Abstract and Keywords

Theories on how time is perceived often lack integration between clock systems and other cognitive mechanisms. Researchers studying time have identified three broad timescales associated with different empirical phenomena, and assumed to be instantiated in different neural substrates. The authors discuss millisecond timing, involved with low-level motor and speech planning, and circadian timing, involved with the sleep-wake cycle, then focus on phenomena associated with interval timing, which ranges from hundreds of milliseconds to multiple seconds or minutes. They then present the integrative timing model, a computational model that can successfully account for the role of time in many simple and complex tasks. Throughout the chapter, the authors base their discussions of ontologies, phenomena, and models on a combination of theoretical evaluations, behavioral data, and neurobiological findings.

Keywords: interval timing, circadian timing, millisecond timing, time, computational models, integrative timing model, neurobiology
Introduction

From saccades taking sometimes just 20 milliseconds to processes involved in solving complex problems that can take minutes or hours, to developmental trajectories taking multiple years, all behavior studied by cognitive scientists takes place in time. In the case of saccadic eye movements, the passing of time is merely a physical necessity because physical laws dictate how long ballistic eye movements take to move visual fixation from one location to another. However, as soon as behavior becomes more complex, time becomes an integrative aspect of cognitive performance, even though it is typically not observed as such unless one is explicitly attending to the importance of time. In the context of public speaking, for example, we have all learned that one can stress important passages by pausing, a strategy that—with some training—most people can master. But even in simple day-to-day dyadic communication, temporal sensitivity plays an important role as speakers synchronize the temporal structure of their utterances. Clark (e.g., 2002), who has extensively studied the role of time in speaking (but see also Tallal, 2004; Wilson & Wilson, 2005), has linked this observation to the notion of the readiness principle proposed by Woodworth (1938). According to this principle, people are faster and more accurate in processing information when they are ready for it. On the one hand, this principle indicates that the supplier of information should allow the receiving party sufficient time for processing before providing additional information. On the other hand, however, this also suggests that the receiving party might use temporal regularities in the incoming information to optimally prepare (see Schirmer, 2004; Wearden, 2008, for further reviews). This adjustment to the temporal regularities of the environment is not specific to the domain of linguistic processing, but also can be observed in many other contexts, such as the entrainment to the pace at which stimuli are presented in an experiment (e.g., Grosjean, Rosenbaum, & Elsinger, 2001), the pace of specific aspects of computer games (e.g., Moon & Anderson, 2013), or the temporal structure in a complex technical system (e.g., Russwinkel, Urbas, & Thuring, 2011).

Within cognitive psychology, preparation in time has been studied extensively, most explicitly in the context of studies in which it is assessed how presenting a signal at a fixed duration before the actual stimulus can benefit processing. Already in 1981, a review paper by Niemi and Näätänen (1981) listed more than 125 papers focusing on these foreperiod effects. Although Niemi and Näätänen concluded their review by stating that what exactly causes foreperiod effects is unknown (see Nobre, Correa, & Coull, 2007, for a more recent review), they explicitly mention early work (e.g., Kornblum, 1973; Ollman & Billington, 1972; Snodgrass, 1969) that proposes that the presentation of the warning signal starts a time estimation process that either triggers a response at the temporally expected onset of the target or drives the preparatory processes that enables a quick and efficient processing of the target as proposed by Woodworth (1938). This link between foreperiod (and hazard) effects and timing theories has also been explored more directly in the recent work of Los, Kruijne, and Meeter (2014) and is an important aspect...
of current theories on the influence of predictive coding on subjective duration (Matthews et al., 2014).

But what cognitive faculty allows humans to estimate time? And, as the examples have indicated, given that this type of time interval estimation is often implicit, automated, and tightly interwoven with other aspects of cognition such as perception (e.g., Van Rijn, 2014) or decision-making (Shi, Church, & Meck, 2013), how can we integrate time estimation into a more general account of cognition? Before addressing these questions, we will first sketch a global outline of the different time ranges distinguished in research and then, focusing on interval timing, explore which psychophysiological laws describe human temporal performance. Because a series of recent reviews (e.g., Buhusi & Meck, 2005; Buonomano, 2013; Coull, Cheng, & Meck, 2011; Merchant, Harrington, & Meck, 2013; Van Rijn, Gu, & Meck, 2014; Wittmann, 2013) have extensively covered the neurophysiological foundations of temporal performance, we will discuss the neurophysiology of timing to the extent that it supports or contradicts existing timing theories.

**Taxonomy of Time**

Although time might seem a unitary concept, ranging from the milliseconds required for a saccade to minutes or hours involved in performing complex tasks, behavioral and neuroscience research on timing has provided evidence of at least three different timing systems (e.g., Buhusi & Meck, 2005, Buonomano, 2013; note that Buonomano also discusses microsecond timing important for sound localization, a topic not discussed here) that we will discuss in this chapter: Although the following categorization is mainly in terms of associated durations, another distinction that is often made is between timing that is “automatic” versus timing that is “cognitively controlled” (e.g., Lewis & Miall, 2003; Rammsayer, 1999), a topic that we will address as well.
Millisecond Timing

The shortest intervals studied in the domain of timing are those that have an upper bound of a couple of hundred milliseconds and that are involved in speech (see, for a review, Schirmer, 2004) and music (e.g., Shaffer, 1984) and in motor control (Ivry & Spencer, 2004; see, for a review, Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). As an example of the role of timing in speech perception, some phonemes are recognized on the basis of their temporal characteristics. For example, the word “rabbit” is typically pronounced containing a very short period of silence (~20 ms) that signals the intraword stop consonant “b.” If this silence is experimentally lengthened (>80 ms), the utterance is perceived as “rapid” (Liberman, 1996). In a German functional magnetic resonance imaging (fMRI)-analogue of the “rabbit–rapid” study, Mathiak, Hertrich, Grodd, and Ackermann (2002), using the German words “Boden” and “Boten,” demonstrated that the right cerebellar hemisphere is sensitive to the encoding of temporal parameters of verbal utterances. Because a number of cognitive tasks that require some type of verbal representation (e.g., verbal working memory tasks) are associated with activity in similar regions, Mathiak et al. hypothesized that the fine-grained temporal structure of speech sound sequences might still play a role in tasks that are often considered to be in the slower, interval timing or cognitive band (Newell, 1990, see also Anderson, 2002).

The notion that the cerebellum guides millisecond timing is also supported by studies on the timing of motor actions such as repetitive tapping tasks. In these tasks, participants are presented a series of tones at equidistant intervals and are asked to tap in synchrony with the tones. After a number of tone presentations, the tones stop and participants are asked to continue tapping. Although some of the observed variability will obviously be due to motor noise, the accuracy of both the motor processes involved in executing the tap and the underlying timing process can be established by analyzing the variance structure of the performance in both phases (Vorberg & Wing, 1996). In line with the localizations observed in the speech studies, patients with (medial) cerebellar lesions show more variable performance on this repetitive tapping task (Ivry & Keele, 1989).

Although these studies might sketch a picture that the cerebellum is responsible for motor timing, not all motor functions show reduced temporal accuracy after cerebellar lesions. For example, patients with cerebellar lesions show no deterioration in continuous circle drawing performance, a task that requires temporal consistency of the involved motor actions (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). This has resulted in the hypothesis that the cerebellum is involved in discrete, event-based timing in which an explicit temporal representation can be formed between the onset and offset of an interval (Ivry et al., 2002).

It is noteworthy that there is some evidence from lesion studies (Nichelli, Alway, & Grafman, 1996) that suggests that the cerebellum is also involved in interval comparison tasks using long intervals (i.e., >8 sec). Because these durations are typically considered
to be outside the range of motor timing, this work suggests that millisecond timing and interval timing might be partially based on similar neurological structures.

**Interval Timing**

The term “interval timing” is used to describe the temporal processes that deal with the estimation and reproduction of durations in the seconds-to-minutes range. These durations are critical in the accurate representation of more complex action sequences and slightly longer term rhythmical structures (Matell, Meck, & Nicolelis, 2003), but also in the estimation of the duration of longer term activities (e.g., gaming or Internet browsing; Bisson & Grodin, 2013). Interval timing is found in a wide variety of species, from humans and primates to bees and fish. Within the animal literature on interval timing, one of the best-known experimental setups is the fixed-interval procedure in which a reward can only be obtained after a fixed temporal duration since the last reward. Animals can discover the temporal structure involved and withhold their response immediately after a reward, initiating responding only after a proportion of the interval has elapsed. Because this behavior is observed even in the absence of any external time cues, the subject must have access to an internal representation of the passing of time. A variant of this task that is more suited for studies with human participants is the peak-interval procedure (e.g., Hinton & Meck, 2004; Malapani, Deweer, & Gibbon, 2002; Malapani et al., 1998; Rakitin et al., 1998). In this procedure, participants are first presented a duration a couple of times and are then asked to reproduce this duration. A typical operationalization of this experiment is to present a participant with the duration using a light that is on for a certain time during the learning trials. During the reproduction trials, the light is again turned on, and participants are asked to turn the light off by pressing a button after the same duration has passed. If all responses of a participant are averaged and plotted, a slightly right-skewed Gaussian distribution is observed, of which the mean indicates the participant’s accuracy and the spread indicates the precision.

Although this task might seem rather artificial at first, the properties of this task can easily be mapped on time-critical sequential multitasking (e.g., Kushleyeva, Salvucci, & Lee, 2005; Salvucci, Taatgen, & Kushleyeva, 2006), a complex but common task: for example, checking a flight instrument gauge with a frequency appropriate to the expected frequency of fluctuations in the gauge’s measurements (e.g., Miller & Fu, 2007; Salvucci, 2005). Another example is that a driver has to make sure to check the rearview mirror regularly (every 2 to 5 seconds according to the California Driver Handbook, although empirical studies suggest that glances are much less frequent—e.g., approximately once per 25 seconds when driving on a highway; Recarte & Nunes, 2000). In the section on Models of Interval Timing, we will discuss a model that can account for the complexities involved in these types of tasks.
Whereas the earlier descriptions mainly focus on the time ranges of the durations, another way to categorize intervals is by the extent to which the temporal behavior is automatic versus cognitively controlled. This distinction is partly based on differences observed in neuroimaging studies that compared shorter and longer (i.e., multiple seconds) intervals, that assessed whether the temporal task requires a motor response, and that manipulated the predictability of the task (Lewis & Miall, 2003). According to this distinction, automatic timing is mainly guided by the (pre-)motor circuits and sensory cortices and does not require the involvement of prefrontal or parietal cortex. According to Lewis and Miall, this type of timing might use a number of different time sources, such as time sources in the cerebellum (as discussed earlier), but it might also utilize recurring temporal patterns, such as the temporally predictable increase or decrease of activity in cells or cell clusters. The prefrontal and parietal cortices are, on the other hand, critical for cognitively controlled timing because they might provide the system with the memory and attentional requirements necessary for timing on longer intervals (Duncan, 2001). An interesting hypothesis put forward by Lewis and Miall is that most timing is based on the less flexible automatic system but that more flexible modules can be used to provide a versatile but more effortful clock system when attention is directed to a timing task.

Circadian and Infradian Timing

Two more often-distinguished timescales are circadian (~24-hour cycles) and infradian (>24-hour cycles) timing, with circadian timing being more closely linked to cognitive processing. Circadian rhythms are endogenous, entrainable oscillations with a 24-hour phase and are typically in phase with an external cue that provides temporal calibration (such as a light–dark cycle) although, even in the absence of such a cue, the oscillation remains largely intact. Circadian rhythms control many aspects of our daily behavior, from easily observed behavior associated with sleep and wakefulness (and the accompanying underlying factors such as body temperature, brain wave activity, and hormone production) to more subtle processes such as cell regeneration.

Whereas debate is ongoing regarding the clock that drives interval and millisecond timing, the clock driving circadian rhythms is uncontested. In mammals, the circadian clock is located in the suprachiasmatic nucleus (SCN), a distinct group of cells in the hypothalamus that receives information about the light–dark cycle via the rods and cones in the retina but also via retinal ganglion cells (Berson, 2003). Although it has been generally believed that the intrinsic phase of the SCN is about 25 hours, recent studies indicate that, under controlled conditions, the intrinsic period of the human circadian rhythm is very close to 24 hours (24.18 hours; Czeisler et al., 1999).

A well-known effect of the circadian rhythm, although not often taken into account in cognitive science, is that cognitive performance covaries with time of day (for reviews, see Carrier & Monk, 2000; Schmidt, Collette, Cajochen, & Peigneux, 2007; for references to earlier work, see Pöppel & Giedke, 1970). The phase of the circadian rhythm affects...
attentional capacities, executive functioning, and memory potentially via a slowing of central cognitive processing (e.g., Bratzke, Rolke, Ulrich, & Peters, 2007). Although these effects can partly be caused by fatigue or the increase in sleep loss during long testing sessions, studies with long periods (i.e., >36 hours) of constant wakefulness and controlled behavioral and environmental conditions have shown that even if effects associated with sleep loss are partialed out, the circadian phase influences cognitive performance (e.g., Bratzke, Rolke, Steinborn, & Ulrich, 2009). By combining biomathematical models of the modulatory effects of circadian phase with cognitive architectures that model “normal” cognitive behavior, Gunzelmann and colleagues (e.g., Gunzelmann, Moore, Gluck, Van Dongen, & Dinges, 2009; Kronauer, Gunzelmann, Van Dongen, Doyle, & Klerman, 2007) are able to explain a large proportion of the effects of circadian phase and sleep loss.

Interestingly, large interindividual variations can be observed in the phase of circadian rhythms, with early chronotypes waking up when late chronotypes fall asleep (Roenneberg, Wirz-Justice, & Merrow, 2003). Although this might seem at odds with the role of the light-dark cycle as a Zeitgeber, increased shielding in modern societies from the high light intensities found outdoors reduces the normalizing role of the light–dark cycle and results in a wider distribution of chronotypes (Roenneberg et al., 2007). Chronotype has a direct influence on cognitive performance, even predicting blood oxygenation levels in the supplementary motor area (SMA), parietal cortex, and rolandic operculum during a self-paced finger tapping task (Peres et al., 2011). Given that societal constraints tie certain activities to particular times of the day (e.g., start of the working day) and that these constraints fit the behavioral profiles of early chronotypes, enforced work or school schedules will interfere considerably with the biologically determined sleep times of about 75% of the populations, a phenomenon coined “social jetlag” (Wittmann, Dinich, Merrow, & Roenneberg, 2006). Obviously, this misalignment is in general even stronger in shift workers (e.g., Kantermann, Juda, Vetter, & Roenneberg, 2010; Vetter, Juda, & Roenneberg, 2012), but it is also particularly strong in adolescents (e.g., Carskadon, Wolfson, Acebo, Tzischinsky, & Seifer, 1998). Because the effects of this misalignment range from impaired learning on cognitive laboratory tasks (Wright, Hull, Hughes, Ronda, & Czeisler, 2006) and school grades (Dorsett, Perminova, & Kosova, 2010) to changes in metabolic and cardiovascular functioning (Scheer, Hilton, Mantzoros, & Shea, 2009) and obesity (Roenneberg, Allebrandt, Merrow, & Vetter, 2012), it is clear that proper alignment is important.

With respect to the interaction between circadian timing and interval or millisecond timing, although circadian and interval timing are typically considered to be distinct phenomena, circadian phase influences interval timing (e.g., Agostino, Golombek, & Meck, 2011; Lustig & Meck, 2001; Tucci, 2011), although the exact mechanisms behind this interaction are yet unknown.
Psychological Present

Whereas millisecond, interval, and circadian timing are defined in terms of objective units of time, another often used categorization of time is the “subjective present” (Pöppel, 2009). In a long tradition of biologists (e.g., Von Baer, who, in 1860, came up with the theoretical concept of the longest possible time interval that is considered a single “time point”), physicists (e.g., Mach, who, in 1865, determined that durations shorter than 30–40 ms are indeed observed as a single time point), philosophers, and psychologists (Fraisse, 1963; James, 1890; Michon, 1978), Pöppel (see also Pöppel, 1978) proposed that these time points (instead of “intervals” or “durations”) are the basic building blocks of the “mental machinery of humans,” potentially based on oscillations (e.g., Matell & Meck, 2004; Miall, 1989). Based on a series of empirical results (for an overview, see Wittmann, 1999), Pöppel further argued that the subjective “now” lasts about 2 or –3 seconds. For example, all events happening within an interval of up to 2 or 3 seconds can be grouped into a singular event, whereas events that last longer than this duration are typically observed as consisting of a series of sequential events. A similar distinction between intervals shorter and longer than 3 seconds has been proposed by Fraisse (1984). According to Fraisse, intervals up to approximately 3 seconds can be directly perceived, whereas longer intervals have to be processed or estimated because the onset of the interval will no longer be available at the offset of the event. Both Fraisse’s and Pöppel’s two-process theories are based on the notion that a low-frequency binding mechanism integrates cognitive events into a temporal gestalt (Pöppel, 1997). Although many studies provide evidence in favor of a distinction between the processing of intervals shorter or longer than 3 seconds, other work has questioned this view. For example, Eisler (1976) fitted psychophysical functions for subjective behavior to the data of 111 studies published between 1886 and 1975. Because a single power function (with fitted exponent, averaging to ~0.9) described all datasets, these empirical results question the existence of two distinct temporal mechanisms (see also Rammsayer & Ulrich, 2005).

Details of Interval Timing

Although all categories of timing discussed so far are associated with cognitive functioning, interval timing is the category most typically studied in cognitive science because it shares its time ranges with many cognitive processes. Instead of covering all details associated with interval timing (see, e.g., Allan, 1979; Grondin, 2010, for reviews), we will focus our discussion on two psychophysical laws that are often cited in the context of temporal processing: the scalar property (which is related to Weber’s Law) and Vierordt’s Law. This will be followed by a discussion of retrospective and prospective timing, two types of timing that can be described as “estimating the duration of an event that was completed in the past” or “estimating an event that is still ongoing.”
The Laws of Time
Weber’s Law and the Scalar Property

Weber’s Law is one of the best known psychophysical laws, stating that the smallest noticeable difference between two stimuli is proportional to the magnitude of the stimuli. In many domains, Weber’s Law is tested by presenting participants with a stimulus and measuring the minimum amount of change in the magnitude of the stimulus to detect the change. According to Weber’s Law, the ratio of this just noticeable difference (jnd) and the magnitude of the baseline stimulus is constant, with potentially different constants for different sensory domains. An alternative measure of relative variability is the coefficient of variation (CV), a measure proportional to the Weber fraction. Within the time domain, the CV can be calculated when a participant has been asked to reproduce a certain temporal interval, typically called the standard, a number of times. By dividing the observed standard deviation by the mean of the distribution (or the standard), the CV is obtained. Based on this regularity, distributions of reproduced durations should superpose when they are normalized based on the time of the peak; if a distribution of reproduced durations based on a standard of 3 seconds is divided by the mean (or mode) of the observed reproductions, and the same is done for a distribution based on a standard of 6 seconds, the plots of both distributions should overlap.

On the basis of a large number of (mainly) animal studies that adhere to the properties described earlier, Gibbon (1977) proposed the scalar timing theory (see Gibbon & Church, 1990; Gibbon, Church, & Meck, 1984; Van Rijn et al., 2014, for discussion; and see Gibbon & Church, 1981, for quantitative details). This theory, to which we later will return, assumes that temporal processing is at the heart of most cognitive functioning since in most tasks timing and expectancy (of the onset of stimuli or of potential rewards) play important roles. Gibbon showed that the behavioral profiles of animals are nicely described by the assumption that the temporal expectancy of an upcoming stimulus adheres to a scalar property (i.e., a constant CV: the standard deviation of estimations scales linearly with the mean).

Grondin (2001) has provided an extensive discussion of the applicability of Weber’s Law to interval timing in humans, concluding that it holds well for intervals between .2 and 2 seconds, with some deviations for longer and shorter durations. According to Grondin, the violations from Weber’s Law, or “fragmented time,” could either indicate that other cognitive aspects start playing a role at durations longer than 2 seconds (e.g., counting, or participants failing to remain focused on the timing task at hand) or that multiple internal time sources contribute to different durations. This latter explanation nicely fits the assumed distinction between millisecond and interval timing discussed earlier. The explanation that cognitive factors are at the root of the differences in human-derived CVs between intervals shorter or longer than 2 seconds is supported by the finding that this distinction is not observed in animals. For example, Gibbon (1977) discusses a number of studies with pigeons in which stable CVs are found for durations up to approximately 1 hour. At the same time, a more extensive account of the scalar timing theory (Gibbon et al., 1984) takes into account that not just noise in the temporal system affects behavior, but also that the observed behavior, even in the context of a temporal reproduction task,
involves many other cognitive faculties (e.g., memory for earlier experienced intervals), all with their own specific noise characteristics (see Gu, Van Rijn, & Meck, 2015 and Van Rijn, 2016, for a discussion and review of the interactions between memory and interval timing; and Taatgen & Van Rijn, 2011, for a computational model in which memory noise influences temporal performance). However, the temporal information still adheres to the scalar property, so the observed variance is considered a mixture of a component that depends on the stimulus magnitude and components independent of magnitude (see also Wearden & Lejeune, 2008, for a review of scalar properties in human temporal performance).

Vierordt’s Law

In a paper on “The Central Tendency of Judgement,” Hollingworth (1910) posed that all judgments have the tendency to gravitate toward the mean of the presented magnitudes. Part of this claim is based on the work by Vierordt (1868, in Lejeune & Wearden, 2009), who presented one of the first monographs explicitly focused on the experimental study of (human) time perception and production. Vierordt’s Law, based on the work presented in his book, states that short durations, presented among longer durations, are judged as longer than they really are, whereas the long durations are judged as shorter, with an “indifference point” (at which durations are judged veridically) being found somewhere around the midpoint of the duration range. This distortion is also referred to as the contraction bias (e.g., Poulton, 1979, who discusses a series of possible biases in perception) or just “regression toward the mean.” In interval timing, this phenomenon is found both for relatively short durations and for durations up to 1 hour. Interestingly, this indifference point varies depending on the exact experimental conditions, which might be one of the reasons why even current-day theories of interval timing have difficulty capturing all effects associated with Vierordt’s Law (Lejeune & Wearden, 2009).

Although not framed in the context of Vierordt’s Law, a recent paper by Jazayeri and Shadlen (2010) has provided a formal model of Hollingworth’s ideas that a measure of central tendency derived (p. 157) from all previous stimuli affects the perception and reproduction of new stimuli. Framed in a Bayesian context, this model explains the observed gravitation by the influence of the prior (based on previous stimuli) on the likelihood (representing the currently observed stimuli). Based on assumptions similar to the scalar property (longer durations are represented as wider likelihood distributions), this model can explain a number of detailed features in the Vierordt’s Law-like data. However, this ideal-observer model also makes a number of assumptions that are difficult to align with empirical and biological constraints (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012). Interestingly, when participants are particularly well trained or sensitive to time, the gravitation toward the mean of the distribution is much smaller, and, in some subpopulations, even completely absent (e.g., percussionists, Cicchini, et al., 2012).

Forward or Backward Timing
When talking about the estimation of time, two types of time estimation should be distinguished. The examples discussed earlier all relate to prospective time estimation, the perception of the passing of time when, at the start of the interval, it is known that an estimate will have to be made. Since a person is actively aware of the need to estimate the passing of time, Block (see Zakay & Block, 2004) referred to the subjective estimate of time in prospective tasks as “experienced duration.” In contrast, in the retrospective paradigm, only after the interval has ended does the person become aware of the need to judge a duration, as if one would be asked to estimate how much time has passed since starting to read this chapter. Obviously, since it is unlikely that a person actively times all possible events, retrospective timing has to rely on information retrieved from memory to assess “remembered duration.” Although the distinction between prospective and retrospective time estimation is fairly recent (see Wearden, 2008, for a discussion) and some work has suggested that one temporal processing system underlies both retrospective and prospective timing (e.g., Tobin, Bisson, & Grondin, 2010), other researchers stress that the differences between both processes suggest distinct processes (see Zakay & Block, 2004), an observation which is supported by observation that a number of critical variables differentially influence experienced and remembered duration. Moreover, work that provides evidence that retrospective and prospective timing are related often uses long durations for both retrospective and prospective tasks. When using multi-minute durations, it’s likely that the person who is asked to time an interaction in the prospective condition engages in other tasks during the interval, making it more likely that a memory-based strategy is also used for the prospective timing task. Nowadays, in the words of Ivry and Hazeltine (1992), retrospective timing is often seen as “timing without a timer” and prospective timing as “timing with a timer.”

**Retrospective Timing**

The notion of “timing without a timer” is based on the observation that people can make a temporal judgment in retrospective timing even though they probably did not engage any specific timing mechanism. However, where does the temporal information underlying the retrospective judgments come from? The prototypical explanation found in the literature can be traced back to Ornstein’s (1997) “storage size” account of duration judgments. According to Ornstein, retrospective time judgments are based on an assessment of how much information has been stored during the time period. Although this proposal did not specify what type of information would be stored during the time period assessed retrospectively, it still aligns well with current theories on retrospective timing that typically assume that some sort of quantity judgment is made. For example, one account of retrospective timing assumes that the amount of memory storage that is used during the retrospectively timed interval might be guiding the retrospective assessment of duration, whereas another account assumes that the number of contextual changes or cognitive events (e.g., Zakay & Block, 2004) is quantified and used to assess “remembered duration.” Both accounts seem to rely much more on explicit processing than what is assumed for the automatic process involved in “timing with a timer.”
One of the major difficulties involved in studying retrospective timing is that a retrospective timing judgment can only be elicited once within an experiment; after that, the participant is alerted to time and thus subsequent judgments are likely to be (partly) driven by prospective timing. Together with the large variability observed between participants in retrospective timing studies, these methodological issues seem to have hindered research on retrospective timing (Wearden, 2008).

An interesting perspective on retrospective timing is provided by Tobin, Bisson, and Grodin (2010) who argue that, instead of the dichotomy sketched earlier, retrospective and prospective timing do differ but only on a quantitative level. To appreciate the argument of Tobin et al., one should know that one of the main arguments for the distinction is that prospective timing was shown to be affected by the amount of attention directed to timing, whereas similar effects were not observed for retrospective timing (see literature reviewed in Tobin et al., 2010). However, Tobin et al. argue that although all tasks might be timed, if the amount of attention directed to time is small to start out with—as it is in retrospective timing—no or only very small effects of the manipulation of attention would be expected. An attractive aspect of this view is that it would provide an important step toward unifying models of prospective and retrospective timing (see also Block & Zakay, 2001).

**Prospective Timing**

In the context of “timing with a timer,” many researchers have simply surmised the existence of a clock system and have tried to identify the properties of this underlying system. An experiment done in this domain can typically be categorized as an instance of one of four general paradigms, as identified by Allan (1979):

1. **Verbal estimation**: After exposure to a time interval, reporting how much time has elapsed in a well-known quantity (“this lasted 3 seconds”; note that this paradigm is comparable to the typical paradigms used in retrospective timing)
2. **Interval production**: Producing an interval of a certain, specified duration (“click on the button after 15 seconds have passed”)
3. **Interval reproduction**: Perceiving an interval of a certain duration (e.g., the length of a tone) and then reproducing it (by pressing a button to end the tone)
4. **Interval comparison**: Perceiving the duration of two intervals (e.g., two tones that are played sequentially) and reporting which is longer

The interval comparison paradigm is often further subdivided by contrasting the above-mentioned direct comparison-based discrimination task with temporal generalization in which participants are asked to judge durations relative to (i.e., “longer than,” “equal to,” “shorter than”) an earlier learned standard duration.

Interestingly, although all these tasks are typically assumed to tap into the same mechanisms, it is important to realize that the first two paradigms assume that participants in these experiments have an accurate representation of how long one unit of the response scale lasts and also assume that these units can be used to generate a
(linear) timeline that can be “read out” during the estimation of an interval. This notion is at odds with the observation that people typically have a representation of the duration of 1 second and employ different types of strategies to estimate longer durations. Because a well-known strategy is to repeatedly (sub)vocalize certain words that are assumed to last 1 second (e.g., “one one hundred, two one hundred, three ...”), researchers using this method have to be even more ingenious to ensure that their participants are not keeping track of time by simple counting. Given the potential reliance on explicit, memorized representations and counting strategies in these two paradigms, one can wonder whether results obtained with these paradigms accurately reflect the underlying properties of the clock. Based on these concerns, most current studies involved with prospective timing use reproduction or comparison paradigms.

As mentioned earlier, prospective timing is the focus of the lion’s share of the timing studies reported in the literature. This might be partly due to the methodological difficulties involved in testing retrospective timing, but another possible explanation is that prospective timing in its broad definition—being aware that time is important in the current context—is omnipresent in the cognitive sciences.

Models of Interval Timing

If an agent has the capacity to experience time without external input, an internal source of time has to be available to this agent. This source of time, sometimes referred to as the internal Zeitgeber, analogous to the external cue for the circadian clock, is typically assumed to be a cognitive faculty that either emits ticks not unlike a metronome, or it is assumed to be a derivative of a more continuous measure such as the change in temperature or activity of memory traces. However, because the ticks of a metronome can only be used to track the passing of time if one counts the number of ticks, and the passing of time can only be derived from a continuous measure if values associated with the beginning and end of an interval can be compared, additional structures are necessary to keep track of time.

Already in the 1920s and 1930s initial ideas were developed that proved influential (see, Wearden, 2005, for an historical overview) in the development of the first comprehensive model of interval timing. This model, which is highly cited, was developed by Treisman in the earlier 1960s (1963). Treisman’s model assumes a metronome-like pulse generator that sends quantized ticks to an accumulator that counts the number of ticks passed since the onset of a temporally important event. In this type of model (see also Creelman, 1962, for a similar proposal), it is typically assumed that the pacemaker continuously sends pulses but that these pulses are only accumulated when attention is focused to time; thus, a gate is opened that allows the pulses to reach the accumulator. Because the counts stored in the accumulator can be copied to a long-term memory store, new durations can be compared to earlier perceived durations, thus giving rise to
temporal behavior. Figure 8.1 shows the basic outline of this information processing model of interval timing.

Another type of model that has been proposed to account for interval timing is the multiple timescales (MTS) framework (Staddon & Higa, 1999). According to the MTS, the basic source of temporal information is the activation that is associated with a decaying memory trace. By inspecting the activation of a trace and assuming a relatively stable decay function, the activation of a memory trace can provide information on the time that has passed since the creation of the trace. In the MTS model, the information of multiple traces is combined to account for a number of properties of interval timing (see also Marr, 1999).

Other types of models are the behavioral theory of timing (BeT; e.g., Fetterman & Killeen, 1995; Killeen & Fetterman, 1988, 1993) and the learning to time (LeT) model proposed by Machado et al. (Machado, Malheiro, & Erlhagen, 2009). The BeT model assumes that temporal discriminations are governed by sequences of behaviors evolving through time, with behavioral state transitions determined by reinforcement rates. The LeT model has a slightly different perspective because whereas the BeT and the MTS model focus on alternative sources of the internal clock, the LeT model emphasizes the often neglected role of learning in temporal tasks. Although these models have a number of attractive properties (e.g., in the context of the MTS model, it is not necessary to use a specific start signal since the activation of any trace that has entered memory can be inspected), most of these models are not as widely applied as the pacemaker/accumulator model. We will therefore mainly focus on information processing models of time processing that build on the original work of Treisman.

**Information Processing Models of Time and Time Processing**

As depicted in Figure 8.1, information-processing models of interval timing typically consist of a source that is generating discrete events or pulses at predictable, but not necessarily constant, intervals and a container system that accrues these events. By storing the amount of pulses associated with a certain interval in long-term memory, this information can be used to prepare for the offset of subsequent presentations of the same interval. Despite its simplicity, this model has proved extremely powerful in explaining human and animal interval timing and has been extended to account for or used to
explain the effects of memory processing, attention, emotion, and neuropharmacological on interval timing. An extensive description of this type of model and contrasts with more modern accounts can be found in Van Rijn, Gu, and Meck (2014).

However, the application of this model has been limited to tasks in which time is the main focus, often even the only focus of cognitive processing (as in the tasks described in the section “Prospective Timing”). In daily life, however, timing is often a secondary aspect of a more general goal, as when one assesses the urgency of a phone call by estimating how long the other party keeps the phone ringing before giving up. To allow for the study of interval timing in the context of these more complex, real-life tasks, it is necessary that the interval timing model is able to account for the interactions between interval timing and other cognitive faculties, ranging from visual perception and attention (Wierda, Taatgen, Van Rijn, & Martens, 2013) to working memory limitations when multiple concurrent constraints have to be satisfied (Borst, Taatgen, & Van Rijn, 2010) and from deciphering the intended content of linguistic input (Van Rij, Van Rijn, & Hendriks, 2013) to the low-level aspects of decision-making in the light of conflicting information (Van Maanen & Van Rijn, 2007). To be able to embed temporal information in these types of task, the integrative timing model was developed.

**Integrative Timing Model**

As discussed earlier, models of time estimation typically consist of several components that together explain how time is perceived, compared, and reproduced. Each of these components therefore requires a mini-theory of how that component contributes to overall performance. The integrative timing theory and model of Taatgen, Van Rijn, and Anderson (2007) takes a different approach. Taatgen et al. point out that most of the components of time estimation models are not specific to time estimation; in particular, these components also appear in models of attention, memory, and comparison/decision-making. Only some sort of clock or Zeitgeber seems to be particular to time estimation, and even that component shares common laws with other types of perception, in particular Weber’s Law.

The integrative timing model therefore takes memory, attention, and decision-making from existing psychological theories, more specifically as they are implemented in the Adaptive Control of Thought-Rational (ACT-R) cognitive architecture (Anderson, 2007). Time estimation in that model consists of an additional module that is added to ACT-R, which only contains a timer and a means to read out and reset the timer. In the following sections, we will discuss each of the components in some detail.

**The Clock**

The integrated timing model takes a very direct approach to implementing the clock component of the model. In order to achieve Weber’s Law, it combines the classical pacemaker-accumulator model with the idea of a nonlinear internal timescale (Church & Deluty, 1977; Staddon & Higa, 1999). Instead of a pacemaker that produces pulses at a
fixed rate, the pacemaker in the integrated timing model produces pulses with a gradually decreasing rate according to geometric series (note that, already in 1883, Galton suggested the use of geometric series in the context of the perception of quantity that adheres to the scalar property). As a consequence, it produces many pulses in the first few seconds after the start of an interval (which resets the pulse rate) but fewer pulses per second later in the interval. A small amount of noise is added to the process to reproduce the typical variability in time estimation.

In essence, the clock in the integrated timing model transforms a time interval into a number on a nonlinear scale, where longer intervals seem more similar to each other than smaller intervals. This clock naturally reproduces several time estimation phenomena. The scalar property and the slightly right-skewed distribution in peak-interval experiments are a natural consequence of a nonlinear scale with noise. Bisection experiments are a second category of experiments that is naturally explained by this model. In bisection, subjects are first trained on a short and a long interval (e.g., 2 and 8 seconds, respectively). They are then presented with several intervals between the short and the long interval and have to judge whether the presented interval is closer to the short or the long interval. A typical result, depicted in Figure 8.2, is that the interval that is judged to be in the middle between short and long is at the geometric mean between the short and long intervals, a natural consequence of a nonlinear representation that follows a geometric series.

Attention

Several theories assume that time estimation requires sustained attention and that other distracting tasks therefore directly suspend or at least affect the accumulation of pulses. This is, however, at odds with the notion that time estimation is often not a conscious process and therefore does not always need attention to sustain it. For example, Grosjean et al. (Grosjean, Rosenbaum, & Elsinger, 2001) found that subjects unknowingly time the interval between trials in a choice reaction task. In their experiment, a slight deviance in interstimulus interval affected performance, even though the deviance was not consciously noticed by the subjects.

The integrative time model offers an explanation that is more in line with general effects of attention. Take, for example, the well-known invisible gorilla test of selective attention in which subjects fail to notice a man in a gorilla suit walking through a scene because they have to pay attention to basketball player passing a ball. Similarly, even though the accumulator in the clock may give an accurate representation of time, it may be ignored if the cognitive demands of other tasks or other aspects of the task are too high (see Taatgen et al., 2007, for examples of how this can explain several time estimation experiments in which attention plays a role).
In order to compare or reproduce time intervals, representations of time have to be stored in memory, either long- or short-term. Several different specialized memory models for time have been proposed (Jones & Wearden, 2003, 2004), but they all had the problem of being too simple to cover more than a subset of experiments.

ACT-R has a theory of declarative memory with a long history of development that is very well suited to also storing time intervals. In this memory, each experience with a time interval is stored as a separate memory trace. If two experiences are identical, a single, more activated copy is retained. Memory traces decay over time, which means that the most recent and most frequent traces are most active.

When an interval has to be retrieved from memory, a method called blending is used (Lebiere, Gonzalez, & Martin, 2007). Blending combines several memory traces and weighs them according to their activation and how well they match the retrieval cue. This combination is capable of modeling fairly complex phenomena of remembering time intervals. Taatgen and Van Rijn (2011) taught subjects in their experiment two intervals, a short interval of 2 seconds and a long interval that was initially 3.1 seconds (for additional modeling details, see Taatgen & Van Rijn, 2011). Subjects then had to alternate between reproducing the short and the long interval. Feedback was provided on whether the reproduced interval was correct (within ±12.5%), too short, or too long. After several trials, however, the criterion for the long interval was gradually changed, first upward, then back to 3.1 seconds, and then downward (subjects didn’t know this would happen). The results, shown in Figure 8.3, show that subjects adjust their estimates accordingly, but also that the changes in estimate for the long duration affect the estimates for the short duration, even though this interval was never changed. In other words, the long interval contaminates the short interval (a more detailed statistical analysis showed that this was true the other way around as well: the short interval contaminates the long interval).

The memory model accommodates all the relevant phenomena in the results. It adapts its representation of a particular interval on the basis of the feedback, and the recency effect ensures that recent experiences trump older experiences. More importantly, the blending
mechanism ensures that a small amount of the changes in one interval carry over to the other interval.

**The Role of Time Estimation in Complex Tasks**

Incorporating time perception in a cognitive architecture has more advantages than just being able to reuse cognitive components: it also offers a means to model the role of time perception in more complex tasks or the manipulations with time intervals that would require separate theories otherwise.

An example of the latter is a study by Van Rijn and Taatgen (2008). In their experiment, subjects had to produce two intervals, but they were partially overlapping in time. In other words, subjects received a start signal for one interval and then, some variable time (stimulus onset asynchrony, SOA) later, a second start signal for a second interval. Their task was to indicate the end of both the first and second intervals. The results showed that the first interval was produced accurately but that the reproduction of the second interval was biased by the SOA. If the SOA was long, the reproduction of the second interval was longer than with short SOAs.

Figure 8.4 shows how a combination of adding up the pulses that represent the interval and the SOA, combined with the bias introduced by the nonlinear scale, can explain the phenomenon.
Fig. 8.4 Illustration of how the model produces two overlapping intervals. The model has a representation of the interval (2 seconds = 17 pulses). It uses this to reproduce the first interval. To reproduce the second interval, it measures the SOA in terms of pulses (5 pulses in the case of a 0.6-second SOA and 13 pulses in the case of a 1.3-second SOA) and adds this to the end of the first interval. However, due to the nonlinear scale the estimate of the second interval becomes longer with increasing SOA.

A second example of the advantage of a cognitive architecture is a study of the role of time perception in driving, particularly multitasking in driving. Salvucci, Taatgen, and Kushleyeva (2006) gave subjects the task of driving in a simple simulated driving simulator. As a secondary task, they had to enter addresses in a simulated navigation device. In order to do the navigation task without driving off the road, subjects had to engage in the navigation task for brief amounts of time during which they could not look at the road. The experiment showed that subjects were sensitive to the conditions of the road: if driving required frequent steering corrections, they engaged in the navigation task for periods averaging 2 seconds. If steering corrections were required less often, they extended the period during which they worked on the navigation task to 3.5 seconds.

The model of this experiment assumes that subjects build up a representation of how long they can look away from the road based on experience. If the car is still perfectly in the middle of the lane after looking back following a navigation action, the assumption is that the period can be extended the next time. If the car is too far out of the center of the lane, the interval has to be shortened. Otherwise, the interval is kept the same. The nice aspect of this model is that it incorporates multiple aspects of cognition with a supporting but critical role for time perception.

Neurobiological Foundations

Because all information processing models assume a critical role for the pacemaker and an accumulator, a lot of effort has been invested in localizing the biological implementation of these components. Because the preparation for an upcoming response or stimulus is typically reflected in a buildup of negativity (either called the contingent negative variation or the Bereitschaftspotential) in the electroencephalogram at electrodes measuring the activity of the (pre-)SMA, early work has focused on finding support for the notion that the accumulator is reflected in the activity of the (pre-)SMA. Initially, a series of studies seems to have provided strong support for this claim; however, more recent work questions this claim both on empirical grounds (Kononowicz, Sander, & Van Rijn, 2015; Kononowicz & Van Rijn, 2011, 2014; Miniussi, Wilding, Coull, & Nobre, 1999; Ng, Tobin, & Penney, 2011), but also based on theoretical inconsistencies (e.g., Mento, 2013; Muller & Nobre, 2014; Van Rijn, Kononowicz, Meck, Ng, & Penney, 2011). However, elegant TMS studies have shown that the (pre-)SMA does play a critical role in interval timing (Wiener et al., 2012), although the exact nature remains unclear.
Whereas the biological analogue of the accumulator is still under debate, a more promising proposal has been made regarding the internal source of time. The striatal beat frequency (SBF) model by Matell and Meck (Matell & Meck, 2000, 2004; see also Oprisan & Buhusi, 2011) proposes that a cortico-striatal network is the primary source of temporal information. This SBF model is built around the notion that cortical neurons or neuron ensembles oscillate at relatively stable (over time) but different (over oscillators) frequencies and that striatal neurons act as detectors that become active if a certain pattern is observed 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 oscillatory patterns, thus allowing for the association between a certain coincidence pattern among the oscillators and a temporally salient event. Instead of counting pulses, this model assumes that time is perceived by a process of pattern matching. Although this account might seem far removed from the information processing models described earlier, Van Rijn, Gu, and Meck (2014) describe how the integrated timing and SBF models can be combined to provide a biologically plausible explanation for the nonlinearity assumed in the integrated timing model. More recent explorations related to the SBF model have proposed a close link between working memory-related brain oscillations and interval timing (Gu et al., 2015), thus providing a potential further integration of interval timing with other cognitive faculties.

**Conclusion**

In this chapter, we discussed the different categorizations of time, from micro- and millisecond timing relevant for motor control to circadian timing and their influences on cognition. We note that this categorization corresponds to the way that both Newell (1990) and Anderson (2002) have categorized cognitive phenomena into biological, cognitive, rational, and social bands, at different timescales. Because most behaviors studied by cognitive scientists take between a couple of hundred milliseconds up to a number of minutes, we have specifically focused on interval timing and discussed the theories that focus specifically on timing and also extensively discussed newer theories that consider interval timing in the context of more general cognitive functioning. Since the proposal of these integrated accounts, this type of model has led to a surge of computational models that use aspects of interval timing in their explanation of other tasks. Given that this model has also proved to be in line with neurobiological constraints on interval timing, we are confident that these types of integrated models will continue to inform future accounts of complex cognitive performance.

**Future Directions**
1. How can information processing theories be integrated with the constraints provided by the neurobiology of interval timing? Although some neurobiological components of interval timing models have been identified, the exact mechanisms have escaped detection. On the one hand, recent reviews (e.g., Wittmann, 2013) have emphasized that the activity of many brain regions correlate with the passing of time, but we have recently demonstrated that at least one of these accumulation patterns is unlikely to be causally involved in interval timing and have shown that alternative electrophysiological markers provide more promising indices (Kononowicz & Van Rijn, 2014, 2015). Although many proposals have been made regarding the neurobiological substrate underlying interval timing, an all-encompassing theory that can explain the myriad of phenomena associated with timing while being true to biological constraints is still lacking.

2. How does the passing of time influence decision-making? Although timing might play a role in many complex tasks, it has been suggested that interval timing is specifically relevant in decision-making that is based on the sampling of evidence. In these sampling models, a decision is made whenever sufficient evidence has been sampled in favor of one of the response alternatives (for an integrated sampling model, see Van Maanen, Van Rijn, & Taatgen, 2012). However, especially if the evidence does not favor any of the response alternatives, the sampling process can continue indefinitely. Knowledge about this aspect of the task could be used by the decision-maker in that, if it takes long to come to a decision, the alternatives will most likely have a similar subjective value. Thus, the passing of time could be used to lower the response thresholds. Although these general ideas have been around for some time, mathematical models of this phenomenon are currently under active development in the decision-making field.

3. Can preparation for an upcoming stimulus be distinguished from “pure” interval timing? The initial work on interval timing was based on studies focusing on response preparation. Obviously, timing is important in these types of temporal preparation studies, but it might be that this type of timing is different from pure timing in which no motor response needs to be given (see also Kornblum, 1973). In recent literature, the distinction between “pure timing” and “preparation-based timing” is not typically made nor discussed. This discussion has recently been revived, for example by Boehm et al. (Boehm, Van Maanen, Forstmann, & Van Rijn, 2014) who have shown that one of the main neural markers of interval timing is a predictor of cognitive preparedness and not a predictor of the passing of time.

4. What are the genetic markers of interval timing? Although genetic markers for circadian timing have been identified, little is known about the genetic markers for interval timing. To answer this question, a good animal model of interval timing needs to be identified, a process which—to our knowledge—has not been initiated yet.
An Integrative Account of Psychological Time

5. How can the human mind time multiple interval simultaneously? Earlier, we discussed experiments showing that human participants can time multiple intervals by invoking “temporal arithmetic,” which is based on the idea that one main interval is timed, and another interval is estimated on the basis of the deviation from this main interval. However, this experiment was performed using a typical interval timing setup in which participants were specifically attending to the passing of time. In real life, humans estimate many intervals at the same time, ranging from the time that the coffee needs to percolate, to the pauses in the utterances of a spouse, to the time it takes for a stove burner to ignite, to the realization that one’s children are too quiet for too long and that they therefore must be up to something. All these processes must be timed, and it is unlikely that all these intervals are estimated relative to one main interval.

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