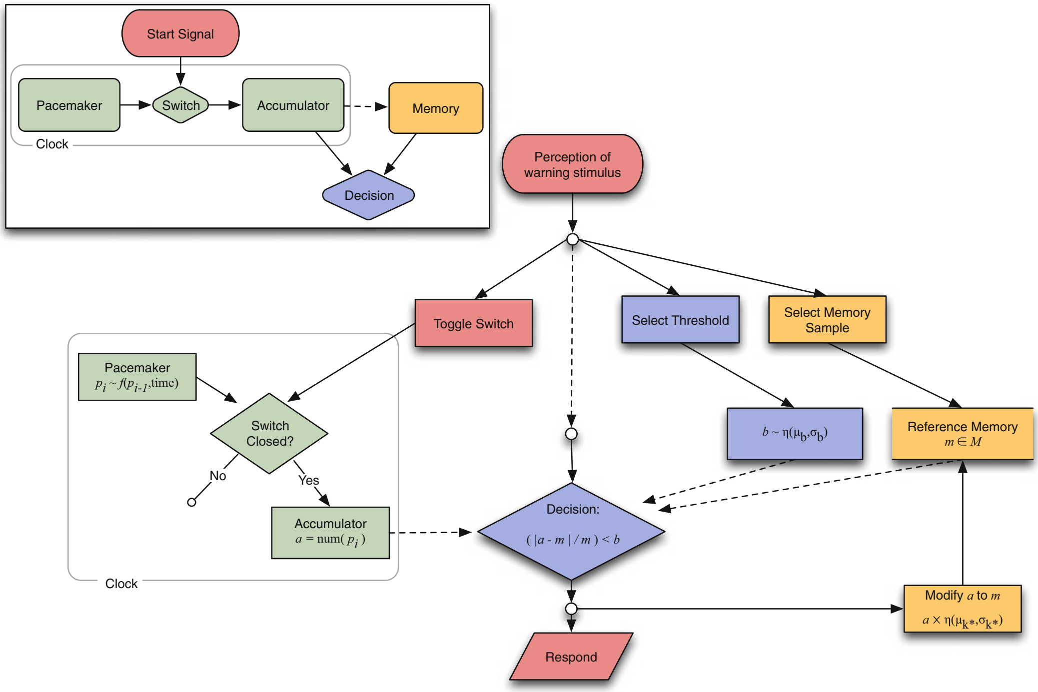

Fig. 1 *Top-left box* shows the outline of most information-processing models of interval timing based on a triad of clock, memory and decision stages [6, 17, 20, 64]. The main picture depicts one instance of these models; the Scalar Timing Theory as described in Church [24]. The main clock components are shown in *green*, the boxes processing input and output in *red*, the memory components in *yellow*, and the decision components in *blue*

environmental events. To allow for these predictions, an internal signal has to exist that provides the organism with a sense of time in order to anticipate these events. In the case of state-dependent models, categorically defined internal states are associated with specific behavioral actions attributed to each of the states [6]. By the pacing of transitions from one state to the other, behavior emerges that is attuned to the temporal regularities of the environment without the need of a dedicated clock or timing circuit (e.g., the behavioral theory of timing [7, 8]). In other state-dependent models, timing is an intrinsic property of the neural dynamics that elapse over the course of tens of milliseconds to a few seconds following the onset of a timed event (Buonomano, this volume; [9]).

However, the majority of dedicated models of time perception (for comparisons between dedicated vs. intrinsic models [6, 10–12]) assume that interval timing can best be described by a triad of clock, memory, and decision stages as depicted in the top-left box of Fig. 1. Most of the work that adheres to this triad can be traced back to the pioneering work of Creelman [13] and Treisman [14] who proposed the first information-processing (IP) models of interval timing. In these models, a dedicated clock stage provides a continuous or an interval-scale index of the passing of time since the onset of a temporally relevant event. Whenever the offset of the to-be-timed interval is observed, the clock reading is taken and stored in memory. After sufficient experience, the onset of upcoming stimuli can be predicted by comparing the current clock reading to the previously stored memory values. Although in the early work on interval timing most studies focused on the role of the pacemaker/accumulator, it was soon acknowledged that all stages of information processing (e.g., clock, memory, and decision) could contribute to the behavioral profiles observed in the temporal control of behavior [15]. One of the best developed theories that fits this general description and specifies how the different IP components contribute to observed behavior is Scalar Timing Theory [16, 17]—sometimes referred to as Scalar Expectancy Theory as originally developed by Gibbon [18, 19]. The general properties of these interval-timing systems have been described by Church [20] and more recently by Allman et al. [21].

Scalar Timing Theory

Description of the General Outline

A detailed version of Scalar Timing Theory is shown in Fig. 1 in order to provide an appreciation of the model's various levels of complexity [16, 22, 23]. This outline and the following description are based on the computational implementation of Scalar Timing Theory described by Church [24], although slightly modified versions have been described elsewhere [25]. According to Scalar Timing Theory, the "internal clock" of an organism that is engaged in the measurement of the physical duration of an external event (T) is comprised of a pacemaker that emits pulses at a regular rate. Whenever a temporally salient event is observed, a start signal is sent that closes a switch (or gate) between the pacemaker and an accumulator, allowing for pulses to reach the accumulator where they are integrated as a function of time. As the switch has to be closed in order for an event to be encoded, a process that is assumed to take some time, the model accounts for variation in the duration between the physical onset of the event and the first pulse passing the switch. This duration is assumed to be normally distributed: $t_1 = \eta(\mu_{t1}, \sigma_{t1})$—see papers by Meck and colleagues [26, 27]. Any pulse that passes the switch is thought to increase the value of the accumulator by one. By means of this coupled pacemaker/accumulator process, a measure of subjective duration (D) is available to the organism. When the imperative stimulus is observed, the organism can read out the accumulator, noticing that the time between the warning and imperative stimulus took, for example, 32 pulses. Of course, perceiving the imperative stimulus might also have taken time, reflected in switch opening latency: $t_2 = \eta(\mu_{t2}, \sigma_{t2})$, so that the subjective duration is assumed to be $D = T - T_0$ [27], with T_0 representing $t_1 - t_2$.

As most psychophysical phenomena, interval timing adheres to Weber's law, with shorter durations being estimated with less variability than longer durations. As this is typically demonstrated by observing identical response distributions after a scale transform (e.g., divide all distributions by the mean of the distribution), such superimposition of timing functions is referred to as the scalar property of interval timing [17, 28–30]. In contrast to many other psychophysical theories that assume that the subjective percept is non-linearly related to the objective input [31, 32], Scalar Timing Theory puts forward that the clock stage provides a veridical mapping of objective, external time to subjective, internal time [18]. Although it is sometimes claimed that the veridical time assumption is supported by experiments in which subjects have to compare the amount of time that is still left during the perception of a previously learned interval with another previously learned interval—the Time-Left experiments by Gibbon and Church [33]; see also Wearden's study [34]. It has been argued that the behavior observed in these procedures might also stem from strategies that do not tap directly into the underlying time scales [35–38]. A stronger case for the support of a linear encoding can be found in studies in which empirical response distributions were observed that are similar to the theoretical distributions associated with the linear encoding of time [39, 40].

Because all of these accounts assume veridical timing, the clock stage typically isn't used to account for the scalar property. Instead, Scalar Timing Theory assumes that the memory stage is the source of the scalar property—see papers by Gibbon and Church [16, 22, 33] for general details, or more specifically, that the scalar property is induced by the process that copies values from the accumulator to the memory store. When the offset of a temporal interval is observed, the current value of the accumulator, a, is multiplied by a memory translation constant k*—drawn from a normal distribution $\eta(\mu_{k*}, \sigma_{k*})$ [26, 41–43] before the value is copied to reference memory. This multiplication results in wider memory distributions for longer durations than for shorter durations, providing the basis for the adherence to the scalar property of interval timing. In the default version of Scalar Timing Theory, the memory store is considered to "consist of a large number of unorganized samples" [24, p. 9] although the samples must of course be associated with the environmental events that they encode for.

Whenever the organism wants to respond simultaneously with the onset of an upcoming event, it retrieves a random sample from memory that is associated with previous experiences with that event, and starts the accumulation process as soon as the warning signal is observed. However, since m, the sample from memory has been multiplied by the k* memory translation constant, a direct comparison between a, the value in the accumulator and m is not informative. Instead, Scalar Timing Theory assumes that a ratio comparison is made between m and a that is subsequently compared to a threshold parameter b to decide whether or not a response has to be made (i.e., if $(|a - m|/m) < b$, then make a response). Like the other parameters, the threshold is assumed to be sampled from a random distribution: $b = \eta(\mu_b,\sigma_b)$.

Although Scalar Timing Theory was originally developed within the context of animal learning and conditioning procedures, it has been successfully applied to temporal processing in humans, in both healthy and clinical populations [44–46] and has aided in the interpretation of the changes in interval timing capacities over lifespan development, including age-related declines [47–49]. In these settings, Scalar Timing Theory has accounted for many different phenomena associated with interval timing, such as the effects of different experimental contexts and procedures [50, 51], of pharmacological manipulations [52–56] and of emotional [52–58] and attentional [59–62] influences.

Challenges for the Information-Processing Models of Interval Timing

In any task related to interval timing, all (or most) of the processes and stages mentioned above play a role. As these different processes and stages interact, it is sometimes not straightforward or even possible to attribute a particular empirical observation to a particular aspect of an IP model of interval timing because any change in a particular procedure can be mimicked by a change in another aspect of the model. Nevertheless, it is important to critically evaluate any model or theory, and especially assess the validity of those components that are central to the phenomena covered. Like in other complex domains, the approach has been to isolate particular components and to specifically manipulate the experimental setup so that conclusions can be drawn relating to that component. This approach has obviously been an important line of research in the field of interval timing, with for example studies (see also [63]) showing that the scalar property should be captured in the memory components instead of in the accumulation process associated with Scalar Timing Theory [33], that a single sample is selected from reference memory on each trial instead of multiple [64], and that memory samples stored in reference memory affect other memory samples [65].

Stable Representation and Modularity

Scalar Timing Theory could be seen as a self-contained module that provides temporal information to a cognitive system or architecture that performs a more general task which relies on temporal information. Although one could, of course, still study the components of this black box, this approach would allow for using the output of Scalar Timing Theory without worrying about which internal processes have given rise to that particular output. However, this does require that irrespective of the task that is modeled using Scalar Timing Theory, the components should always function in the same way, cf., Figure 3.2-1.2 in [24].

Although rarely explicitly acknowledged, but see [63], the inclusion of a more cognitive decision component makes it difficult to adhere to this strong claim. Let's take, for example, human performance in a duration bisection task [66]. In a bisection experiment, participants are presented durations that they have to classify as either more similar to a previously learned "short" duration or as more similar to a previously learned "long" duration. When the proportion of "more similar to long" responses is plotted as a function of the length of the physical duration, a smooth sigmoid psychometric curve is typically observed, but see [67] with almost none of the shortest durations being classified as "long" (and vice versa for the longest duration), and with the bisection point (i.e., the point at which both answer options are equally often chosen) typically at the geometric mean of both standards [30, 66]. At first sight, it might seem that Scalar Timing Theory can quite straightforwardly account for the performance observed in bisection tasks: at the onset of the to-be-judged duration, the switch is closed and pulses will be accumulated. However, on the basis of what information will Scalar Timing Theory make a decision? Since this is a judgment task (and not a reproduction task), one might assume that the participant just waits for the offset of the presented duration, and then decides "short" if the observed a is closer to a memory sample associated with the short standard than to one associated with the long standard. That is, if $(|a - m_{short}|/m_{short}) < (|a - m_{long}|/m_{long})$ then choose "short", otherwise choose "long". Although at cursory inspection it might seem that this process fits nicely with the outline presented in Fig. 1, it requires that the decision process compares a to both m_{short} and m_{long}, requiring two retrievals from memory and a more complex comparison than the typically assumed simple comparison to a preset threshold. One could, of course, assume that this comparison isn't made within Scalar Timing Theory, but that the output of the clock is transferred to later stages. However, this would then assume that "non-timing" processes have access to the memory stage that is embedded in the timing module, violating basic assumptions of modularity. A third alternative hypothesis entails the creation of a bisection criterion [68], which could act as an internal, subjective representation of the point of subjective equality. According to this view, participants could internally commit to a "long" response as soon as this bisection criterion has passed. This criterion could be based on the geometric mean of the samples representing the short and long standards—i.e., $\mathrm{sqrt}(m_{short} \times m_{long})$. To allow for scalar variance, this point of subjective equality would have to be recalculated for each trial from two sampled values. Thus, to allow for this interpretation of the duration bisection task, the timing model outlined in Fig. 1 would have to be extended to represent a process that would result in a subjective bisection criterion that could take the place of m, but that is based on two retrievals from reference memory.

Although all three of these accounts would require modifications to the basic outline of Scalar Timing Theory illustrated in Fig. 1, recent electrophysiological data indicate that additional changes to the model might be necessary. Ng et al. [69] recorded EEG during a duration bisection task. From earlier work, it is known that during timing tasks a slow brain potential wave of negative polarity develops, referred to as the contingent negative variation (CNV), which resolves after a temporal decision has been made [70, 71]. If a bisection criterion is used by participants, one would expect the CNV to resolve at or around the point of subjective equality (e.g., geometric mean of the short and long standards). This pattern was indeed observed by Ng et al. [69], supporting the hypothesis that a comparison to the bisection criterion drives performance. However, the results also indicated that participants temporally prepared for the possible offset of the short tones, because the CNV increased starting at the onset of the comparison duration and reached its maximum amplitude around the time when the offset of the shortest duration would be presented. These results suggest that on the one hand a comparison is made based on a $m_{criterion}$ based on m_{short} and m_{long}, but on the other hand also indicate that a sample representing m_{short} is still available to the decision-making system given that value seems to be used to prepare for the upcoming stimuli.

Obviously, one could modify Scalar Timing Theory to account for these changes, and, as argued by Wearden [63], the basic properties of the timing system would still be the same. However, if one allows arbitrarily complex modifications to the original system (such as including a sequential timing process that first retrieves and estimates m_{short} and then retrieves m_{long} and estimates the average of m_{short} and m_{long}), a model consistent with Scalar Timing Theory can be constructed to fit almost any data set [63]. Moreover, because this more complex model provides considerable flexibility in decision processes, temporal arithmetic and, for example, the number and type of retrievals from reference memory, new parameters will need to be introduced that account for the latencies associated with these new processes. The inclusion of these parameters would make it difficult to constrain the model on the basis of empirical data from timing studies.

Degrees of Freedom Problem in Models of Interval Timing

The issues outlined above can be reduced to a straightforward "degrees of freedom" problem: although timing studies provide a wealth of data that can constrain theories of interval timing, the number of degrees of freedom enables Scalar Timing Theory to easily cover most or all possible outcomes of these studies, cf., non-constraining models in [72]. Two approaches can be taken to solve this problem that both focus on reducing the degrees of freedom. First, by introducing new behavioral measures that the theory should be able to account for, one can decrease the overall degrees of freedom. For example, if a particular model has 6 degrees of freedom, a new behavioral measure might require a certain parameter of that model to be set to a particular value to allow for a good fit, thus reducing the number of degrees of freedom to 5 for all other behavioral measures because that value has become fixed. This strategy can be seen as constraining the number of degrees of freedom by bringing in additional, potentially external constraints. Second, any process assumed by Scalar Timing Theory should eventually be identifiable in the neurobiology of the organism that demonstrates the capacity to time durations in the hundreds of milliseconds-to-minutes range. For example, if no brain area can be identified that corresponds to the accumulator as proposed by Scalar Timing Theory, one might need to reconsider the existence of an accumulator [73, 74] or if some proposals for the working of the memory stage are implausible from a neurobiological perspective, these alternatives might be rejected and thus constrain the theory. These constraints are derived from a reevaluation of the components already present in a theory, and could therefore be described as additional internal constraints.

In the remainder of this chapter, we will focus on four recent developments that focus on providing additional constraints on theories of interval timing by either incorporating additional external or internal constraints, or by providing cross-validation. First, we will discuss an integrated model of interval timing that embeds a dedicated clock structure consistent with Scalar Timing Theory in a more general cognitive architecture that provides externally validated constraints on the memory and decision stages [75]. Although this model could be seen as more complex than Scalar Timing Theory, this integrated model allows for modeling the interactions between non-temporal and temporal aspects of cognition. By incorporating the constraints that have been identified by fitting the cognitive architecture to other domains and tasks, models of interval timing become more constrained. Second, we will discuss how a model based on cortico-striatal interactions can replace Scalar Timing Theory's traditional clock and memory stages [44, 54, 76], removing a number of degrees of freedom from the original model because the basic properties of this clock have been directly derived from neurobiological observations. Third, we will discuss how this cortico-striatal model can be integrated into the architecture-based model and how a number of elementary neurobiological constraints bring about the scalar property in interval timing.

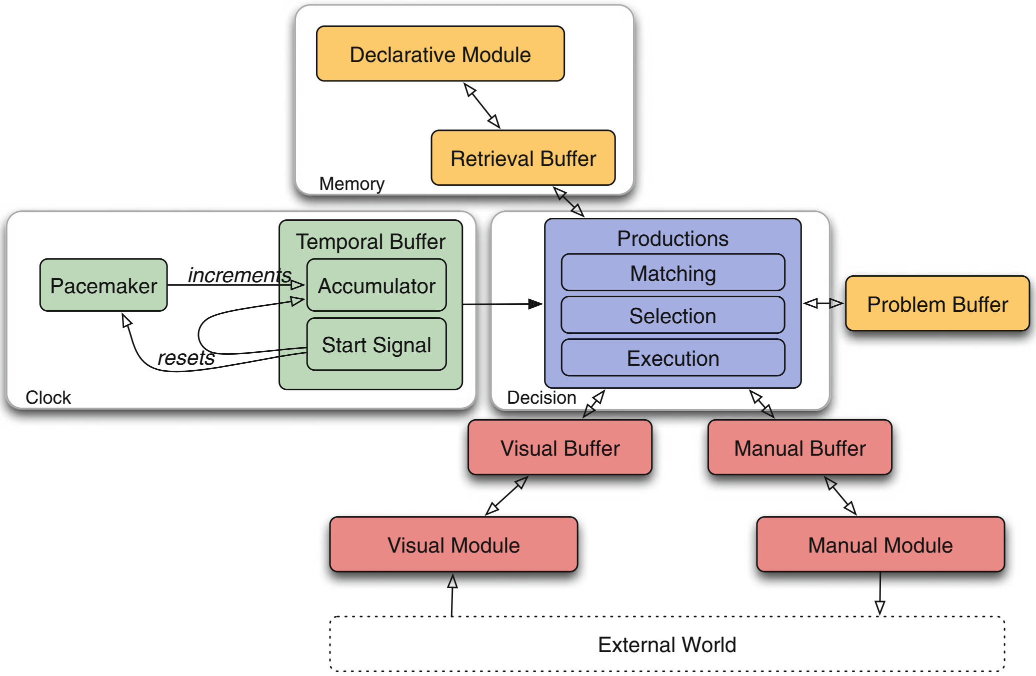

Fig. 2 An outline of the integrated-architecture timing model. The Clock component is similar to the clock stage found in Scalar Timing Theory [17], but with inter-pulse intervals approximating a geometric sequence. The Decision and Memory components are implemented by the decision rules and declarative memory system of ACT-R, the architecture that also provides the other components [75]. The color of the components matches the colors used in Fig. 1

Fourth, and finally, we will present the outline of a model that integrates interval timing in a more general framework of oscillation-driven cognitive behavior.

Integration of Cognitive Architectures

While working on computational models of behavioral tasks that were at first sight not obviously time dependent, Taatgen et al. realized that a number of phenomena they encountered were partly driven by their participants' sense of time. For example, Van Rijn and Anderson [77] had human participants perform a lexical-decision task at either normal speed or under speed stress and found evidence that the likelihood of guessing could be described as a function of the temporal distance to the response deadline. Given that Adaptive Character of Thought-Rational (ACT-R) [78, 79], the cognitive architecture frequently used for modeling these tasks, didn't provide any straightforward way to account for the passage of time, Taatgen et al. [75] extended ACT-R with a clock module based on the dedicated clock stage found in Scalar Timing Theory. Although Scalar Timing Theory also includes a memory stage, and several memory models have been proposed [80, 81], no model of temporal memory has been proposed that captures the more general features of memory systems utilized in human cognition. In contrast, the ACT-R theory provides an advanced and more constrained framework for modeling both memory and decision-making processes. Consequently, these default ACT-R components were used instead of incorporating the memory and decision stages from Scalar Timing Theory. The combination of both "internal clock" and ACT-R frameworks thus provides a best-of-both-worlds approach to modeling interval timing-based behavior. An outline of this integrated-architecture model of interval timing is illustrated in Fig. 2.

Although we discuss the three most important components of the integrated-architecture model of interval timing below, it should be noted that this architecture also provides for components that are involved with observing and acting on the environment. As a result of these additional components, models developed using this integrated-architecture can provide principled predictions about t_1 and t_2 which reflect the time that it takes to perceive and act on the onset and offset of a temporally salient event. That is, any visual event in the "External World" has to be observed via the "Visual Module", before decision rules in the Decision component can relay the start signal to the Clock component (see Fig. 2). As each component is based on formal theoretical work in the respective fields, the amount of time associated with t_1 (and t_2) can be predicted based on previous work instead of having it sampled from a normal distribution. Similarly, the incorporation of motor components (e.g., the "Manual Module") allows for estimating the delays associated with the actual response, an aspect of behavior not typically included in Scalar Timing Theory or similar models.

One of the challenges faced when integrating different theoretical approaches or frameworks is that certain assumptions that are necessary in the one framework, are difficult to account for in the other framework. For example, Scalar Timing Theory assumes that the accumulator value is multiplied by a before it's being copied to reference memory. In contrast, the ACT-R theory states that output from any module is automatically copied to memory, potentially subjected to some additive noise. However, the memory translation constant k* has a multiplicative effect [i.e., $a \times \eta(\mu_{k*}, \sigma_{k*})$, instead of $\eta(0, \sigma_a)$], and thus is not in line with the constraints of the architecture. Although one could, in principle, add explicit strategies that implement this multiplicative strategy, this process would be rather cumbersome, and add significant processing time. In addition to this, using the memory translation constant would imply the use of ratio rules for comparisons, a process that is also not easily accounted for (see also [82], which argued that ratio-rules are difficult to account for in neurobiological models). That is, a ratio-rule requires that whenever the system checks whether a particular duration has passed, (1) the current value from the accumulator has to be retrieved, (2) the reference value has to be retrieved from memory and (3) subsequently subtracted from the accumulator value, (4) divide the outcome of the subtraction by the reference value, to finally (5) compare the division to a threshold. Apart from requiring considerable processing and working memory resources, this suggests that timing an interval is a highly obtrusive process that would severely affect other cognitive tasks executed in parallel. This caveats could be perceived as a negative point for the integrated-architecture model, but it is also indicative of the consequences of adding external constraints to a theory: sometimes additional constraints require a change of thought.

In the sections below, we will discuss the three major components of the integrated-architecture model of interval timing, but we refer the interested reader to Taatgen et al. [75] and Van Rijn and Taatgen [83] for additional background.

Clock Stage

As the memory system in the integrated-architecture model cannot easily account for the scalar property of interval timing, the main source of scalar variance has to be found in the clock module. Therefore, a pragmatic approach was taken in which a pacemaker produces pulses with a gradually decreasing rate according to the following formula: $p_n = p_{n-1} \times a + \eta(0, p_{n-1} \times b)$ where p_n indicates the time between pulse n and $n - 1$ (and p_0 represents the initial value), a represents the pulse multiplier (the common ratio), and b the parameter determining the width of the noise distribution. It is important to note that although this function does provide a non-linear mapping, the non-linearity of this mapping is much dampened in comparison to the non-linearity suggested by logarithmic mappings of objective to subjective time. In fact, apart from the noise component, the subjective experience of time follows a geometric series, as a particular pulse count n in the accumulator will be observed at time $\Sigma_{x \times \{1..n\}} (p_x \times a^x)$. By fitting this model to empirical data [83], the p_0 was determined to be 100 ms, a was set at 1.02, and b at 0.015. Interestingly, this set of parameters indicates that the average inter-pulse time for short event durations (i.e., around 1 s) is shorter (~120 ms) than has been suggested in the literature [27] but at longer durations (i.e., around 5 s), the average inter-pulse duration is about 200 ms indicating that the assumed pulse length for typical interval timing durations is comparable to previously identified values. Regardless of the precise values, this non-linear mapping of objective to subjective time results in a higher temporal resolution immediately after the onset of an event than at later phases. This non-linearity gives rise to scalar effects on subjective duration, since an interval of about 5 s can only be estimated with a precision of 200 ms, whereas an interval with a duration of about 1 s can be estimated with a precision of 120 ms. Together with the inherent noise in the system, which also scales up with event duration and has a multiplicative effect in the geometric sequence, the scalar property of interval timing emerges [84–86].

Memory Stage

As mentioned above, the integrated-architecture model incorporates the ACT-R memory mechanism. Although a full discussion of this mechanism is beyond the scope of this chapter (see [87] for an introduction, and [88] for more recent discussion of the functioning of declarative memory), the main aspects of the declarative memory system from the perspective of interval timing are that all facts stored in the system as memory traces are subject to decay, and that various forms of memory mixing (i.e., the blending of different facts) are accounted for [89]. The psychological processes underlying this memory system have been extensively tested, both at the level of aggregate behavior and at the level of between-trial effects [90]. It should be noted however, that a separate working memory—as proposed in Scalar Timing Theory [43, 91–93]—is difficult to align with ACT-R, because the most similar component or "problem state" [94, 95] plays a different functional role.

The "memory mixing" mechanism takes an average of several memory traces, weighted by the activity of each trace and how well they match the current experimental context. As the traces contain pulse counts copied from the clock system, this blending process will adjust the count associated with a particular interval downwards if that interval is presented in the context of "shorter" alternatives, but upwards if "longer" alternatives are present. This way, the memory system, developed outside of the context of interval timing, naturally accounts for Vierordt's law [96–98]. Moreover, the memory system also naturally predicts trial-by-trial effects, with estimates of more recent trials having a stronger effect than older trials that have been subjected to decay for a longer period of time [98, 99]. By means of statistical modeling, Taatgen and Van Rijn [100] showed that the impact of older trials quickly wanes, as the influence of two trials ago is about half the size as the influence of the previous trial. To summarize, by incorporating an existing memory system into the integrated-architecture model of interval timing, both existing (e.g., memory mixing [50, 65, 98]) and new (e.g., feedback-based contamination of reference memory [100]; see [99] for other phenomena associated with feedback processing) timing phenomena can be quantitatively explained without having to introduce additional cognitive processes or model parameters.

Decision Stage

Although ratio-rules are favored [67] in Scalar Timing Theory, the variable m to which the value of accumulator is compared (i.e., $|a - m|/m$) is not strictly defined, and can range from a simple count retrieved from memory (e.g., m_i) to the earlier discussed point-of-subjective-equality (e.g., sqrt($m_{short} \times m_{long}$) in duration bisection studies. Although these choices imply different processes and will most likely be associated with different latencies, the choice of m is not separately

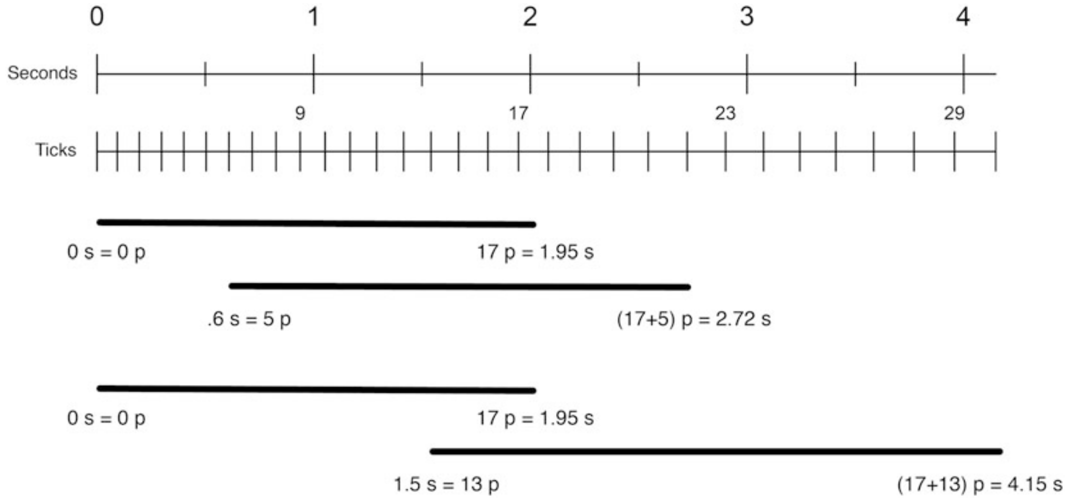

Fig. 3 Outline of the experimental procedures used to investigate the timing of multiple overlapping event durations [83]. In this example, the standard duration of 2 s is estimated to be 17 pulses. In the example shown at the *top*, the second duration starts 600 ms or 5 pulses after the first duration has started. The model thus estimates the end of the second event at 5 + 17 pulses, resulting in a duration estimate of 2.72 − 600 = 2.12 s. In the *bottom* example, the second event only starts at 1.5 s (13 pulses), so the response that signals the perceived offset of the second event duration is given at 13 + 17 pulses, resulting in an estimate of 4.15 − 1.5 = 2.65 s. This subjective lengthening result was attributed to a non-linear representation of time

modeled. In contrast, ACT-R's decision rules cannot perform complicated processes in a single step. For example, it is straightforward to test whether the current value in the accumulator is similar to a value retrieved from the memory store. However, multiple decision rules are needed to test whether the value of the accumulator is similar to the mean of two samples (e.g., separate steps for retrieving the samples, calculating the mean, etc.). Because this process is likely to take a reasonable amount of time (depending on the level of expertise, but probably more than 500 ms), ACT-R provides testable predictions regarding the nature of m and many other parameters.

Putting Everything Together

By integrating Scalar Timing Theory's clock stage into the ACT-R architecture, one can create models of tasks (e.g., peak-interval and other temporal generalization procedures) that have been typically analyzed using Scalar Timing Theory [75]. More interesting, the additional "non-clock" components also allow for creating models of more complicated behavior. For example, participants in a study reported in Van Rijn and Taatgen [83] had to reproduce durations with the start of the duration cued by the appearance of a stimulus on either the left or right side of a fixation point. On most trials, the next cue was presented before the duration associated with the previous cue had passed, resulting in partially overlapping intervals as shown in Fig. 3. This diagram also illustrates one of the main results from this study, which is that the later the secondary event started, the longer its estimated duration.

Obviously, there are many potential sources of variance in this model, ranging from how the onsets of the two events are perceived, to the time it would cost to retrieve memory traces or to calculate intermediate values, to the noise associated with motor responses. However, earlier work with the ACT-R architecture has provided us with reliable default parameters for all these components, so the integrated-architecture model can focus on explaining those aspects of the task that are most closely related to interval timing. In this particular task, the main question is, of course, how participants

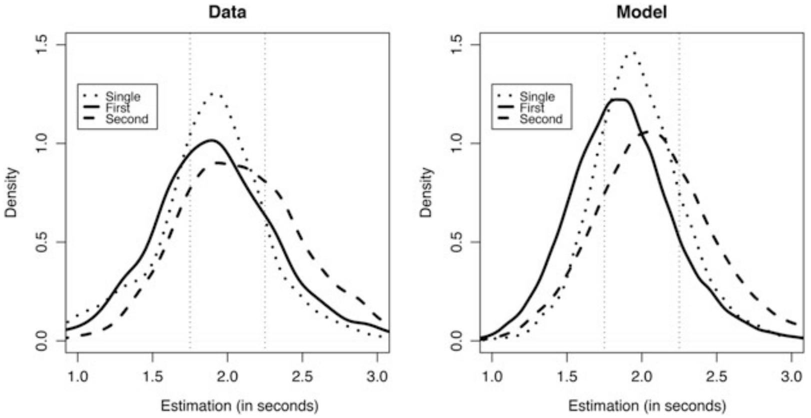

Fig. 4 Main results of the Van Rijn and Taatgen study [83]. The *left panel* shows the distributions for the empirical data, the *right panel* for the model fits. The *dotted line* shows the distribution during the last blocks of the training session, the *solid line* shows the distribution for the event duration that ended first, and the *dashed line* for the event duration that ended last. The model's explanation for the leftward shift of the *solid line* is based on the updating of the standard due to feedback, the rightward shift of the *dashed line* is due to the proposed non-linear representation of time. Adapted from Figure 4 in Van Rijn and Taatgen [83]

manage to estimate two (or more) event durations in parallel. A theoretical possibility, although not directly supported by either the integrated-architecture model nor by Scalar Timing Theory, is that the two durations would be estimated independently, as if a secondary clock-system was spawned [92, 101, 102].

Although recent findings from rats have provided strong evidence for simultaneous temporal processing, i.e., the use of multiple clocks that can be run, paused, and reset independently [101, 102], findings from human participants have tended to support sequential processing [83]. In this case it appears that when participants time overlapping event durations, the value of the accumulator is read out at the onset of the secondary duration, and that after finishing the first duration wait for the same number of pulses previously stored to determine their response. Because of the geometric series-based subjective time, the duration of the pulses added at the end will be longer than the duration of the same number of pulses integrated at the beginning of the interval, thus explaining the effect demonstrated in Fig. 3. Obviously, the later the onset of the second event, the more pulses have to be added at the end of the distribution, and thus the larger the overshoot of the estimation. At the same time, as participants were provided feedback based on their performance, it is to be expected that they would try to optimize their timing behavior, thus shortening their internal representations of the standard durations. Figure 4 shows the main results of the experiment and the model fit. The narrow distribution of the dotted line in the left panel indicates that participants had mastered reproducing the 2-s-interval during training. During the experimental phase of the experiment, the response distributions for the first and second event durations differ. The response distribution for the first event duration is shifted slightly forwards, whereas the response distribution of the second event duration is shifted backwards. As can be seen in the right panel, these patterns are well-described by the model. In the model, the forward shift is caused by the incorporation of the feedback. Each time an event duration is over- or underestimated, participants received feedback (either "too long" or "too short"). As on many trials the second duration was overestimated, participants often received "too long" as feedback, and as a result updated their memory representation of the standard event duration. The backward shift shown by the dotted line can be explained by inferring a non-linear timescale, as discussed earlier. Although individual parameters could have been adjusted to improve the fit to this specific dataset even further, the parameters were chosen to provide the best fit to a series of experiments. Most importantly however, the best fit was obtained with a parameter larger than 1.0, reflecting a non-linear subjective time scale. Since this experiment, we have considered this estimate as fixed and have used the same parameters in all subsequent models [100], as have other researchers [103].

To summarize, using the integrated-architecture model of interval timing makes it possible to create models that provide quantitative estimates of behavior that allow for a much more thorough testing of alternatives than would be possible if one is limited to qualitative predictions. Nevertheless, even when computational models are constructed that provide a reasonable fit the empirical data, the underlying mechanisms should always be scrutinized to make sure that they still align to the latest insights in neuroscience (see Hass and Durstewitz, this volume).

Neural Mechanisms of Interval Timing

The central tenet of both Scalar Timing Theory and the integrated-architecture model of interval timing is that a dedicated clock or timing circuit provides access to an index of subjective time, but neither theory has made any specific claims on the neural instantiation of this timekeeper. Interestingly, the neuroscience literature has suggested that the (pre-) supplementary motor area (SMA) might be part of the neural instantiation of the clock as it has been suggested to act as the accumulator [54]. The main observation supporting this notion was that the amplitude of a slow electrophysiological wave (the contingent negative variation, CNV) that is supposed to originate from the (pre-) SMA appears to covary as a function of the event duration that was estimated, e.g., CNV magnitude effect [104–106]. However, more recent work questions this interpretation because the CNV magnitude effect has proven difficult to replicate [73] and more recent electrophysiological data fails to align with the assumption that the CNV represents the accumulation process proposed by Scalar Timing Theory [69], but see also [107]. As a consequence, the interpretation of the original CNV results and its specificity of this slow wave potential to interval timing remains uncertain [74, 108]. It is clear from the empirical data that this slow wave develops over time and that it quickly resolves after a criterion duration has passed. However, this assumption could also be explained by assuming that the buildup observed in the SMA is driven by another source and only serves as an indirect measure of time. This explanation aligns nicely with the original notion that the buildup of the CNV reflects expectancy [109, 110]; and see for more recent reviews [111, 112], something that requires a sense of time, but is not necessarily time itself. This explanation is also supported by fMRI-EEG co-recordings on the basis of which it has been suggested that thalamo-cortical interactions regulate CNV amplitude ([113], see also the next section). Obviously, this line of argument can be followed for any accumulation or ramping patterns observed in neural substrates: the accumulation could be the source of time as hypothesized in the Scalar Timing Theory or the integrated-architecture theory discussed above, or it could be a derivative of time—Hass and Durstewitz, this volume; [74].

Although the instantiation of the clock stage is the most critical, several other difficulties remain when attempting to integrate the IP models discussed above with neurobiological mechanisms. For example, no neurobiological mechanism has been identified that can perform the ratio comparisons as hypothesized by the Scalar Timing Theory [76, 82]. Although the possibility remains that the required neural mechanisms may be identified in the coming years, another view that has emerged assumes that interval timing is based on the coincidence detection of patterns of oscillating neurons in cortico-thalamic-basal ganglia circuits [12, 44, 54, 71, 114–116].

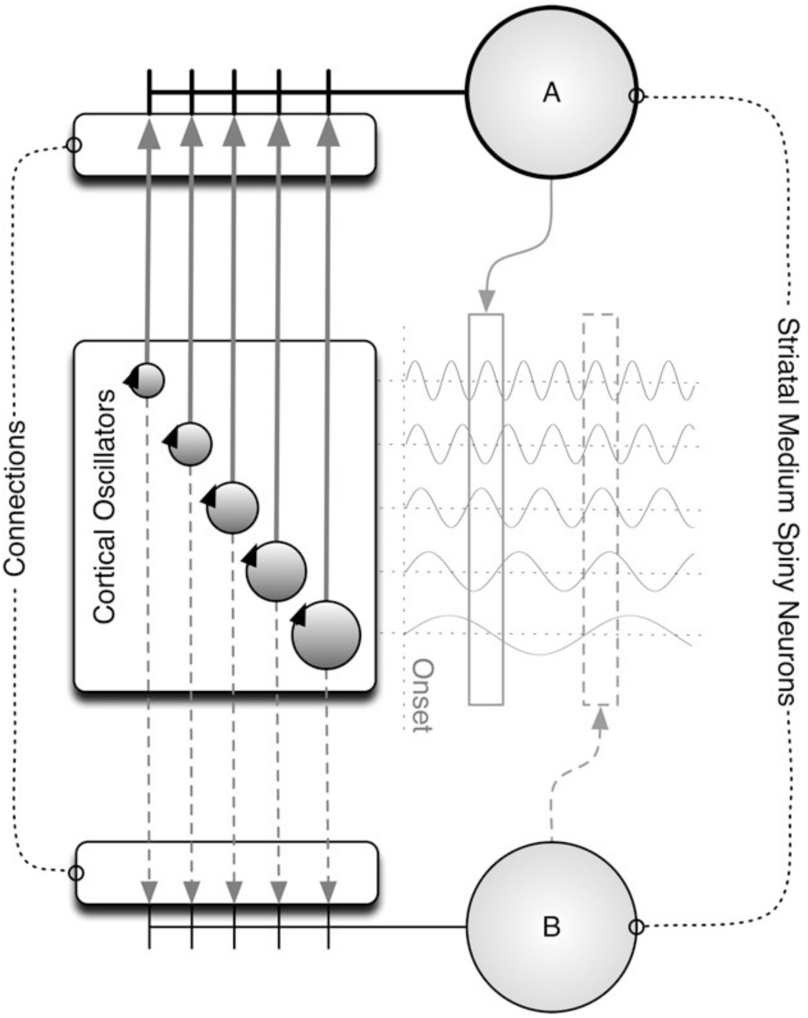

Fig. 5 Schematic depiction of the oscillatory-based timing circuit of the Striatal Beat-Frequency model [6, 76, 117]. At the start of an event, the phase of the Cortical Oscillators is reset after which the oscillations recommence. The different frequencies of the oscillators give rise to different activity patterns over time, depicted to the right of the Cortical Oscillators. Striatal medium spiny neurons (*A* and *B*) receive input from the oscillators via glutamatergic Connections. By dopaminergic input to the striatal neurons (not shown) after temporally salient events, the striatal neurons become sensitive to specific patterns in the oscillators (illustrated with *boxes* outlining activity patterns). In this illustration, striatal medium spiny neuron *A* has been reinforced to detect a coincidence pattern that occurs just after the onset of the event, and neuron *B* is sensitive to a pattern associated with a slightly longer event duration

Striatal Beat-Frequency Model

Based on the work of Miall [117], Matell and Meck [76] have proposed an alternative neural instantiation of the clock stage that assumes a cortico-striatal network as the primary source of temporal information. Although the full model is more detailed, especially with respect to the role of certain nuclei of the basal ganglia and the thalamus, the main outline is shown in Fig. 5. This SBF model is built around the notion that cortical neurons or neuron ensembles (the “Cortical Oscillators” in Fig. 5) oscillate at relative stable (over time) but different (over oscillators) frequencies, and that medium spiny neurons (MSNs –labeled A and B) act as detectors that become active if a certain pattern is observed (via "Connections") among the oscillators. Because the oscillators have different frequencies, different points in time after resetting the phases of the oscillators will be associated with different patterns, thus allowing for the association between a certain coincidence pattern among the oscillators and a temporally salient event.

In the following sections, we will discuss the neurobiology and the functional properties of these different components of the SBF model.

The Oscillators

When discussing the role of oscillators in keeping track of time, the first concept that might come to mind is the suprachiasmatic nucleus (SCN), a tiny region in the anterior part of the hypothalamus. The SCN has an approximate period of 24 h and acts as the central timekeeper for circadian mediated behavior and body functions [118, 119]. In contrast to the SCN, which provides a single oscillating 24-period output signal, the oscillators in SBF models are assumed to play a more indirect role in the tracking of time from milliseconds to hours [120].

In the beat-frequency model proposed by Miall [117], populations of high-frequency (~10 Hz) oscillators are assumed to underlie the perception of event durations in the range of milliseconds to tens of seconds or minutes (i.e., durations > 0.1 Hz). Each oscillator is assumed to have its own frequency, to become active when its activation has reached a certain threshold value, and will stay active until its activation drops below the threshold (this typically results in each oscillator being active for about 1–2 % of each cycle). In this basic beat-frequency model, all oscillators are connected to a single output unit or integrator. At the start of a to-be-timed event, the phase of all oscillators is reset after which the oscillations recommence. At the end of the event, Hebbian-type learning adjusts the connections between active oscillators and the output unit towards 1, and the other oscillators towards 0. After sufficient training, this model can reproduce the perceived duration of the event by resetting the phases of the oscillators at the start of the reproduction and responding when the integrator receives sufficient input from the oscillators. The simulations presented by Miall [117] elegantly demonstrate that populations of high-frequency oscillators with between-oscillator variation in period can act as a "clock" for interval timing as the system can accurately represent durations in the range of milliseconds to hours [12].

Using this basic beat-frequency model as a foundation, Matell and Meck [6, 76] have proposed the Striatal Beat-Frequency (SBF) model. Although the main extension is the augmented output unit (see the section "Striatal Medium Spiny Neurons"), these authors also refined what information is provided by the oscillators to later portions of the clock stage. Instead of assuming a binary output function per oscillator, with a single active period for a small proportion of every cycle and no activity during the remaining part of the cycle, the SBF model assumes a sinusoidal output pattern. This assumption is based on the idea that instead of a single neuron acting as an oscillator, each oscillator could be considered as an ensemble of neurons with a similar frequency (similar to the volley principle in auditory perception). Because neurons are known to fire probabilistically, with a firing rate that is a function of the phase [121], the output of each ensemble-based oscillator will follow a sinusoidal pattern [76, 122–124]. This idea has been further tested by Oprisan and Buhusi [85, 86], who have implemented this process using biophysically realistic Morris-Lecar (ML) cortical neurons [125, 126].

Assuming a similar Hebbian-type process for learning the connections between the output of the ensemble-oscillators and the output unit, Matell and Meck [6, 76] demonstrated that this extension was sufficient to elicit a more Gaussian-shaped pattern of activity in the output unit that is similar to what was observed in single cell recordings in the dorsal striatum. Moreover, by adding some global variability in the dopaminergic control of clock speed

[127–130]—resulting in all oscillators running either slightly faster or slower on each trial—longer durations are represented by a wider shaped distribution in the output unit, reflecting the scalar property even at the single-cell level [131]. Matell and Meck [76] have analytically shown how the scalar property can emerge from the SBF model of interval timing. In their implementation of the SBF model, they assume that virtually all of the cortical neurons that project onto MSNs fire regularly at frequencies in the 8–12 Hz band. Moreover, the output of each of these cortical neurons is modeled by a continuous sine curve oscillation. In contrast, the output of real neurons occurs as spikes, which are usually described by a point process. Although the sine wave description is used for its mathematical simplicity, each beat has a temporal width (e. g., ~50 ms broadening for a 10 Hz oscillation), which will likely have a significant influence on the timing variance. More recently, Buhusi and Oprisan [84] have examined the Morris-Lecar (ML) model for neuron firing, which generates non-linear, action potential-like beat oscillations. The “beats” produced with this ML model should also exhibit temporally broadening and hence affect timing variance in a manner currently unaccounted for. As a consequence, a more biologically realistic way to implement the SBF model would be to describe the output of cortical neurons by regular spikes (with a small jitter); each spike transmitted to the MSN evokes a postsynaptic excitatory current (EPSC); coincident spikes produce superimposed EPSCs that lead to spike discharge of the MSN, by which target durations are discriminated using the coincidence-detection mechanism described within the original SBF model [76].

Striatal Medium Spiny Neurons

Although the changes in the functioning of the oscillators are probably equally important in the development from the basic beat-frequency model to the SBF model, the Striatal Beat-Frequency model is named after the more precise neurobiological grounding of the output unit. According to the SBF model, striatal MSNs are the neurobiological implementation of the output unit of the basic beat-frequency model. This link is well supported by neurobiological evidence [54, 71, 132]. For example, the striatum is considered to be the main input system for the basal ganglia, with each striatal MSN receiving input from up to thirty thousand different cortical and thalamic units. The large number of connections aligns well with the assumption that the output unit is connected to a large number of oscillators. Second, the basal ganglia—and more specifically the dorsal striatum—are often considered to be a perceptual filtering system, with clear evidence that the striatal MSNs need a large number of coherent input signals before they fire. This, of course, is required to prevent the MSNs from firing as a result of limited oscillator input. Most importantly, Matell et al. [131] have shown that about 20 % of the measured dorsal striatal cell ensembles showed a temporally specific modulation in firing rate, with particular ensembles becoming active around 10 s after a signal, and other ensembles after around 40 s. This indicates that there are neurons in cortico-striatal circuits that are tuned to specific event durations [132, 133].

In the basic beat-frequency model, the output unit only fired when a specific number of output units were active at the same point in time. Using striatal MSNs as the output unit, Matell and Meck [6, 76] updated the temporal integration and detection process. Based on earlier work, the integration window for coincidence detection was set to 25 ms, reflecting the observation that multiple input signals need not arrive at exactly the same point in time to still be processed as if a coherent input pattern was observed. Moreover, based on the observation that less input is required to keep a MSN active once it has become active, an asymmetric threshold was implemented which results in a slight right skew in the output unit firing distributions. Such coincidence-detection processes and oscillatory processes are ubiquitous in the brain and are a major advantage for the SBF model [9, 44, 76, 134–136].

Connections

In both the original SBF model [6, 76] and in the SBF-ML model [84–86], the input to the striatal MSNs is mediated by the synaptic strength of the connections between oscillators and MSNs. In the SBF model, the synaptic strength is determined by averaging the state of the oscillators at previous times of reinforcement. This learning is driven by long-term potentiation modulated by the dopamine that is released upon the registration of a temporally salient event. The synaptic strengths will represent a distribution of oscillatory states, as global noise in the frequencies of oscillators will result in slightly different oscillatory states on different trials. As a result, the detection of longer event durations will more heavily rely on oscillators with lower frequencies. Because slower oscillators will have a longer period of higher activity, the MSNs encoding a long event duration will receive input for a longer period of time and thus stay active longer, giving an additional source of scalar variance.

Given that these simulations involve all striatal MSNs having identical properties (such as the way incoming information is integrated and similar firing thresholds), and each MSN could be connected to any oscillator, each MSN could, in principle, represent any event duration unless they are chronotopically organized [132]. Therefore, the ability to represent a particular event duration depends on the learned synaptic strengths. In both SBF and SBF-ML, the synaptic strengths of a particular MSN are based on a memory representation of all previous experiences with the event duration that that particular MSN encodes for. As such, these cortico-striatal synaptic strengths have the same functional role as the pulse counts stored in reference memory in Scalar Timing Theory [17] and in the integrated-architecture account of timing [100]: i.e., the synaptic strengths serve as a filtering mechanism that constrains the firing of a MSN to times associated with a particular event duration, in the same way as the pulse counts constrain a response to a particular accumulator value or clock reading stored in memory.

Interval Timing within the Striatal Beat-Frequency Model

In IP theories of interval timing, the memory stage links the clock—implemented as a combination of a pacemaker and accumulator—to the processes that should perform a certain action at a particular point in time: only when the value stored in the accumulator is equal to or similar enough to the value retrieved from memory will the decision rule be applied. The three main components of the SBF model can be straightforwardly mapped onto this description [44, 54, 76]. First, the oscillators provide the same type of information as the combined pacemaker-accumulator in the IP models—a unique pattern of activation versus a unique integer count for different event durations. Second, as mentioned above, the cortico-striatal connections serve a similar role as the memory traces in the IP models, with synaptic strengths acting as a filtering mechanism that constrains the firing of a MSN to times associated with a particular event duration, in the same way as the pulse counts constrain a response to a particular accumulator value. And third, the firing of a MSN is synonymous with the decision stage in the IP models. In Scalar Timing Theory, the firing of a decision rule indicates that later, unspecified processes can perform the action that was associated with the reproduced duration (i.e., start pressing a lever to receive the food reward), whereas in the integrated-architecture account, observing that the values in the accumulator and the retrieved memory trace are identical will cause a decision rule to be applied that sets in action the execution of the temporally constrained action.

The main difference between the SBF model and pacemaker-accumulator models is that pacemaker-accumulator models implicitly assume that there is one decision rule which could, in principle, be used for estimating different event durations. That is, the same ratio rule in Scalar Timing Theory or the same decision rule in the integrative-architecture theory could be used to estimate different event durations as long as these durations can be uniquely encoded in and retrieved from memory. In the SBF model, the synaptic strengths are unique to each individual receiving MSN, which means that each subjectively unique event duration has to be encoded by a unique MSN. One could therefore say that after experiencing a particular duration *D* a number of times, which will have resulted in well-learned synaptic strengths, the associated MSN has become a temporal "feature detector" that will always fire after *D* time has passed. If, at a later point in time, another event has the same temporal structure, this particular MSN could be linked to that event as well, suggesting that striatal MSNs act in a very similar manner as feature detectors or perceptrons for other types of sensory input [137, 138].

Integration of Striatal Beat-Frequency and Models of Complex Interval Timing

Although the SBF and SBF-ML simulations focus on learning and reproducing a single duration, any timing system should be able to distinguish between or estimate multiple intervals. As acknowledged by Matell and Meck [76] and Oprisan and Buhusi [85, 86], and shown in Fig. 5, multiple striatal MSNs could be connected to the same set of oscillators. By means of different reinforcement patterns, each MSN would have different synaptic strengths and thus be attuned to different event durations. This raises the question as to whether each event will be associated to its own MSN, or whether different events that share a relatively similar temporal pattern will be encoded using the same MSN. It might be clear that it is theoretically impossible to have a separate MSN for each possible event duration this would require an infinite number of MSNs. At the same time, objective event durations that are sufficiently different should also be perceived as being different. The minimal objective duration that reliably results in subjective differences is called the just-noticeable-difference (JND) and, as described by Weber's law, is proportional to the length of the two to-be-distinguished durations. This would suggest that temporal precision is higher for shorter durations than for longer durations. That is, the distance between the event duration to which a MSN is most sensitive and the event duration of its direct neighbor should increase with the length of those durations.

This theoretical rationale for a nonlinear distribution of the MSNs is supported by computer simulations. Based on assumptions derived from the SBF model, we have constructed a novel variant of the SBF model (SBF*n*) that can learn to encode multiple ("*n*") distinct event durations. The initial state of this SBF*n* model is depicted in the left panel of Fig. 6. Each smaller distribution reflects the receptive field of a single detector that is modeled after the MSNs in the SBF model. Based on the simulations presented by Matell and Meck [76]—see for example their Figure 3.2-12, we expressed each neuron's sensitivity for a particular event duration as a skewed-normal distribution with a mean equal to the encoded duration, a standard deviation that is scalar in the mean, and a slight skew of 2. The left panel of Fig. 6 also shows the initial a-theoretic linear distribution of the detectors over the range of event durations for which they are sensitive. After creating this initial distribution, the SBF*n* model is presented with randomly drawn event durations, uniformly sampled from the entire range. For each sampled event duration, the MSN with the most active receptive field is selected, simulating that this particular objective duration is perceived as the subjective duration represented by that detector. In line with the idea that the synaptic strengths will be updated each time an event duration is encountered that results in the firing of a MSN, the mean of the distribution is updated following a simple reinforcement learning algorithm. The distributions shown in the right panel of Fig. 6 represent the detectors of SBF*n* after sufficient training has been provided and a relatively stable pattern has emerged. Clearly, a nonlinear pattern is exhibited, starting with high temporal resolution at shorter durations with a negatively accelerating decrement in temporal resolution for longer durations. The dotted line shown in the right panel of Fig. 6 is a best fit

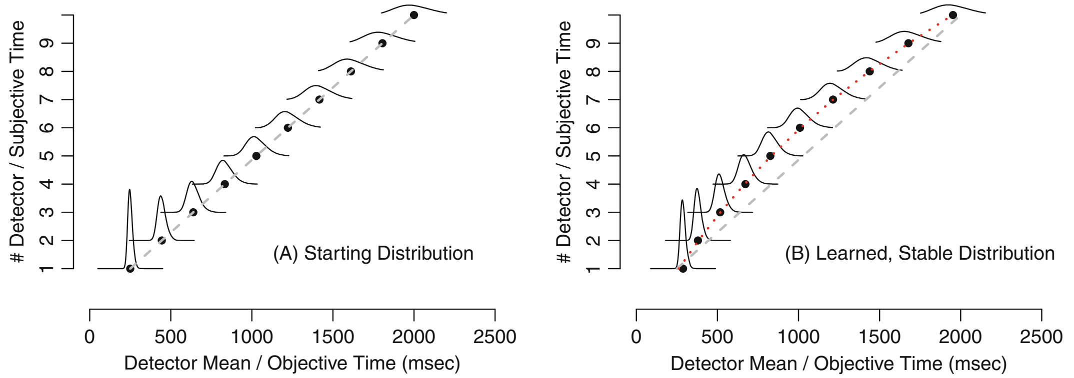

Fig. 6 Starting distribution (*left panel*) and learned, stable distribution (*right panel*) of an extended Striatal Beat-Frequency model that can represent multiple durations (SBF*n*). The x-axis depicts the objective time to which each of the ten simulated detectors modeled after striatal medium spiny neurons is sensitive. Each of the detectors has a skewed-normal receptive field that scales with the represented event duration. The initial state of the SBF*n* model, depicted in the *left panel* reflects linear temporal precision. The stable distribution of detectors, shown in the *right panel*, emerges after training. This distribution follows a geometric series as can be seen by the *dotted line* that follows the function $\sum(110 \times 1.1^{n}) + 150$

geometric series, indicating that the temporal resolution closely resembles Fechner's observation that the subjective experience increases arithmetically for geometrically increasing physical stimuli. Interestingly, many of the basic assumptions of these different SBF models could also be applied to the IP models of interval timing. For example, the assumption of global variability in the frequencies of the oscillators could be translated to variability in clock speed between trials in Scalar Timing Theory as was proposed by Matell and Meck [76]. This would remove the need for the memory translation based on k^*. However, to account for other effects associated with the scalar property, such as the JND effect, a ratio-rule would still be required.

As the distribution of simulated detectors in the SBF*n* model follows the same pattern of nonlinearity as was used in the integrated-architecture model of interval timing, it is straightforward to update this model to match the properties of the neurobiologically constrained SBF*n* model. That is, where the original integrated-architecture model assumed that the clock module provides a readout on an interval scale that represents the current time, an updated version could simply be provided with an indication of which MSN fired most recently. Because these feature detectors will always fire in sequence, the model will be able to predict which detector will fire next, thus providing an index of the passage of time even before the target detector has fired (concept of "shorter" than) as well as after it has fired (concept of "longer" than). This information could drive expectancy-based processes as it might provide the thalamocortical-based input to decision processes that regulate the CNV amplitude as hypothesized by Nagai et al. [113]. Although a complete SBF model as implemented by Matell and Meck [76] and Oprisan and Buhusi [85, 86] could be included in the integrated-architecture model, a more pragmatic approach would be to update the parameters of the geometric series in the model so that the mapping of objective to subjective time follows the distributions of the MSNs of the SBF*n* model.

Integration of Interval Timing and Models of Working Memory

One of the remaining questions is related to the source of the oscillations that provide the input to the MSNs as neither the SBF nor SBF*n* model identifies the exact source. Interestingly, both theoretical and empirical work suggests that working memory and interval timing rely not only on the same anatomical structures, but also on the same neural representation of a specific stimulus [139, 140]. Specifically, cortical neurons may fire in an oscillatory fashion to form representations of stimuli, and the MSNs 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. Based on this link between working memory and interval timing [140], the SBF and SBF*n* models of interval timing can be extended to an oscillatory model of interval timing and working memory (SBF*m*). The principles derived from these biologically based models also fit well with a family of models that emphasize the importance of time in many working-memory phenomena [141–143].

Neural oscillation is an important feature in both interval timing and working memory. In particular, the activation of working memory is associated with increased gamma oscillations (e.g., 25–100 Hz) in the frontal cortex that are entrained to the hippocampal theta-frequency range (e.g., 5–12 Hz) in multiple brain areas including the cortex, striatum, and hippocampus—all relevant to interval timing [139, 144]. Recent evidence suggests that phase-amplitude coupling (PAC) of theta and gamma occurs during working memory maintenance [145–147]—where PAC refers to the phenomenon of coupling between the amplitude of a faster oscillation and the phase of a slower oscillation. Such a relation between different frequency ranges has been shown to be a prevailing feature of neural activity associated with cognitive function. Penttonen and Buzsaki [148], for example, showed a natural logarithmic relationship in the periods of delta, theta, gamma, and ultra-fast oscillations, while Lakatos et al. [149] have shown hierarchical relations in delta, theta, and gamma bands of activity. In this regard, the relations among these different frequency categories are thought to be important in controlling patterns of neural activation.

Computer simulations suggest that multiple oscillators with different frequencies produce these logarithmic and hierarchical relationships. Moreover, the simulated relation between different frequency ranges appears to be fractal, i.e., gamma oscillations are entrained within theta, which is, in turn, entrained within delta oscillations [139]. Consequently, it has been hypothesized that interval timing and working memory are decoded from different ranges of these oscillatory periods. More specifically, MSNs in the striatum could detect cortical target representations from the spatio-temporal patterns of gamma spikes entrained with theta (for stimulus attributes in working memory) or from synchronous patterns of theta oscillations entrained in slow oscillations (for event durations in interval timing). In this manner, the same patterns of oscillation in cortical networks can represent stimulus attributes and event durations simultaneously. Moreover, an optimal strategy for detection can distinguish between interval timing and working memory, i.e., a diverse range of delta–theta frequencies is favorable for encoding event duration, whereas synchronous theta oscillations are better for maintaining one or more items in working memory because this effectively increases the size of neuronal network. Therefore, the observed interference between interval timing and working memory [150–154] can be explained in terms of how the range of theta-oscillation frequencies is set (e.g., multiple theta frequencies or a single theta frequency synchronized with cortical oscillations). We suggest that network synchrony analyses, as described by Burke et al. [155] and Gu et al. [139], are able to distinguish between two types of spectral modulations: (1) those that reflect synchronous engagement of MSNs in the striatum with cortical or hippocampal neurons and (2) those that reflect either asynchronous modulations of neural activity or local synchrony accompanied by disengagement from other brain structures. The basic idea is that these different spectral modulations within cortico-thalamic-basal ganglia circuits have distinct spatiotemporal profiles during the timing of event durations and the encoding of specific stimulus attributes in working memory [99, 132, 140], thus providing an integrative format for the representation of time and other types of episodic information.

Summary and Conclusions

In this chapter we have shown how over the years the original IP model of interval timing has been extended. At the basis of this work lies the original theory proposed by Treisman [14] which specified, in verbal terms, how the combination of clock, memory and decision stages could give rise to temporal behavior. Gibbon et al. [17] further developed this model in a series of papers that refined the original theory by providing specific and quantitative implementations of the different IP stages. A large proportion of the current work in the field of interval timing is still based on the ideas put forward in the context of this Scalar Timing Theory. Two lines of work can be identified that branched off from this original model. Work in one branch focused on improving the neurobiological foundations of Scalar Timing Theory. The main example of this work is the Striatal Beat-Frequency model [6, 76] which demonstrates that a cortico-thalamic-basal ganglia network can implement the clock stage as proposed in Scalar Timing Theory. The other branch has focused on complementing the IP-models of interval timing with an integrated cognitive architecture [75, 83]. On the one hand, this integrated-architecture allows researchers to create models of more complex tasks in which interval timing plays a crucial role, whereas on the other hand this integration provides further constraints on interval-timing theories as the putative processes need to be filled in with greater detail. This requirement can also result in new explanations for existing phenomena. For example, the processes underlying the long-term declarative memory system of the integrative- architecture model allow for the precise modeling of the memory effects [100] observed in interval timing (i.e., the “memory mixing” effect—[50, 65, 98]).

Current work in this field is focused on reuniting these two branches. In the SBF*n* model, the SBF and integrated-architecture model of interval timing are combined, providing a neurobiology-based model that can be used to model complex time-based tasks. Although extending the integrative-architecture model to include a SBF-based clock stage does not change its functional properties, the neurobiological basis of the SBF model provides further constraints for this architecture-based model. Another approach to unification is the proposed SBF*m* model. The idea for this model is based on extensive work that links working memory to oscillations in the same cortico-striatal network that serves as the basis of the SBF model. The SBF*m* model links working memory processes and interval timing by assuming that the firing patterns of the oscillating neurons could encode for content in the working memory system, whereas the phase of these oscillations could encode for temporal properties [139, 140]. Future work will focus on the implementation of this SBF*m* model, and at the same time testing the predictions of this model using, for example, network synchrony analyses [139, 155] and model-based fMRI analyses [156–158] in an attempt to unify prospective and retrospective time estimation [159–163].

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