

## 3.2 Memory for time

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### Abstract

The brain maintains a record of recent events including information about the time at which events were experienced. We review behavioral and neurophysiological evidence as well as computational models to better understand memory for time. Neurophysiologically, populations of neurons that record the time of recent events have been observed in many brain regions. Time cells fire in long sequences after a triggering event demonstrating memory for the past. Populations of exponentially-decaying neurons record past events at many delays by decaying at different rates. Both kinds of representations record distant times with less temporal resolution. The work reviewed here converges on the idea that the brain maintains a representation of past events along a scale-invariant compressed timeline.

It has long been appreciated that our experience of time is central to mnemonic functioning. Indeed awareness of the passage of time requires memory—how could one appreciate the “past” in relation to the “present” without the ability to simultaneously apprehend both (Husserl, 1966). Many philosophers arrived at the notion that our internal experience of time is in some sense organized analogous to the way a spatial dimension is organized, with information about distance and order (see also Bergson, 1910). James (1890) proposed something that sounds roughly akin to a short-term memory with temporally-ordered slots: “Objects fade out of consciousness slowly. If the present thought is of A B C D E F G, the next one will be of B C D E F G H, and the one after that of C D E F G H I—the lingerings of the past dropping successively away, and the incomings of the future making up the loss.” Similarly, considering the phenomenology of time, Husserl (1966) notes that our experience of the recent past has a temporally ordered character. Events further in the past are not merely weaker, but “feel” further in the past and recede further from the present as time elapses. Moreover, Husserl (1966) argues that when the future can be predicted—for instance while listening to a familiar melody—our anticipated future similarly has a temporal character. Events further in the future “feel” more distant and they approach the present with the passage of time. To summarize, James and Husserl argue that as time unfolds our experience of the recent past is organized like a timeline with information about what events happened at what temporal distance from the present—i.e., our experience of the present contains a record of what happened when in the recent past. One may imagine this

timeline as something like a musical score that tells the player what notes to play when. Imagine how the song would sound if the score contained only information about what notes to play and how often to play them without providing information about when and in what order to play them!

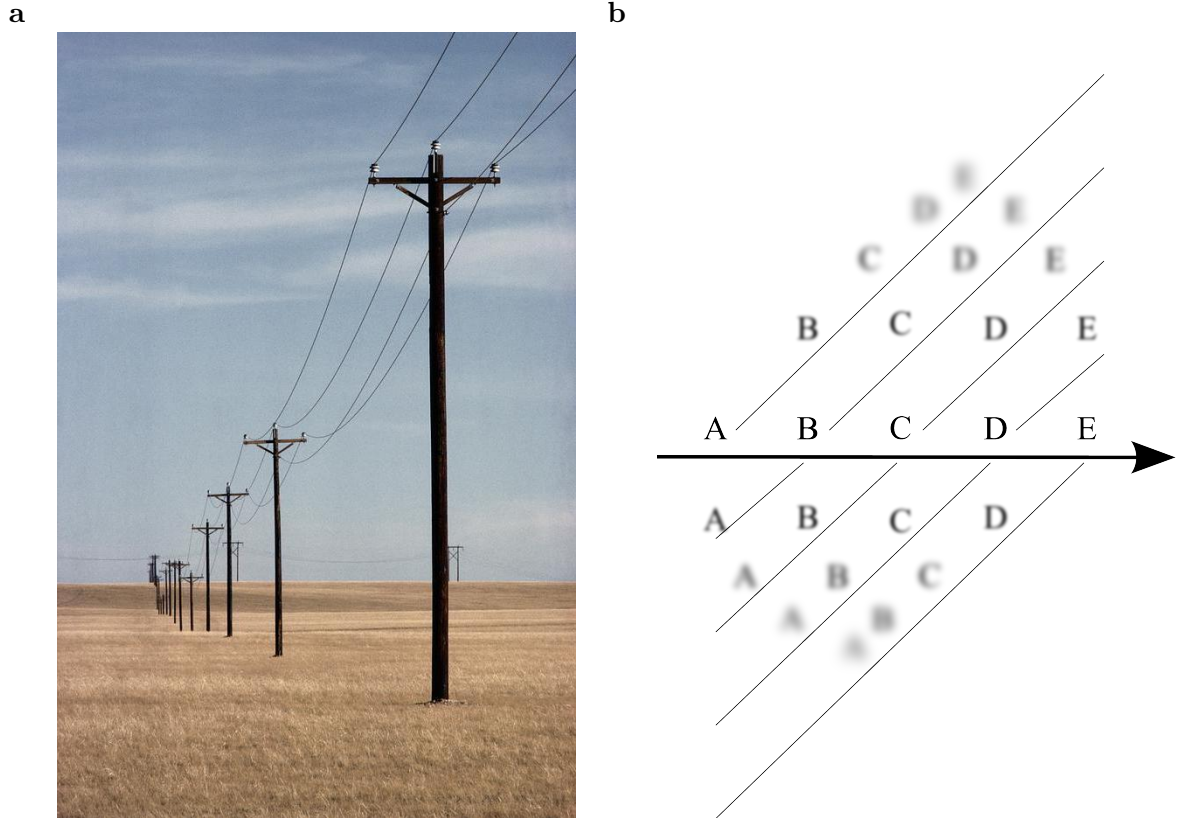
Evidence from psychological and neural science converges on the idea that many forms of memory rely on a timeline of the recent past, with many of the properties James and Husserl proposed from simply observing our internal experience of the passage of time. Although we will consider other hypotheses in this chapter, they will all have serious limitations. In the end, this chapter is not so much about people’s memory for the time of events, but about how memory for the time of events, in both the mind and brain, could affect many different forms of memory. We review behavioral evidence that bears on this question, even though in many cases the tasks do not require the participant to rate the time of events in memory. The primary result is that many tasks could be understood as a consequence of a timeline, much like that hypothesized by James and Husserl with the added constraint that the timeline is compressed. That is, as they suggested, memory for the past contains information about order. And, as they both suggested, memory for events further in the past are less well-remembered than events closer in time to the present. In addition, however, the neural and behavioral evidence suggest that the timeline grows more compressed for events further in the past such that the resolution of *when* an event took place is less clear for events further in the past. The visual image of a line of telephone poles has been suggested as a visual metaphor to understand what is meant by compression (Figure 1a,b Crowder, 1976).

### Behavioral paradigms that constrain the neural representation for time

In this section, we will start by reviewing data from the interval reproduction task, in which participants reproduce delays of various lengths. This subsection will introduce the concept of scale-invariance and logarithmic compression, which will be important later on. The next subsection covers judgments of recency (JOR), in which participants explicitly rate how long in the past probe stimuli were experienced. We will find that data from the JOR task over long time intervals support logarithmic compression. Moreover, data from the short-term JOR task suggest that participants perform the task by sequentially examining an ordered timeline of experience, not unlike scanning one’s eyes along a visual display. Following this, we will review evidence from classical conditioning paradigms which support the “temporal encoding hypothesis.” Briefly, the temporal encoding hypothesis states that associations between stimuli are not direct, but are mediated by a timeline of the past. Finally, we will discuss temporal effects in episodic memory. The vivid experience of episodic memory has led to it being described as “mental time travel” (Tulving, 1983). If the experience of the present is a consequence of the current state of a compressed timeline, then it would stand to reason that reinstating a previous state of the timeline would result in the re-experience of that prior moment from one’s life.

#### *Interval reproduction*

Many behavioral paradigms have been developed to evaluate the ability of animals and humans to time intervals over the range of a few hundred milliseconds up to about an



*Figure 1. Compressed timeline of experience. a.* A compressed timeline can be visualized by analogy to a row of telephone poles. Suppose that you walk along a row of evenly-spaced telephone poles at a constant rate. The amount of time between each pole is objectively the same. But now if you stop and look back at your path, the poles you passed more recently are easy to distinguish because they are close to you in space. In contrast, the details of telephone poles you passed further in the past are more difficult to distinguish. So too, the distance between pairs of adjacent poles experienced further in the past is compressed into smaller regions of the visual image. *b.* A compressed timeline describing the past and the future, inspired by the work of Edmund Husserl. Here the horizontal line A B . . . corresponds to objective reality. At each moment, our experience of the past (diagonal line below and to the left of the present) carries information about events in the recent past and when they occurred. More recent events are represented more clearly in memory; as items recede into the past, their identity (blur of the letter) and time of occurrence (position along the line) become less distinct. In addition to retention—memory for the past—Husserl also discussed protention—anticipation of the future. If the sequence has been experienced many times (such as a familiar melody), we can anticipate the future, corresponding here to the diagonal line above and to the right of the horizontal line.

hour. A number of paradigms have been developed to evaluate this ability. We focus here on a task referred to as interval reproduction. In interval reproduction, the participant is presented with some stimulus with a characteristic duration. For instance a square might change color for some interval  $\tau$  and then terminate. After experiencing the interval  $\tau$ , the participant is instructed to reproduce it. For instance the participant might press a button to change the color of the square and then press it again after a time  $\tau$  has elapsed. In human participants care is typically taken to prevent the participant from simply counting during the interval (for instance, by requiring the participant to say random numbers aloud at irregular intervals). In order to decide when to press the button the participant must compare their current memory for the time since the square changed color to a stored memory for the instructed interval. That is, to learn the temporal interval the participant must store something like “the square changed to this color at a time  $\tau$  in the past”. After pressing the button, the participant compares their current memory for the time since the button press to this memory for the instructed interval and respond when the match is sufficiently strong. Accuracy is measured in interval reproduction by comparing the time at which the participant responds to the actual delay. Analyses of accuracy take into account not only the mean response, but the distribution of responses across trials and participants.

Perhaps the most remarkable finding in interval reproduction is the fact that participants can reproduce intervals over a large range of intervals. In a particularly heroic experiment Lewis and Miall (2009) had participants reproduce intervals over an extremely wide range from 68 ms (much faster than typical human RTs) up to 16.7 minutes. Not surprisingly participants were not able to reproduce the extremely fast intervals with any precision—68 ms was chosen based on the refresh rate of the monitor on which the stimuli were presented! However, from about a couple of hundred milliseconds up to 16.7 minutes, participants’ mean responses were about the same proportion of the true duration—roughly  $0.7\tau$  despite changes in  $\tau$  over about four orders of magnitude.

This type of finding led to the extremely influential idea that the brain’s representation of time is scale-invariant (Gibbon, 1977; C. R. Gallistel & Gibbon, 2000; Balsam & Gallistel, 2009). That is, if we prepare an experiment described by a time series of events  $f(t)$ , the results of the experiment will be comparable if we rescale time as  $f(at)$ . Note that the factor of  $a$  “stretches” the time axis if  $a > 1$  and “squashes” the time axis if  $a < 1$ . This property is not what one would expect if temporal memory at different values of  $\tau$  were supported by different memory systems—such as short-term memory and long-term memory (Atkinson & Shiffrin, 1968). Note that if time is equally spaced on a logarithmic scale, this leads naturally (but not uniquely) to a scale-invariant representation of time; on a logarithmic scale the distance between 2 and 20 is the same as the distance between 10 and 100.

Scale-invariance predicts not only that the mean reproduction time is a constant proportion of  $\tau$ , but that the errors should also rescale. That is, if in one condition we find that participants’ errors in reproducing an interval  $\tau_1$  is  $\delta_1$ , scale-invariance requires that the error would rescale with the interval such that  $\frac{\delta_2}{\tau_2} = \frac{\delta_1}{\tau_1}$ . Interval timing experiments have frequently observed this rescaling of errors (see Gibbon, Malapani, Dale, & Gallistel, 1997; Buhsu & Meck, 2005, for reviews). For instance, Rakitin et al. (1998) observed this strong form of scale-invariance for intervals ranging from 8 s to 12 s to 21 s. In this experiment they were interested not so much in the mean response time, but the distribution of errors. Although the errors in timing the 21 s interval were wider than the errors in the 8 s

interval, they were of the same proportional width. When the responses in each condition were plotted as a function of  $t/\tau$ , where  $\tau$  was set to 8, 12, or 21 s as appropriate, the curves aligned very closely. Note that this empirical property is a natural consequence if the Weber-Fechner law (Fechner, 1860/1912) holds for the mind’s estimate of elapsed time, such that our internal estimate of time is a function of  $\log \tau$ . The Weber-Fechner law is one of the oldest quantitative relationships in psychology and holds at least roughly for a number of sensory dimensions, such as brightness, loudness, etc. Although scale-invariance is not always observed in timing experiments (for excellent reviews, see Lejeune & Wearden, 2006; Wearden & Lejeune, 2008), it has been an important concept in computational models of timing and memory for time (C. R. Gallistel & Gibbon, 2000; S. Brown, Steyvers, & Hemmer, 2007; Howard, Shankar, Aue, & Criss, 2015).

### *Judgment of recency*

Interval reproduction depends on participants’ ability to compare a stored memory trace for an interval with the memory for a current interval. The judgement of recency (JOR) task asks participants to rate how far in the past a stimulus was experienced (absolute JOR) or to select which of two probe stimuli was experienced more recently (relative JOR). JOR asks participants to explicitly report on the duration between a past event (or events in the case of relative JOR) and the present. Although there has been some work on animal models of judgments of recency (e.g., Templer & Hampton, 2012; Fortin, Agster, & Eichenbaum, 2002) this chapter will focus on human work.

The JOR task was introduced to the human memory literature in the early 1960s by Yntema and Trask (1963). The most important conclusions from this pioneering study were that 1) participants can readily report on the relative recency of different probe stimuli, 2) all else equal, participants’ judgments got worse as the probe stimuli receded into the past, and 3) all else equal, participants’ judgments improved as the temporal separation *between* probes increased. Yntema and Trask (1963) explained their results in the context of a “time tags” hypothesis. At retrieval, participants retrieve a time tag associated with each of the probe stimuli that provide information about its time of presentation relative to the present. Then the participant compares the tags retrieved by each of the probes to one another in order to determine which probe to select. Note that a compressed timeline of the past would serve quite effectively as a time tag. After learning A B C D E, the probe B might recover a tag corresponding to “four steps in the past” whereas the probe D might recover a tag corresponding to “two steps in the past”. If time in the past is compressed (Figure 1), it would be more difficult to distinguish events separated by the same objective distance as they recede further in the past.

*Logarithmic scale for absolute judgements of recency.* In subsequent years, researchers studying absolute JOR studied strength models. Rather than relying on time tags, which are presumed to carry detailed temporal information, in a strength model each entry in memory is associated with a scalar strength that decays as time passes. Put another way, in light of the telephone pole metaphor, a strength model would presume that memory retains information about the size of the telephone pole, but does not have a space-like dimension devoted to representing the time of past events. At test the participant presumably evaluates the strength of the probe stimulus in an absolute JOR task to determine the response. If the

“telephone pole appears large” in memory, it was presumably presented more recently than a telephone pole that appears smaller. As we will see later, data from short-term JOR is extremely difficult to reconcile with a strength model and we will discard this hypothesis—a conclusion reached by most researchers studying the problem in the 1970s. However, the key finding from this early work for our purposes is that to account for the behavioral data with a strength model, strength must decay with the logarithm of the probe’s recency, consistent with a logarithmically-compressed timeline implementing a Weber-Fechner scale for the past.

The first question one may ask in JOR is how ratings of recency change as a function of the actual recency of the probe. Hinrichs and Buschke (Hinrichs, 1970; Hinrichs & Buschke, 1968) observed that numerical estimates of the recency of a probe presented  $\tau$  steps in the past increase like  $\log \tau$ . As a consequence, they proposed a strength model in which the strength of a memory trace decays like  $-\log \tau$ . This model is consistent with the Yntema and Trask (1963) results.

Despite the intuitive simplicity of logarithmic strength models, it is clear that strength models (whether logarithmic or not) are insufficient to describe many phenomena in human JOR performance. For instance, Hintzman (2010) did an experiment in which probes in an absolute JOR task were presented more than once (see also Flexser & Bower, 1974). In this experiment, probe items can be presented three times, corresponding to the initial presentation, the first test and the second test. Let us refer to the time lag between the initial presentation and the first test as  $\tau_1$  and refer to the time between the first test and the second test as  $\tau_2$ . On the first repetition, the well-known logarithmic relationship between absolute rating and actual  $\tau_1$  was observed. If JOR relies on a strength for each probe item, and if that strength decays with time, we would expect repeated items to be judged as much more recent than non-repeated items. In contrast to this prediction, on the second presentation the judgment depended on  $\log \tau_2$ ; repetition of an item, and the lag at the first presentation  $\tau_1$  had a barely measurable effect on participants’ ratings of recency. The results are as if participants can remember multiple occurrences of the same nominal stimulus as distinct events, as predicted by multiple-trace models of memory (e.g., Hintzman, 1986). One can account for these findings with a memory store that contains multiple traces of the past if the traces are spaced appropriately to give the logarithmic relationship.

*Scanning along a timeline in short-term JOR.* Consistent with these conclusions from JOR in list learning experiments, evidence from short-term JOR experiments suggests that different events give rise to separate traces in a temporally-organized memory store, much like the timeline proposed by James and Husserl. In short-term JOR experiments, a short list is presented, usually quickly (e.g., Hacker, 1980; Muter, 1979). In many cases the stimuli come from a small pool that are reused across many lists (e.g., consonants). The qualitative patterns observed by Yntema and Trask (1963)—that all else equal pushing the two probes into the past decreases accuracy and increasing the separation between probes increases accuracy are both observed. The interesting finding comes when one considers RT data which support a self-terminating serial scanning model (Hacker, 1980; Muter, 1979; Hockley, 1984). According to this account, memory for the list is organized like a timeline. Given a pair of probes, participants compare the probe stimuli one-by-one to the contents of

memory starting with the entries closer to the present and moving towards the past. When they find one of the probe stimuli in memory, they terminate their search. In this model, errors happen because occasionally degraded memory traces cause the match to fail; under these circumstances the search continues.

This self-terminating serial scanning model makes a number of straightforward predictions. First, the RT for a correct response should increase as the more-recent probe becomes less recent. Second, correct RT should not depend on the recency of the less-recent probe. Third, the pattern for error RT, in which one selects the less-recent probe, should depend on the recency of the less-recent probe but not of the more recent probe. All three of these phenomena are consistently observed (Hacker, 1980; Muter, 1979; Hockley, 1984; Singh, Oliva, & Howard, 2017).

The basic premise of the self-terminating model is that memory has a temporal organization and that participants can sequentially direct attention to different parts of this timeline, analogous to the way people can shift their gaze through the visual field. This interpretation is bolstered by evidence that when the instructions are reversed, so too does the apparent direction of scanning. That is, in the standard JOR experiment the participant is asked to pick the more recent probe and RT goes up as if the participant starts “looking at the timeline” close to the present and gradually “moves their attention” towards the beginning of the list. In one set of experiments Caplan and colleagues asked about what would happen if participants were asked which of the probes came *earlier* in the list (M. Chan, Ross, Earle, & Caplan, 2009; Y. S. Liu, Chan, & Caplan, 2014). They found that participants were now faster to choose the items at the *beginning* of the list. That is, when asked to choose the probe closest to the beginning of the list, participants were *slower* to select probes that were closer in time to the present. The pattern of results is just as one would expect if the participants first “directed their attention to the time of the beginning of the list” and then sequentially moved their attention forward in time towards the present.

*JOR data are consistent with a logarithmically compressed timeline.* So, there are these two streams of evidence from JOR. The argument from absolute JOR is that memory uses a logarithmic scale to measure the amount of past time but that a strength model is insufficient to account for important properties of JOR. The argument from short-term JOR is that memory consists of a temporally-organized representation that can be examined sequentially not unlike how people can direct attention to different parts of visual space. It has been proposed (Howard et al., 2015; Howard, 2018) that these two findings can be reconciled if memory consists of a temporally-organized representation that is logarithmically compressed. That is, memories for different events are organized in multiple traces along a timeline, but the timeline is not evenly-spaced. Logarithmic compression, like that seen in the visual system as a function of distance from the fovea (Daniel & Whitridge, 1961; Hubel & Wiesel, 1974; Van Essen, Newsome, & Maunsell, 1984), means that the amount of objective distance covered moving from one cell’s receptive field to the next goes up quickly, like the numerical sequence 1, 2, 4, 8 . . . . This suggests that the time it takes to scan to a particular time in the past goes up more slowly than linear because each subsequent step travels further into the past. To test this hypothesis (Singh & Howard, 2017) replicated the standard short-term JOR experiment and found that the indeed the

rate of scanning was sublinear, consistent with sequentially directing attention along a logarithmically-compressed timeline.

It should be noted that although the “short-term” JOR (e.g., Hacker, 1980; Muter, 1979) results and “long-term JOR” (e.g., Hintzman, 2010; Yntema & Trask, 1963) results emphasize different aspects of performance, they do not contradict one another. Indeed a scanning model built on a logarithmically-compressed representation of temporal context can account for both sets of results (Howard et al., 2015).

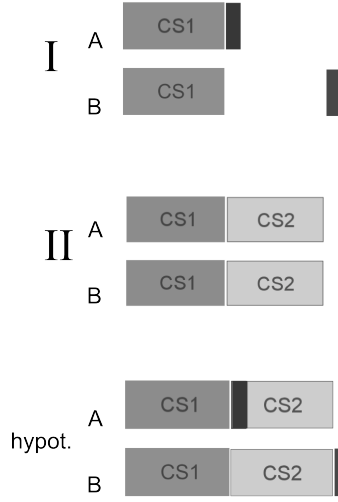
### *Classical conditioning and “temporal mapping”*

JOR explicitly evaluates participants’ memory for the time of past events. However, tasks that do not explicitly require assessment of the time of past events can also shed light on how the brain and mind maintain information about the past. Pavlov’s dog learned a temporal relationship between the bell and the food. If the time of the bell and the time of the food were uncorrelated there would be no association. In this sense even simple classical conditioning expresses memory for time. It is not necessary that the conditioned stimulus (CS, e.g., the bell) and the unconditioned stimulus (US, e.g., the food) are experienced simultaneously. In delay conditioning, the US is presented at the time the CS terminates, so they do not overlap. In trace conditioning, there is a nonzero temporal gap between the offset of the CS and the onset of the US. We know a great deal about the neurobiology of simple Pavlovian conditioning in rodents and the neural circuitry that supports these associations (see Thompson, 2005, for a review of the pioneering work). At the end of the day, however, the animal’s goal is to predict the future—the bell in the present predicts that food will become available five seconds in the future. Viewed in this way, at least some forms of classical conditioning could also utilize an ordered timeline of the past, with functional associations between stimuli (the bell and the food) mediated by the effect these stimuli have on timelines.

The centrality of temporal relationships in classical conditioning has led to the *temporal encoding hypothesis* (e.g., Arcediano & Miller, 2002), which argues that time is a fundamental component of even simple associations. Evolutionarily, this property is adaptive insofar as it enables animals to learn contingencies between events and thus better predict the future (Balsam & Gallistel, 2009). Mechanistically, one can understand the temporal encoding hypothesis as the idea that connections between two stimuli are formed not by directly linking the representations of the stimuli, but by linking and aligning timelines including the two stimuli. This proposal is dramatically supported by findings from second order conditioning. These experiments falsify the hypothesis that the association between a CS and a US is a simple scalar value. Because this point is extremely important in understanding the relationship between memory and time, we explain this phenomenon in some detail.

Consider an experiment by Cole, Barnet, and Miller (1995); Figure 2 provides a schematic of the experimental design. Two groups of rats learned a relationship between a conditioned stimulus (CS) and an unconditioned stimulus (US, in this experiment a mild footshock). Because there will be two conditioned stimuli, we will refer to the CS in this first phase of learning as CS1. In group A, the US was presented immediately after offset of CS1. In group B, five seconds intervened between the offset of CS1 and the US. Not surprisingly, the CS1 elicited a greater conditioned response, or CR, for group A than for group B. In





*Figure 2.* **Schematic of the two-phase conditioning experiment described in the text.** Each block shows the experience of two groups of subjects, group A and group B. The top block, labeled I, shows the experience of each group in Phase I of the experiment. The middle block shows the experience in Phase II. The bottom block shows the representation hypothesized to guide behavior if the subject is able to somehow 1) construct a timeline of experience and 2) integrate the timelines from Phase I and Phase II of learning on the temporal position of CS1.

this experiment, because the US is a shock the CR is freezing behavior that spontaneously accompanies the shock. If the CR results from a simple association, the strength of that association must be weakened by the inclusion of a delay. In a second phase of learning, each group learned another association between CS1 and a new conditioned stimulus, CS2. For each group, CS2 lasted for five seconds and its onset coincides with offset of the CS1 (Figure 2, middle). After this second phase of learning the magnitude of the CR to CS2 was observed for each group. There are two important properties of this design. First, because the CS2 was never paired with the US, any CR must be attributable to some kind of information conveyed from the CS1 to the CS2. Second, if association were a simple scalar value, the response to CS2 for each group should just be a function of the magnitude of the CR to CS1 for that group. However, if temporal relationships between CS1 and the US are part of the contents of learning, more complex relationships are possible.

Consider the temporal relationship predicted for CS2 if the two temporal experiences were aligned on CS1 presentation. For group A, because the timing between CS1 and the US was the same as between CS1 and CS2, if these two experiences were aligned, the onset of the CS2 and the US would be coincident (Figure 2, bottom). Because CS2 and US happen at the same time, this means that CS2 would not be useful for predicting the US in the future. However, in group B, because the delay from CS1 to US was greater than the delay from CS1 to CS2, the CS2 would “fit in the gap” between CS1 and the US if the two experiences were aligned. In group B, the offset of the CS2 would align with the onset of the US and CS2 would be a good predictor of the US. The empirical results are unambiguous; the CR caused by CS2 was greater for group B than for group A, despite the fact that the CS1-CR association was greater for group A than group B. Across many different variants of

this kind of experiment the findings are consistently in favor of the idea that “associations” are not simple links, but rather convey information about temporal relationships between events (e.g., Barnet, Cole, & Miller, 1997; Savastano & Miller, 1998; Arcediano, Escobar, & Miller, 2003).

The temporal encoding hypothesis has been formalized by Balsam and Gallistel (2009). They argued that the degree of association between a CS and a US ought to be a consequence of the amount of information that observing the CS conveys about the *time* at which the US will occur in the future. For instance, if the US is presented at random times and there is no correlation between the time of the CS and the time of the US, the best estimate one could make of the time of the US will occur is a uniform probability distribution proportional to its rate of occurrence. However, if the CS and US have a consistent temporal relationship (for instance every time the CS is presented the US follows five seconds in the future) then the estimate of the time at which the US will occur following the CS is more precise than the prediction one can make without observing the CS. One can quantify the difference between the uncertainty in the absence of pairing to the CS and the uncertainty after observation of the CS. The CS predicts the US to the extent the distribution after presentation of the CS is more certain. This hypothesis accounts for many important results in classical conditioning (see C. Gallistel, Craig, & Shahan, 2019).

Another key finding from classical conditioning that bears on the neural representation of time comes from autoshaping. In the autoshaping paradigm, the subject (usually pigeons in these experiments) is presented with a CS, for instance illumination of a light. Some time later—say, several seconds—a food pellet is dispensed from a nearby hopper. After some number of temporally-separated pairings, the pigeon will peck at the CS, as if it has acquired some of the reinforcing value from the food. Let us refer to the time between the CS and the arrival of the food as  $\tau$ . All else equal, the animal learns faster if  $\tau$  is small. Let us refer to the time between one trial and the next as  $T$ . All else equal, the animal learns faster if  $T$  is *large*. The remarkable finding is that the number of reinforcements necessary depends only on the ratio  $\tau/T$  (Gibbon, Baldock, Locurto, Gold, & Terrace, 1977). That is, if  $\tau = 2$  s and  $T = 20$  s the animal learns after as many pairings as it would have required if  $\tau = 10$  s and  $T = 100$  s. This finding implies that there is not a characteristic scale for associative learning—however we change  $\tau \rightarrow a\tau$  we can change  $T$  by the same factor  $a$  and recover the same rate of learning. To the extent classical conditioning can be understood as constructing and aligning timelines relating the past to the future, this finding suggests that the timelines are logarithmically compressed.

### *Episodic memory*

It has long been argued that episodic memory corresponds to “mental time travel” in which the rememberer reexperiences a specific moment of past time. Although we will not dwell on the topic here because it is well-covered in other chapters (see especially Chs. 2.1, 5.5, and 5.12), it is worth noting that the recency and contiguity effects, which are robustly observed in episodic memory paradigms (Kahana, Howard, & Polyn, 2008) may be understood as memory for time. The recency effect is the finding that, all else equal, we remember events that happened more recently in the past than further in the past. The contiguity effect is the finding that, all else equal, when an event is remembered, this brings to mind events that were experienced close in time to the remembered events. It has

been proposed that recency and contiguity effects in episodic memory depend on a gradually changing state of “temporal context”. According to this view, episodic memory is associated with recovery of a previous state of temporal context (Howard & Kahana, 2002; Sederberg, Howard, & Kahana, 2008; Polyn, Norman, & Kahana, 2009). Both recency and contiguity effects are observed over a wide range of time scales (Glenberg et al., 1980; Moreton & Ward, 2010; Unsworth, 2008; Howard, Youker, & Venkatadass, 2008; Healey, Long, & Kahana, 2018), suggesting that temporal context should change over many time scales. This condition would certainly be met by a scale-invariant temporal context; a logarithmically-compressed timeline would function perfectly well as a scale-invariant temporal context in models of episodic memory.

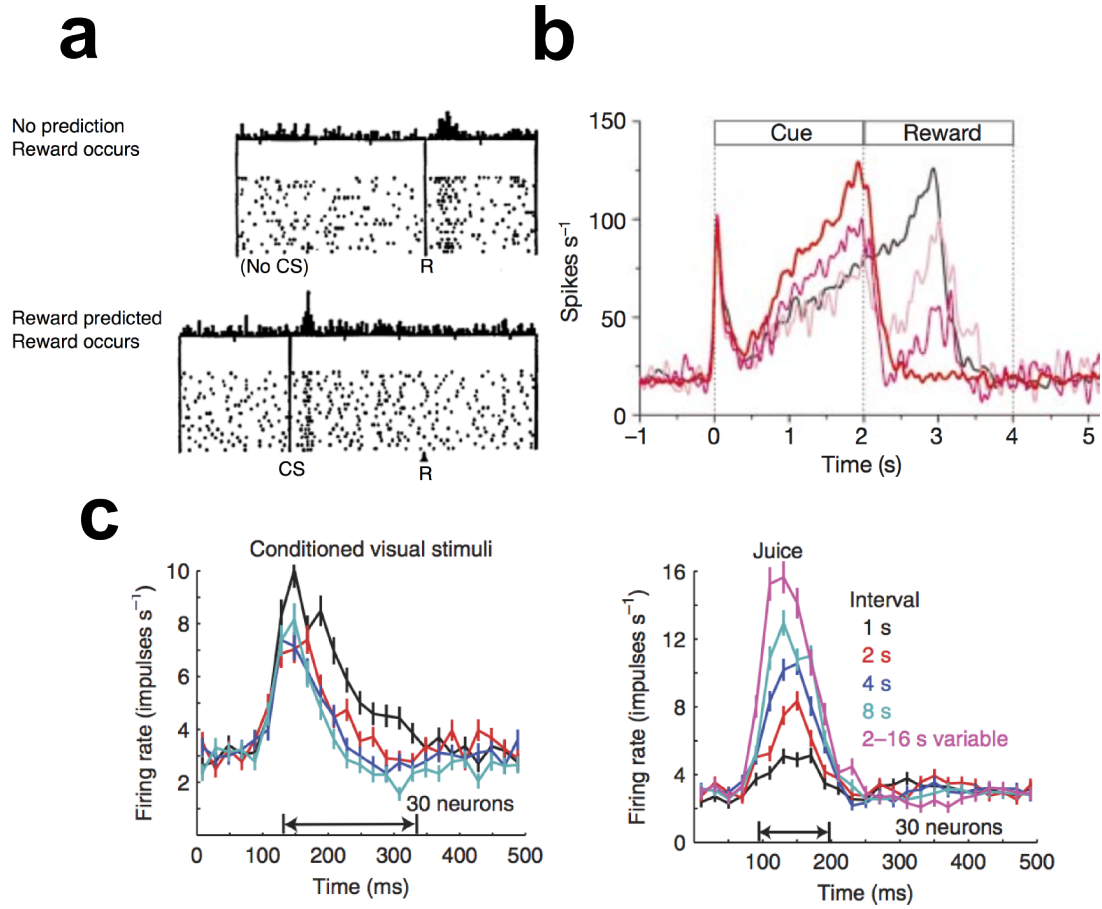
### Neurophysiological signatures of temporal information in the brain

The foregoing section argued that behavioral results from a range of experimental paradigms are broadly consistent with the hypothesis that people have access to a logarithmically-compressed record of the recent past. In this section we review evidence from animal neurophysiology that speak to the question of how the brain records memory for the recent past and learns associations between events.

This section is organized around three lines of evidence. We briefly review neurophysiological evidence from “simple” conditioning tasks touching briefly on the evidence from the mid-brain dopaminergic reward system, the thalamus and cerebellum. In all cases, neural firing reflects information about the time of future events, providing neurophysiological support for the hypothesis that many forms of behavioral association rely on learning of informative temporal relationships. Second, the firing rate of neurons in several regions changes monotonically with the passage of time. Because the firing rates change systematically as a function of time, this could be used to signal the time since the system was perturbed. A critical finding over several studies is that different neurons convey information at different scales. Third, the last decade has seen an explosion of neurophysiological studies showing neurons that sequentially activate carrying information about how far in the past the stimulus that triggered them was experienced. These neurons, referred to as “time cells,” provide direct evidence for a compressed timeline of the past leading up to the present.

### *Pavlovian associations, predictions, and memory for time*

Neuroscientists have long studied “simple” Pavlovian conditioning. Pavlov hypothesized that conditioning could be attributable to the enhancement of reflex arcs in the brain. Indeed, one can develop a minimal neural model for associations using synaptic plasticity and indeed a great deal has been learned about the molecular mechanisms of learning and synaptic plasticity studying behavior in sea slugs (Kandel, 2001), an invertebrate with a very limited behavioral repertoire. It has been argued that under normal circumstances, much of the mammalian brain participates in simple associations (Wagner & Luo, 2020), with the dopaminergic mid-brain, the thalamus and the cerebellum all participating to create predictions that inform the processing of information in widespread regions of the cortex. We briefly review the evidence pointing to the role of dopamine in classical conditioning and then discuss a key experiment suggesting that the dopamine system is sensitive to the delay between the CS and US and uncertainty in the time of the occurrence of the US.



**Figure 3. Neurophysiology of timing information in classical conditioning.** **a.** Dopamine cells respond to unpredicted rewards (top). After learning they no longer respond to the rewarding stimulus, but rather respond to the CS that predicts it. Note that the CS and the reward are separated in time (Schultz et al. 1997). **b.** Non-primary neurons in the thalamus show evidence of temporal predictions. After learning that a CS predicts a reward, the thalamic neuron ramps to the time of the reward (black line). This requires that the neuron has access to the future time at which the reward will be experienced immediately after the CS. After learning, the time to the reward is shortened and the animal gradually learns the new relationship (pink and red lines). Rather than a single peak that gradually moves earlier in time, the firing rate shows two peaks (Komura et al., 2001). **c.** Effect of temporal separation on the dopamine response. In this experiment the time delay between a visual CS and a juice reward was systematically varied. Left: Response to the CS. As the delay increases, there is less response of dopamine neurons to the CS. Right: Response to the juice reward. As the delay increases there is more firing of the dopamine neurons at the time of juice delivery (Fiorillo, et al., 2008).

*Classical conditioning, the dopaminergic reward system and memory for time.* Dopamine is an important neurotransmitter in the mammalian brain and is used by neurons in deep brain regions including the ventral tegmental area and substantia nigra. Dopamine is deeply implicated in both classical conditioning (e.g., Waelti, Dickinson, & Schultz, 2001; Schultz, 2002) and to the perception of time (e.g., Meck, Penney, & Pouthas, 2008; Soares, Atallah, & Paton, 2016). For instance, pharmacological manipulations that affect the dopamine system also affect interval timing (Meck et al., 2008; Meck, 1996). Establishing a direct causal relationship, Soares et al. (2016) optogenetically activated or inactivated dopaminergic neurons and observed that behavioral estimates of the passage of time ran faster or slower (Soares et al., 2016). The involvement of dopamine in both classical conditioning and timing behavior suggests that these are two sides of the same coin, as predicted by the temporal encoding hypothesis (Arcediano & Miller, 2002).

In a series of pioneering experiments, Schultz and colleagues recorded from dopamine neurons in substantia nigra and the ventral tegmental area, relatively deep structures that project broadly to the striatum and frontal cortex (for an early review see Schultz, 1998). These dopamine neurons respond to unconditioned stimuli, in particular reinforcing stimuli. The top panel of Figure 3a shows the response of a monkey dopamine neuron to delivery of fruit juice, a rewarding stimulus. The remarkable finding is that while dopamine neurons respond to the fruit juice when it is surprising, they no longer respond to the same stimulus when it is well-predicted by a CS that precedes it (Figure 3a bottom). After learning, the dopamine neurons do not respond to the fruit juice, but instead respond to the CS that predicts the reward. Because the CS and reward are separated in time, information about the future reward must somehow be transmitted backwards in time to the CS. One way to understand this property of dopamine neurons is that they fire when a reinforcing stimulus first enters the *prospective* timeline (Figure 1b). When a US is poorly predicted, it enters the timeline when it is experienced. However, when it is well-predicted, the US enters the timeline as a future event, distant from the present, at the moment the CS is presented.

Dopaminergic neurons are clearly sensitive to the temporal separation between the CS and the reward. For instance, if reward is predicted, but no reward is delivered on a particular trial, the firing of dopamine neurons dips shortly after the time at which the reward was expected. Similarly if the reward is presented earlier than expected, it evokes elevated firing of dopamine neurons. Both of these findings indicate that the system is able to predict not only that reward will occur, but also the time at which it is expected. Figure 3c shows the results from an experiment by Fiorillo, Newsome, and Schultz (2008) in which the delay between the CS and the reward was systematically manipulated. As the delay increased, the dopamine response to the US fruit juice increased but the response to the CS decreased. As we've seen, the certainty in the time of a predicted event decreases with the delay to that event—in many cases the uncertainty increases proportional to the delay  $\tau$  (Rakitin et al., 1998; Wearden & Lejeune, 2008). Thus, as the uncertainty about the time of the reward increases, the precision of the prediction decreases. The magnitude of the dopamine response to the CS as a function of delay mirrors this temporal uncertainty. Taken together, findings from dopamine neurons in classical conditioning experiments suggest the view that classical conditioning is associated with taking information about the past and predicting a compressed timeline of future events (Fig. 1b).

*Prediction of future outcomes in thalamus, cerebellum, and cortex*

The temporal encoding hypothesis argues that even simple associations between stimuli are mediated by information about time (Arcediano & Miller, 2002) and that classical conditioning reflects an attempt by the brain to better predict the time at which future events will occur (Balsam & Gallistel, 2009). Although the dopaminergic reward system has received a tremendous amount of attention for its role in classical conditioning and learning associations between events separated in time, it is by no means the only brain region involved in learning temporal relationships between events. Here we briefly review evidence beyond the dopaminergic reward system that suggests the thalamus, cerebellum, and cortex are involved in predictions of what *will* happen when.

Komura et al. (2001) studied the firing of non-primary neurons in the rodent thalamus during learning of a Pavlovian association. They found that these neurons responded to the CS if it was from a particular sensory modality; cells in auditory thalamus responded only to an auditory CS and cells in visual thalamus responded only to a visual CS. However, regardless of the modality of the CS, these neurons increased their firing to anticipate the arrival of a rewarding stimulus (see Figure 3b). Let us think about what this firing implies about the nature of temporal information that drives the ramping activity. The simplest explanation is that around the time of the CS, the time in the future at which the reward will happen is conveyed as a simple scalar value—much like a strength model from our discussion of JORs above. If this scalar strength controls the rate at which firing rate grows, the ramp would terminate at the anticipated time of the reward. However, this account is not sufficient to describe what happened when the duration of the delay between the CS and reward was changed. If information about the delay to the time of reward was conveyed by a scalar strength, then if the delay is changed, the slope of the ramp would also change. Under these circumstances, the peak of firing should move gradually across trials from the old time of reward to the new time of reward. Figure 3b shows the results when the delay was shortened. Although the thalamic neurons reflected the new delay interval after learning, they did not show a single peak that moved gradually from the old time to the new time. Rather at intermediate stages of learning they showed two peaks. These results are inconsistent with the view that time of future occurrence is conveyed as a simple scalar value. Rather, the results are consistent with an internal estimate of *both* possible outcomes as a function of future time (Fig. 1b). These ramps may be analogous to neurons in the ventral striatum that ramp their firing in a spatial navigation task in anticipation of arrival at a location where reward may be available (van der Meer & Redish, 2011).

Prediction of future outcomes in the thalamus may result from cooperation with the cerebellum. The cerebellum has long been known to be critical in many forms of simple conditioning (see Thompson, 2005, for a review of the early lesion literature) and skilled motor production which includes the ability to precisely time movements (Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). More recent evidence suggests that the cerebellum cooperates with the thalamus and dopaminergic system to predict the time and identity of future events (for a review see Wagner & Luo, 2020). For instance, neurons in cerebellum fire in anticipation of an expected reward, not unlike the thalamic neurons reviewed above (Wagner, Kim, Savall, Schnitzer, & Luo, 2017). Theories of cerebellar function (Raymond & Medina, 2018) include the hypothesis that cells in the cerebellum provide a “temporal basis

set” that may connect to properties of cortical and hippocampal neurons reviewed later in this chapter (e.g., Bullock, Fiala, & Grossberg, 1994; Kennedy et al., 2014; Guo, Huson, Macosko, & Regehr, 2020). These temporal basis functions correspond well to James and Husserl’s conception of a timeline. In the cerebellum, a great deal of attention has been paid to the possibility that sub-cellular mechanisms rather than network properties could account for its role in timing behavior (Jirenhed, Rasmussen, Johansson, & Hesslow, 2017; Johansson, Jirenhed, Rasmussen, Zucca, & Hesslow, 2014).

Although we usually are able to measure a Pavlovian association in animals only *via* a conditioned response, in principle the nervous system could form associations between any consistently paired events. Recent evidence shows that the response of neurons in V1, primary visual cortex, depends not only on the current stimulus, but also associations formed between preceding stimuli (e.g., Gavornik & Bear, 2014; Homann, Koay, Glidden, Tank, & Berry, 2017; H. Kim, Homann, Tank, & Berry, 2019). In this paradigm a mouse is presented with a series of visually-simple stimuli, such as angled bars of light, that are presented for a short period of time on the order of a few hundred milliseconds. To illustrate the basic result, let us consider two basic conditions. In one condition the stimuli are repeatedly presented in the same order, e.g., ABCDABCDABCD . . . . In another condition, the stimuli are repeated equally often but in a random order, e.g., ABCDCABDACDB . . . . The basic result is that the neural response in V1 is very different when the stimuli are part of a predictable sequence. On average, the response of V1 neurons is reduced for predicted stimuli, although a subset of neurons show the opposite effect. Because the assignment of images to the roles A, B, etc is arbitrary, and the images are equally familiar in both conditions, the change in response must reflect learning that allows the animal to predict the current stimulus from the preceding temporal context. After training on a particular experience, one can probe the properties of memory by perturbing the sequence in different ways and observing to what extent the neural response changes relative to the completely predictable condition.

There are several important properties of memory that one can infer from these studies. Gavornik and Bear (2014) perturbed the timing of the sequence while leaving the order intact and observed large changes relative to the completely predictable sequence, demonstrating that the predictions are sensitive to time *per se* (Gavornik & Bear, 2014). Moreover habituation takes place surprisingly quickly. Homann et al. (2017) showed measurable habituation within a few repetitions of the pattern. Changing the length of the pattern (i.e., ABCD  $\rightarrow$  ABCDE) did not have much effect on the number of presentations necessary to observe habituation, even out to sequences nineteen stimuli long. Critically, learning does simply depend on pairwise associations between adjacent stimuli. H. Kim et al. (2019) changed a stimulus embedded in a learned sequence and then observed the effects on stimuli that followed the novel stimulus. That is, after learning ABCD . . . , they might present AXCD and observe the response to C, D etc. A change in the response to C would be a 1-back effect; a change in the response to D would be a 2-back effect. They found that the response of stimulus-coding neurons was affected by a disruption of the sequence even when the disruption preceded by the studied item by four or five intervening stimuli, extending more than a second in the past.

A number of factors argue that predictions in V1, which depends on memory for the recent past, arise from a distributed network involving many brain regions. Gavornik and

Bear (2014) noted that the earliest signs of predictive habituation arise in the layers of V1 that receive input from the thalamus. Moreover, lesions to the hippocampus, which is not directly connected to V1, impair the sensitivity of habituation to temporal context but do not impair the ability of V1 to distinguish completely novel stimuli from familiar stimuli (Finnie, Komorowski, & Bear, 2021). There is abundant evidence (reviewed later in this chapter) that the firing of hippocampal neurons codes for information about the time and identity of stimulus presentations. Taken together, these results suggest that stimulus processing in V1 is affected by a temporal prediction derived from the recent past that depends on widespread brain structures, that extends at least 4-5 items into the past, and is conveyed to V1 *via* the thalamus.

*Temporal information about the past conveyed by monotonically-changing firing rates*

How does the brain estimate the time of past events? One simple way to build such a model is to have different neurons that are triggered at the time a particular event occurs. As time passes after presentation of the event, the firing rate of these neurons relax gradually as a function of time back to baseline firing. Depending on how the triggering event perturbs the ongoing firing rate, this general procedure could lead to firing rates that increase with the passage of time, analogous to ramping neurons in the thalamus or striatum, or firing rates that decrease with the passage of time, decaying back to their baseline firing rate. If one knows the shape of the function describing a cell's firing rate as a function of time, one could observe the firing rate at a particular moment and infer the time since the neuron was triggered. To the extent different neurons are triggered by different events, a population of such neurons would convey information about what event was experienced in the past. In this way, a population of neurons whose firing rates change monotonically could convey information about what happened when in the past, as demanded by James' and Husserl's description of our experience of the passage of time.

There is ample evidence that cortical neurons in a wide variety of regions express temporal information by monotonically relaxing. Pioneering studies provided evidence for a range of ramping behavior in many different brain regions (e.g., Lebedev, O'Doherty, & Nicolelis, 2008; Leon & Shadlen, 2003; Matell, Meck, & Nicolelis, 2003; Matell, Shea-Brown, Gooch, Wilson, & Rinzel, 2011; J. Kim, Ghim, Lee, & Jung, 2013; Sakon, Naya, Wirth, & Suzuki, 2014; Naya & Suzuki, 2011). In this review, we focus our attention on four recent studies that converge on a common form of coding over many cortical regions. These studies all show evidence for neurons that reflect information about the past time of a triggering event by decaying approximately exponentially after they are perturbed. That is shortly after some triggering event, the firing rate of the neuron changes quickly then relaxes slowly back to its baseline firing rate following an exponential function. If the time of the triggering stimulus is  $t = 0$ , the firing rate changes after  $t = 0$  like the exponential function  $e^{-st}$ . At  $t = 0$ , the exponential function is at its maximum. Near  $t = 0$  its value decreases quickly, slowing down gradually as it falls back to zero. The parameter  $s$  is known as the "rate constant" of the function and its inverse  $1/s$  is known as the time constant. When  $s$  is large, the function decays quickly and has a small time constant. When  $s$  is small, the function decays slowly and has a large time constant.

The important findings common to these studies are that 1) different stimuli trigger different subpopulations of cells, 2) different neurons decay with different characteristic



time scales, and 3) the decay rates of neurons are not evenly sampled. Rather, many more neurons decay quickly and a smaller number of neurons decay more slowly. These results are at least consistent with the hypothesis that time constants are evenly distributed as a function of the logarithm of time (Guo et al., 2020). As we will see later, these properties place strong constraints on computational models of timing.

Figure 4f shows the results of a study from rodent lateral entorhinal cortex (LEC), a region that provides input to the hippocampus (Tsao et al., 2018). In this experiment, the rat explored a series of visually-distinguishable environments, being moving from one environment to another every several minutes separated by brief periods of time in a rest chamber. Neurons in LEC changed their firing in response to events corresponding to entry to an environment and then changed their firing monotonically over long periods of time. For instance, cell 5 in Figure 4f gradually increased its firing every time it entered a new environment. In contrast, cell 7 started firing at an elevated rate every time it entered the environment with the black walls and then decayed gradually. Cell 6 changed its firing rate very gradually over the entire experimental session. Tsao et al. (2018) observed neurons that responded to many different events and also a wide range of decay rates ranging up to tens of minutes. There were relatively few neurons with slower decay rates (e.g., cell 6 decays very slowly) and more neurons that decayed more quickly.

Studying recordings from the monkey entorhinal cortex during presentation of visual images, Bright et al. (2019) found a population of cells that were perturbed by the image presentation. Most neurons that responded to presentation of an image increased their firing rate but a subset were inhibited relative to their baseline firing rate. However, all of the neurons that were triggered by image presentation changed initially very quickly after the image onset (most within 200 ms) and relaxed back to their baseline firing rate as an exponential function of time with a wide range of time constants extending up to several seconds. As in the Tsao et al. (2018) paper, Bright et al. (2019) showed that firing was sensitive to the particular stimulus that triggered the population, decayed with a broad range of rates across neurons, and that slowly-decaying neurons were less frequent than those that decayed more quickly. Taken together, these two studies converge on a common form for representing information about what happened when in two different species, two different behavioral tasks and two different time scales. The fact that different neurons decayed at different rates is also meaningful. Note that the rate of change of an exponential function with a time constant  $\tau$  depends on  $t/\tau$ . For time scales much greater than  $\tau$ , the firing rate is effectively zero and the cell cannot convey much information about the passage of time. If all the neurons had the same time constant, the population would be very good at distinguishing intervals around that value. The fact that there are many time constants across neurons allows the population to convey information about many different time scales. Because there are fewer neurons with long time constants (slow rate constants), it means that the population conveys less information about distant times in the past, indicating a compressed timeline (Fig. 1a,b). Notably, Guo et al. (2020), recording from cerebellar slices removed from the mouse brain, found a distribution of time constants that was quantitatively consistent with logarithmic compression of time out to about ten seconds.

Rossi-Pool et al. (2019) recorded from monkey dorsal premotor cortex during a working memory task in which the animal was required to remember a vibrotactile stimulus for

a brief delay. Different neurons responded to the identity of the different stimuli that were to be remembered. During the delay time the population of neurons changed their firing rate systematically in a way that enabled decoding of the time since the probe stimulus was presented. The neurons within the population did not all change at the same rate. Although the authors of this study did not directly evaluate whether firing rates changed exponentially, examination of the figures (and examination of their raw data which is posted on a public repository) show that the firing rates change quickly after presentation of the first stimulus and then decay monotonically and non-linearly, very much like an exponential function. Rossi-Pool et al. (2019) measured the relaxation time of each neuron, analogous to the time constant of an exponential function, and found that there was a broad range of relaxation times. Although there was not an explicit requirement for the monkey to report timing information in this task, this temporal signal was dramatically reduced when the monkey was not required to remember the probe stimulus, suggesting that timing information in this population is intimately related to working memory maintenance.

Bernacchia, Seo, Lee, and Wang (2011) studied the response of cortical neurons from a number of brain regions, including anterior cingulate cortex, dorsolateral prefrontal cortex and lateral intraparietal cortex, across trials of a task in which reward was available probabilistically. Unlike the foregoing studies, this population of neurons did not maintain an elevated firing rate during the time between trials. Indeed, firing rate for this population changed dynamically throughout the trial with a variety of forms. However, this relatively complicated time course was modulated by an overall value that depended on the recent history of reward on previous *trials*. They estimated the effect of reward history as an exponential function over trials. Critically, different neurons decayed at different rates, with the slowest decaying neurons showing effects from tens of trials in the past; a period of time extending about a minute. As in the previously described studies (especially Tsao et al., 2018; Bright et al., 2019), the distribution of rates was not uniform. As in those studies, relatively fewer neurons had slow decay rates than those that decayed more quickly.

Taken as a group, these four studies (Tsao et al., 2018; Bright et al., 2019; Bernacchia et al., 2011; Rossi-Pool et al., 2019) begin to tell a coherent story about the nature of the timing signal from populations with firing rates that change monotonically over time. To reiterate, all four studies showed roughly exponential decay for a wide range of neurons. However, the firing rates did not decay at the same rate for each neuron; instead a spectrum of rates was observed across neurons. This suggests that scale-invariance at the population level results from different neurons conveying information about different scales. Because there are fewer neurons that decay very slowly, these populations record the distant past with less temporal resolution than the recent past. Moreover, across studies the same type of decay behavior was found to decode the time since different events: a rewarded trial (Bernacchia et al., 2011), a vibroactile stimulus (Rossi-Pool et al., 2019), entry into a room in a spatial task (Tsao et al., 2018) or the presentation of a visual image (Bright et al., 2019). In all of these studies, there was evidence that the population of exponentially-changing cells contained information about the type of event that was experienced in the past, suggesting that the population contains information about what and when. The observation of a similar form of temporal representation in a wide variety of tasks and brain regions believed to support different “forms of memory” (e.g., Eichenbaum, 2012) suggests that this compressed temporal representation serves a general function in different forms of

memory and cognition.

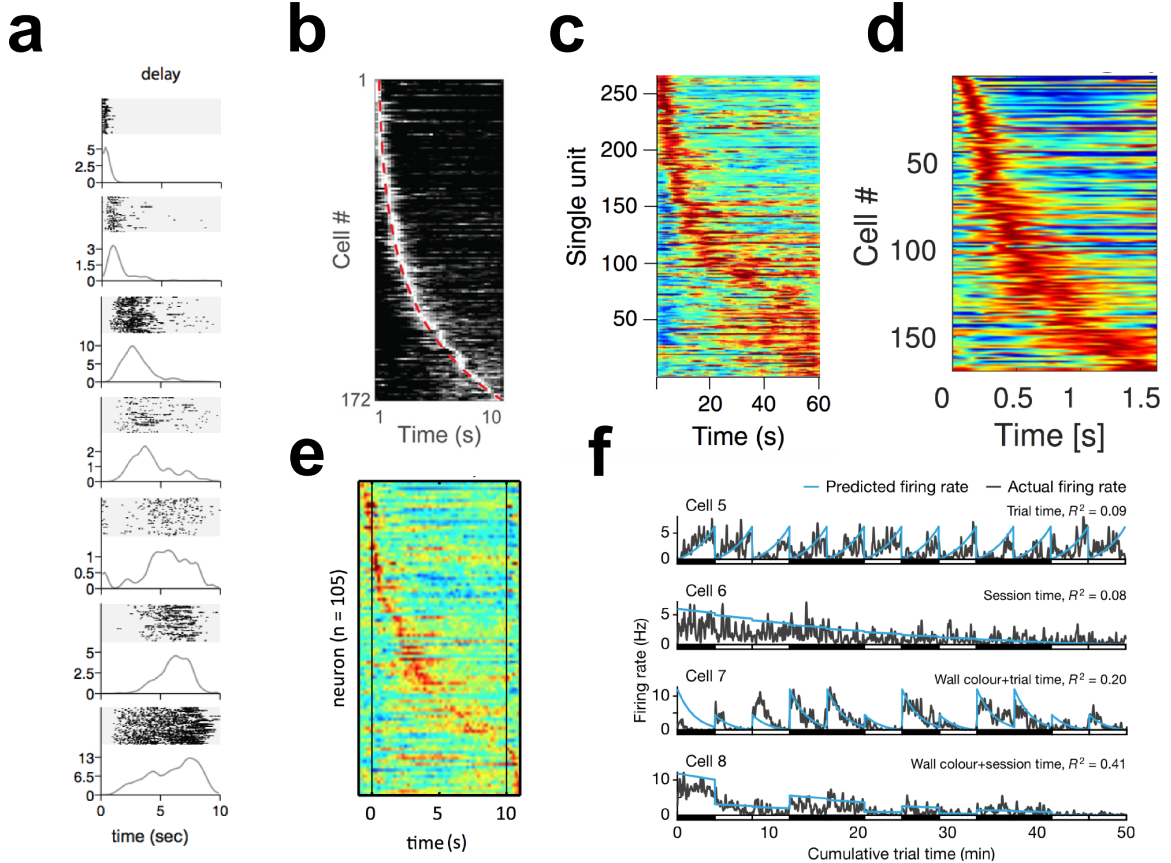
*Sequentially-activated “time cells” in the hippocampus and beyond*

Recent years have seen an explosion of work showing evidence for temporal coding by populations of neurons that fire in sequence rather than changing their firing rate monotonically. The brain represents many continuous variables by supporting those dimensions with the receptive fields of different neurons. For instance, many neurons in the early visual system have receptive fields such that they convey information about the pattern of light in a circumscribed region of retinal space (e.g., Hubel & Wiesel, 1974). Similarly, it is widely believed that hippocampal place cells represent position within an environment (O’Keefe & Dostrovsky, 1971; Wilson & McNaughton, 1993). However, rather than ramping monotonically with position, hippocampal place cells fire when the animal is in a circumscribed region of space. The region of space that is associated with a particular place cell’s firing is referred to as that cell’s place field. From examining the firing of one neuron, one can infer whether the animal is inside or outside its place field. Across many neurons, the place fields tile the environment such that the population carries information about the position of the animal over a region much larger than any individual cell’s place field. Thinking of the population as organized by the center of each cell’s place field, we can imagine the activity of a population of place cells as a “bump” around the animal’s current position.

Time cells are analogous to place cells, but rather than firing in a circumscribed region of space, they fire at a circumscribed period of time after some type of event (Figure 4a). Time cells behave as if they have receptive fields organized in time rather than in space. As a triggering event, such as the stimulus signalling the beginning of a delay interval in a memory experiment, recedes into the past, it first enters and then exits the “time field” of a time cell. Because the time fields for different cells are centered on different times, tiling the past, the population fires in sequence as the triggering event moves through past time.

Time cells (Eichenbaum, 2014) were initially reported in the hippocampus (Pastalkova, Itskov, Amarasingham, & Buzsaki, 2008; MacDonald, Lepage, Eden, & Eichenbaum, 2011), but have since been described in a number of regions including striatum (Mello, Soares, & Paton, 2015; Akhlaghpour et al., 2016; Jin, Fujii, & Graybiel, 2009), and prefrontal cortex (Tiganj, Kim, Jung, & Howard, 2017; Tiganj, Cromer, Roy, Miller, & Howard, 2018; Jin et al., 2009). Time cells have been observed when an animal is moving in place, as on a treadmill or a running wheel (Pastalkova et al., 2008; Mau et al., 2018; Kraus, Robinson, White, Eichenbaum, & Hasselmo, 2013), but are also observed when the animal is not locomoting (MacDonald et al., 2011; Tiganj et al., 2017) and even under conditions where the animal is head fixed (MacDonald, Carrow, Place, & Eichenbaum, 2013; Taxisidis et al., 2018; Tiganj et al., 2018). The diversity of the brain regions that show sequential activity coupled with their observation under many different behavioral demands suggest that time cells play an important role in many forms of memory. This is perhaps not surprising insofar as James and Husserl’s description of an unfolding timeline is so central to our internal experience of the world.

*A compressed record of past events.* Recall from our discussion of behavioral constraints on models of temporal representation that many findings across conditioning, interval timing and judgments of recency could be reconciled with a record of past events



**Figure 4. Coding of time in the brain.** **a.** Rasters of sequentially activated time cells in rat hippocampus. Time cells have receptive fields in time. These fields widen the later a cell fires in the sequence (MacDonald et al., 2011). **b-e.** Sequentially activated cells in a variety of brain regions in a variety of species in a variety of tasks. Each row is the firing field of one unit and the units are sorted according to their peak time. Time cells preferentially represent the beginning of the interval, resulting in a characteristic hook when the units are sorted as a function of their peak time. **b.** A population of simultaneously recorded neurons in mouse hippocampus (Mau et al., 2018). The dashed red line shows the curve that would be expected from logarithmic compression. **c.** Mouse medial PFC (Bolkan, et al., 2017). **d.** Monkey lateral PFC (Tiganj, et al., 2018). **e.** Rat dorsomedial striatum (Akhlaghpour, et al., 2016). **f.** Recordings from rat lateral entorhinal cortex do not show sequentially activated time cells, but rather cells that begin firing shortly following an event and exponentially return to baseline (Tsao et al., 2018).

that is ordered along a logarithmically-compressed timeline. Time cells exhibit many of the properties required for a compressed timeline of the past.

First, in order to contain a record of specific events, different stimuli should trigger different cells. That is, if the population of time cells contains a record of the past, their receptive fields should not only include information about what time an event took place but also the identity of the event. Different stimuli trigger different sequences of time cells in the hippocampus and prefrontal cortex (Terada, Sakurai, Nakahara, & Fujisawa, 2017; Tiganj et al., 2018; Taxidis et al., 2018; Cruzado, Tiganj, Brincat, Miller, & Howard, in press).

Second, the behavioral data suggest that the timeline should be logarithmically-compressed. Recall that absolute judgements of recency increased with the logarithm of the actual recency (Hinrichs, 1970). Recall further that the increase in correct RT in short-term JOR increases sublinearly as the correct probe recedes into the past (Hacker, 1980; Hockley, 1984; Singh & Howard, 2017), as if each step in the scanning becomes larger. This kind of compression implies that the resolution for the timeline should decrease for events further in the past, in much the same way that the resolution of the visual system decreases further from the retina (Howard, 2018). It is clear that time cells provide less accurate representation of time for events further in the past. This can be readily appreciated by examining “heatmaps” that show the temporal receptive field of each time cell sorted by their time of peak firing (Figure 4b-e). If each part of the timeline had the same resolution, the same number of cells would code for each region of time and these heatmaps would show a central ridge that appears as a straight line. As can be seen from examination of the heatmaps in Figure 4 there is a characteristic hook to these curves. Although this compression has not been confirmed quantitatively to be logarithmic, it is certainly consistent with this hypothesis (the red dashed line in Fig. 4b is what one would expect from logarithmic compression). Second, the receptive fields for time cells that fire later in the sequence, coding for times further in the past, are wider than for time cells that fire earlier in the sequence (Jin et al., 2009; Kraus et al., 2013; Howard et al., 2014; Mello et al., 2015; Tiganj et al., 2018; Cruzado et al., in press). The examples in Figure 4a are representative. One can also appreciate this by noting the spread in the central ridge of the heatmaps, which is especially clear in Figures 4c-d (the recording technique in the Mau et al., 2018 paper in panel b does not allow evaluation of time field width). This pattern is what one would expect if the population reflects a compressed timeline; as the triggering event recedes into the past, the population represents its time with less and less resolution.

Notably, all of these properties of time cells correspond to homologous findings related to the populations of exponentially-ramping cells discussed in the previous subsection. Both forms of representation carry information about what happened when. Both types of representation carry information about different time scales expressed across different neurons. Both forms of representation appear to be expressed in a wide range of brain regions and a wide range of tasks. Both types of representation represent distant events with less temporal resolution than more recent events, as if they correspond to a compressed timeline. In the entorhinal-hippocampal circuit at least, populations of exponentially-ramping neurons are directly (and reciprocally) connected to populations of time cells, suggesting that the two forms of temporal representation are intimately related.

*Open questions about time cells central to their cognitive utility.* Although time cells show some properties of a logarithmically-compressed timeline, there are very important predictions that have not yet been evaluated as of this writing. First, although it is known that different stimuli can trigger different sequences of time cells, it is not yet known if sequences triggered by different stimuli can run simultaneously. This property is essential if time cells play a role in laboratory tasks like JOR with many stimuli or in episodic memory more broadly. The exponentially-decaying cells in LEC observed by Tsao et al. (2018) show the ability to time multiple events in parallel—note that some neurons are triggered several times over intervals where other neurons decay smoothly (Fig. 4f). If there is an intimate relationship between exponentially-decaying cells in LEC and time cells in hippocampus, one might expect time cells in hippocampus to maintain multiple sequences in parallel.

Second, it is not known how long time cell sequences can continue. The typical “time cell experiment” has a delay of on the order of ten seconds. The longest delays that have been examined are on the order of a few minutes (Mello et al., 2015; Bolkan et al., 2017; Shikano, Ikegaya, & Sasaki, 2021, see also Sun, Yang, Martin, & Tonegawa, 2020). We know that time cells tile every delay that has thus far been considered, but there is not positive evidence that time cells show the much slower changes that would be necessary to support memory for time over scales up to, say, tens of minutes or an hour (e.g., Glenberg et al., 1980; Unsworth, 2008; Howard et al., 2008; Yntema & Trask, 1963). It is clear that representations in the hippocampus (Manns, Howard, & Eichenbaum, 2007; Ziv et al., 2013; Rubin, Geva, Sheintuch, & Ziv, 2015; Mankin et al., 2012; Mankin, Diehl, Sparks, Leutgeb, & Leutgeb, 2015; Cai et al., 2016; Mau et al., 2018) and other regions (Hyman, Ma, Balaguer-Ballester, Durstewitz, & Seamans, 2012; Rashid et al., 2016) do change slowly over long time scales (see Howard, 2017, for a review), but it is not clear whether these slow sequences reflect sequential activity like that shown by time cells (see Y. Liu et al., 2021). Note again that LEC cells change quite slowly, with time constants up to tens of minutes (Tsao et al., 2018). If there is an intimate relationship between exponentially-decaying cells in LEC and hippocampal time cells we would expect to see very slow sequences in hippocampus.

Third, although there are many conceptual similarities between exponentially-ramping cells like those observed in EC and time cells in the hippocampus, and it is well known that these regions are reciprocally connected, it is not known that there is in fact a causal connection between these representations and, if there is, the direction of causality. As we will see, some spectral models predict that hippocampal time cells are derived from exponentially-decaying cells (e.g., Howard et al., 2014; Tiganj, Hasselmo, & Howard, 2015; Rolls & Mills, 2019). The powerful tools of contemporary systems neuroscience could confirm or refute this prediction about the direction of causation.

### *Episodic memory and a neural “jump back in time”*

Episodic memory has been described as “mental time travel” in which the rememberer vividly re-experiences a moment from his or her existence. The foregoing neural evidence suggests that the brain maintains a record of the past leading up to the present—a compressed timeline of what happened when. If this neural representation is related to our experience of the passage of time as described by James and Husserl then perhaps the re-experience of a specific moment from the past corresponds to recovery of a previous state

of the timeline. Indeed, retrieved context models (Chapter 5.11) have developed detailed descriptions of performance in a range of episodic memory tasks making just this assumption (Sederberg et al., 2008; Sederberg, Gershman, Polyn, & Norman, 2011; Polyn et al., 2009; Lohnas, Polyn, & Kahana, 2015; Healey et al., 2018; Talmi, Lohnas, & Daw, 2019). There is some evidence for this hypothesized “neural jump back in time.”

First, it is important to note that neural representations in a wide variety of brain regions, including the hippocampus, change slowly from one moment to the next over scales ranging from seconds up to hours (e.g., Hyman et al., 2012; Mankin et al., 2015; Cai et al., 2016; Rashid et al., 2016). These changes are observed even during presentation of a randomly-assembled list of stimuli (e.g., Folkerts, Rutishauser, & Howard, 2018). Because these slow changes are observed using many different recording techniques, they are unlikely to reflect a recording artifact.

Several studies in humans suggest that memory is associated with recovery of a preceding state. Electrocorticography studies of recall tasks (Manning, Polyn, Litt, Baltuch, & Kahana, 2011; Yaffe et al., 2014) show that the brain state during memory for an item in the list is similar not only to the brain state during study of that item, but also its neighbors during the original learning experience in both the forward and backward direction. In an fMRI study with list items that could be decoded using MVPA, S. C. Chan, Applegate, Morton, Polyn, and Norman (2017) found that remembering an item from the list was associated with recovery of the list items that preceded it—literally recovery of the temporal context in which an item was experienced. Kragel, Morton, and Polyn (2015) showed in an fMRI study that the degree of hippocampal activation was correlated with parameter of a detailed computational model corresponding to the success of recovery of temporal context. Human single unit studies of recognition memory have shown evidence that memory is associated with a recovery of a prior state of temporal context (Howard, Viskontas, Shankar, & Fried, 2012; Folkerts et al., 2018). In particular, Folkerts et al. (2018) showed that the neural jump-back-in-time was only observed when the participants gave a highly-confident recognition response, presumably reflecting vivid episodic memory for the event.

Evidence for a recovery of temporal context associated with successful memory has also been observed in episodic memory for real-world experiences. Nielson, Smith, Sreekumar, Dennis, and Sederberg (2015) had participants wear a smart phone around their neck for weeks at a time. The phone took pictures periodically. After this experience, participants were brought into an fMRI scanner and their memory was tested for experiences from their actual life. For any pair of memories, the temporal (and spatial) distance between the two events is known. They were also able to measure the distance between activity patterns in the brain using MVPA. They found that the temporal distance between memories correlated with the distance in “fMRI space” in the hippocampus. (Folkerts et al., 2018). For more detailed reviews of this work, see (Polyn & Cutler, 2017; Howard, 2017). This empirical story is still unfolding. As of this writing, the major limitation is that it is not necessarily the case that the slowly-changing signal that is recovered corresponds to neural representations of what happened when. It is possible that there is an additional source of correlated noise in the brain that is recovered in these experiments.

## Computational models of time and memory

Over the last several decades theorists from psychology and neuroscience have developed computational hypotheses for how the brain represents time and uses it to inform behavior. In some cases these hypotheses were developed long before the neurophysiological data that can constrain them was available. This provides a means to evaluate the predictive power of the hypothesis. We will review important early models and contrast their properties to those required for a scale-invariant temporal history. We then discuss in some detail a proposal for a scale-invariant logarithmic timeline constructed *via* the Laplace transform of the past. This proposal is consistent with many of the behavioral and neurophysiological data described above.

### *Clock models*

One large class of models can be described as clock, or timer, models. In these models, some signal initiates the start of a generic timer. The state of this clock when some outcome is observed is stored and used to control future behavior. In the most common variant of the clock model, the clock is operationalized as a counter that retains the value of a scalar—much like a strength model—that changes in time. Because the value of this counter, like the weight of the sand that has passed through an hourglass, is correlated with the amount of time between various events, it can be used to support performance in tasks requiring information about the time of prior events. For instance, in an interval timing task, the stimulus beginning the delay might start a counter. At the end of the delay, the state of the counter is stored in a memory trace. When it comes time to reproduce the interval, the counter is reset and then as time unfolds the current state of the counter is compared to the memory trace.

There are many variants of this basic strategy. The most widely-used variant of this approach is known as scalar expectancy theory, (SET, Gibbon, 1977), which has been widely applied in animal and human timing (Rakitin et al., 1998) experiments as well as conditioning (C. R. Gallistel & Gibbon, 2000). In SET, the counter is abstract. The similarity of the counter process to models of evidence accumulation has led some authors to build models of both tasks (Simen, Balci, de Souza, Cohen, & Holmes, 2011; Luzzardo, Rivest, Alonso, & Ludvig, 2017; Luzzardo, Alonso, & Mondragón, 2017). Given that there is an extensive neurophysiological literature linking ramping neural activity to cognitive models for evidence accumulation (Gold & Shadlen, 2007; Brody & Hanks, 2016), this class of accumulator models predict ramping neurons should contribute to timing. However, they do not predict the other aspects of ramping neurons in cortex—non-linear ramps with a range of rates—reviewed above.

In other variants of clock models, the timer is a set of oscillators with slightly different frequencies. The start signal is understood as resetting the phase of the oscillators. As time unfolds, the phases of the different oscillators go through the same sequence as a function of time since the reset event. Oscillatory clock models have been proposed for timing behavior, where the striatum has been proposed to have an integral role in the control of the oscillators (Matell & Meck, 2004; Meck et al., 2008) and for human list learning paradigms (G. D. A. Brown, Preece, & Hulme, 2000).

While clock models have many appealing properties, they also have some limitations,



both conceptual and neurophysiological. The first conceptual problem is that some delicate fine-tuning is required for the variability in a simple counter to obey the scalar property. Consider the random variable constructed from the sum of  $N$  independent random deviates with mean  $\mu$  and standard deviation  $\sigma$ . The central limit theorem tells us that the mean of the sum goes up like  $\mu N$  whereas the standard deviation goes up like  $\sigma\sqrt{N}$ . The scalar property of timing suggests that the standard deviation should go up like  $\sigma N$  rather than  $\sigma\sqrt{N}$ ; counter models that include a scalar value must address this issue one way or another (Gibbon, 1977; Simen et al., 2011). Moreover, in counter models conceptual issues can arise in deciding what trace to access and update (Machado & Silva, 2007; C. R. Gallistel, 2007). Note that these concerns do not apply to oscillator models, where one can implement scale-invariance by appropriately choosing the distribution of frequencies and different times give rise to distinct states of the phases rather than a simple scalar value.

Other conceptual issues are central to clock models and apply equally well to accumulator models and oscillator models. Suppose that a stimulus has started the clock and another stimulus is presented. Does one reset the clock or allow the clock to continue undisturbed by the new stimulus? With the former choice, one discards information about the time of the first stimulus; with the latter choice, memory for the time of the more recent stimulus is impossible. Perhaps rather than a single clock, there are two clocks? Suppose a third stimulus, or a fourth is presented; what is the limit on the number of clocks that are available? What if a visual stimulus is presented, then, after a long delay the same visual stimulus is repeated. Do those two stimuli access the same clock? How does the model know which clock to access? These questions become quite tricky to answer without discarding the hypothesis of dedicated clock circuits. For these reasons clock models, while often applied to interval timing tasks, are typically not used to account for JORs or episodic memory where many stimuli are experienced (but see G. D. A. Brown et al., 2000).

In this chapter, we have argued that the brain maintains a compressed timeline of the past. As anticipated by James and Husserl, this representation contains information about what happened when. To oversimplify a little, although clock models are well able to describe the “when” in this representation, they struggle to account for the “what” in this representation, and the interaction between what-and-when information.

### *Recurrent networks*

Recurrent neural networks (RNN) are a widely used neural network architecture. RNNs retain an internal pattern of activity that is updated at each time step by the current input to the network as well as its own state at the previous time step. The weights connecting the state at the previous time step to the current state are referred to as recurrent weights. In general the recurrent weights, the weights from the input pattern and the weights from the internal state to the output layer can all be learned. When an input causes a change in the internal state, this can have a long-lasting effect at many subsequent time steps *via* reverberation through the recurrent weights. It is this persistence that endows RNNs with long-lasting memory. Because persistent activity is a pattern across neurons and the recurrent weights can have any configuration, it is possible for RNNs to produce *sequences* of activity rather than simple decays like a strength model. Because an input causes a sequence of activity one can, in principle at least, decode the time since that input, providing a possible model for timing behavior in the brain (Buonomano

& Maass, 2009).

RNNs have found broad use in a range of fields. In cognitive science, RNNs were initially extremely influential in connectionist models of language (Elman, 1990) and later applied to the problem of serial order in list learning experiments (Botvinick & Plaut, 2004, 2006). Under some well-specified conditions, it can be proven that the internal state provides a record of events in the past (Maass, Natschläger, & Markram, 2002) and RNNs can be mathematically tractable (White, Lee, & Sompolinsky, 2004; Rajan & Abbott, 2006). RNNs can have rich dynamics; by setting the weights appropriately they can be used for a number of computational applications and have attracted a great deal of attention in machine learning applications (e.g., Graves, 2013; Graves, Mohamed, & Hinton, 2013; Sutskever, Martens, & Hinton, 2011). In recent years, RNNs have also attracted a great deal of attention in computational neuroscience. Because an input can trigger a sequence of states, RNNs are capable of modeling sequentially-activating neurons that behave like time cells (Rajan, Harvey, & Tank, 2016; Wang, Narain, Hosseini, & Jazayeri, 2018).

There are limitations to RNNs as a model of timing behavior in the brain. The typical method for training RNNs, back-propagation through time, requires that the number of training steps necessary to learn a relationship separated by time  $\tau$  goes up with  $\tau$  (Mozer, 1992). This property does not seem to be consistent with empirical data, leading to proposals to augment RNNs with other mechanisms to identify long-time dependencies (e.g., Ke et al., 2018). In general, RNNs are not scale-invariant, although it is possible to write out RNNs that are scale-invariant (Y. Liu & Howard, 2020). RNNs can be trained to scale-invariant, and to exhibit many different properties (Wang et al., 2018), but this begs the question of how the teaching signal could be constructed. Put another way, if you already had a scale-invariant timeline of the past, you could use it to train an RNN to maintain a scale-invariant timeline of the past. But it is not at all clear how an RNN could generate such a representation *de novo*.

### *Spectral models for temporal history*

One approach to the problem of scale-invariance is to simply have an ensemble of processing elements, each with a different scale (in an RNN, this is analogous to having a wide spectrum of eigenvalues). Across the population, all scales are represented so that the system has similar properties no matter what scale is used in the experiment. Tank and Hopfield (1987) wrote out a set of temporal filters with a wide range of scales for use in an attractor model of sequence learning. The Multiple Time Scale (MTS) model (J. E. R. Staddon, 2005; J. E. Staddon & Higa, 1999) of Staddon and colleagues described conditioning behavior with a strength model in which a stimulus is associated with many strengths, each with a different decay rate (see also Pashler, Cepeda, Lindsey, Vul, & Mozer, 2009). Spectral resonance theory (Grossberg & Merrill, 1992; Bullock et al., 1994; Grossberg & Merrill, 1996) describes a neural network model in which a spectrum of time constants gives rise to sequentially-activated cells, not unlike time cells, which can be used to model behavior in many conditioning and timing tasks. Working primarily in the context of computational models of vision, Lindeberg and colleagues (e.g., Lindeberg & Fagerström, 1996; Lindeberg, 1997, 2016, 2021) proposed that memory for the past ought to be maintained by a population of cells with exponential receptive fields extending over past time. Lindeberg (1997) proposed that these exponential receptive fields could be cascaded to develop compact re-

ceptive fields in time that provide a scale-invariant representation of the past and resembles empirically-observed time cells (see also Lindeberg, 2016).

As discussed above, the behavioral data reviewed in this chapter is consistent with a logarithmically-compressed timeline. Moreover, time cells can be understood as representing the past as a compressed function over past time. It has been proposed that the brain constructs this timeline from a population of exponentially ramping cells with different characteristic scales (Bernacchia et al., 2011; Rossi-Pool et al., 2019; Tsao et al., 2018; Bright et al., 2020). Mathematically, a population of neurons that respond to their inputs and then relax exponentially, as originally proposed by Lindeberg and Fagerström (1996), are the real Laplace transform of the input to the network as a function of past time (Shankar & Howard, 2010, 2012, 2013). To elaborate this point, let us write the stimulus at time  $t$  to be remembered as  $f(t)$ . If a population of neurons each respond to the value of  $f$  available at each moment and if they relax exponentially, but with a variety of relaxation rates across neurons, then the pattern of activity across this population of neurons is understandable as the Laplace transform of the history  $f(t' < t)$  leading up to the present moment. That is, the record of the past as a function of time  $t'$  is written onto the firing rates of the population as a function of the rate parameter  $s$ . The insight that this population contains the Laplace transform of the past is extremely powerful.

An extremely important property of the Laplace transform is that it is invertible. That is, one can start with a function—here an objective record of the past leading up to the present—take the Laplace transform of that function—here the firing rate of the neurons in the population as a function of their rate parameter  $s$ —and invert the transform to recover the original function—here the objective past. In other words, because the Laplace transform is invertible, it means that the population containing the transform in principle retains all the information present in the transformed function. This framework models sequentially-activated time cells as an approximate inversion of the Laplace transform. The method for approximating the inversion is well-understood mathematically (this method is known as the Post approximation; Post, 1930) and can be understood neurally as feedforward weights with center-surround receptive fields in  $s$  (Shankar & Howard, 2012; Y. Liu, Tiganj, Hasselmo, & Howard, 2019). Rather than decaying with a rate  $s$ , neurons approximating the inverse transform have receptive fields centered on a time that is proportional to  $1/s$ . This way of taking the inverse transform results in a blur to the temporal receptive fields such that receptive fields centered on points further in the past get proportionally wider. The inverse transform approximates the function over past time itself—information about different points of past time are written onto different cells. Fortuitously, the form of the blur introduced in the inverse naturally introduces a logarithmic compression to the timeline, naturally resulting in a close correspondence with a great deal of behavioral data reviewed earlier in this chapter.

This computational model (Shankar & Howard, 2010, 2012) predated the empirical observation of most of the properties of hippocampal time cells that are consistent with a logarithmically-compressed timeline, and far predated the observation of cells approximating the Laplace transform in the entorhinal cortex (Tsao et al., 2018; Bright et al., 2019). Using this form of a representation of the past, one can readily construct quantitative behavioral models of many different behaviors, including conditioning, working memory, interval timing, and episodic memory (Howard et al., 2015; Howard, 2018). For

instance, RT findings from the judgment of recency task can be modeled by scanning along a logarithmically-compressed timeline (Howard et al., 2015; Singh, Tiganj, & Howard, 2018). Similarly, one can construct a good model of recency and contiguity across scales in episodic memory by assuming that episodic memory is associated with recovery of a previous state of the timeline (Howard et al., 2015). Temporal mapping experiments (e.g., Fig 2 Cole et al., 1995) can be understood as associations mediated by recovered timelines.

### Summary

Philosophers considering the phenomenology of time have long proposed that the mind constructs a “space-like” internal dimension for time (Husserl, 1966; James, 1890). Behavioral data from a variety of paradigms is consistent with this account, with the added constraint that the internal dimension of time is “compressed” estimate of objective time. The mapping appears to be such that internal time is a logarithmic function of external time, consistent with the Weber-Fechner law. In this view, classical conditioning arises as an attempt to predict the future from a logarithmically-compressed estimate of the past. A wealth of neurophysiological evidence is consistent with this understanding of memory for time. Neurons in many brain regions can be used to decode what happened when in the past. Time cells, observed in many different brain regions, suggest that the brain quite literally places receptive fields along a temporal axis (Eichenbaum, 2014). There is ample evidence that the neural representation of the past is compressed as suggested by behavioral considerations. Computational models that account for time cells have been developed that can be used to both model behavioral data and also predict neurophysiological findings.

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