Cognitive computation using neural representations of time and space in the Laplace domain

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Abstract

Memory for the past makes use of a record of what happened when—a function over past time. Time cells in the hippocampus and temporal context cells in the entorhinal cortex both code for events as a function of past time, but with very different receptive fields. Time cells in the hippocampus can be understood as a compressed estimate of events as a function of the past. Temporal context cells in the entorhinal cortex can be understood as the Laplace transform of that function, respectively. Other functional cell types in the hippocampus and related regions, including border cells, place cells, trajectory coding, splitter cells, can be understood as coding for functions over space or past movements or their Laplace transforms. More abstract quantities, like distance in an abstract conceptual space or numerosity could also be mapped onto populations of neurons coding for the Laplace transform of functions over those variables. Quantitative cognitive models of memory and evidence accumulation can also be specified in this framework allowing constraints from both behavior and neurophysiology. More generally, the computational power of the Laplace domain could be important for efficiently implementing data-independent operators, which could serve as a basis for neural models of a very broad range of cognitive computations.

Connectionist models have had astounding success in recent years in describing increasingly sophisticated behaviors using a large number of simple processing elements (LeCun, Bengio, & Hinton, 2015; Graves, Wayne, & Danihelka, 2014). However, the native ability to perform symbolic computations has long been noted as a key problem in developing a theory of cognition (Fodor & Pylyshyn, 1988; Gallistel & King, 2011; Marcus, 2018). Among other things, symbolic processing requires operators that are independent of the data on which they operate. For instance, a computer program can add any pair of integers whether they are familiar or not. Human cognition also has a powerful symbolic capability that allows us to perform many data-independent operations. To take a concrete situation, after focusing on Figure 1 one could close one's eyes and implement a huge number of operations on the contents of memory. For instance, one could choose to imagine Moe Howard's

face translated by 5 cm to the left. Or decide if the thought bubble in **A** is above or below Moe's tie. Operations like translation (e.g., imagining Moe's face moved by 5 cm to the left) or subtraction (e.g., the relative position of the thought bubble and Moe's tie) would have obvious benefits in computational problems like spatial navigation, where we have learned a great deal about functional correlates of neurons in the hippocampus and entorhinal cortex (O'Keefe & Dostrovsky, 1971; Wilson & McNaughton, 1993; Hafting, Fyhn, Molden, Moser, & Moser, 2005). If cognitive data of many different types used the same form of neural representation then if we knew how to build data-independent operators in one domain, the same computational mechanisms could be reused across many domains of cognition. A complete set of operations would constitute a "cognitive map" that could be used for many different types of information (O'Keefe & Nadel, 1978; Behrens et al., 2018).

This paper reviews recent evidence that suggests a common form of neural representation for many types of information important in cognition. The basic idea is that the firing rate of populations of neurons represent functions out in the world. Some populations do not represent these functions directly, but rather represent the Laplace transform of functions. Because we know a great deal about the properties of the Laplace transform, this lets us understand the computational capabilities of these populations at a relatively deep level. This paper proceeds in three sections. In the section entitled "Computing with functions in the Laplace domain" we sketch out in non-technical language the ideas behind this hypothesis. This section will explain what it means to say the brain "represents a function," and what it means for the a population of neurons to estimate "the Laplace transform of a function." In the second section, we describe recent neurophysiological evidence from the hippocampus and entorhinal cortex. The data show evidence that hippocampal time cells behave as if they are estimating a function over past time. Moreover neurons in the entorhinal cortex behave as if they were estimating the Laplace transform of this function over past time. To the extent one accepts this empirical account, it means that the brain has a transform/inverse pair for functions of time one synapse away in the medial temporal lobe. In the third section, we will review modeling work describing how to construct transform/inverse pairs to represent functions over not only time, but spatial position, other kinematic variables, and accumulated evidence for use in decision-making circuits. We suggest that the reader should seriously consider the idea that the brain might use transform/inverse pairs to perform cognitive computations in many different domains.

Computing with functions in the Laplace domain

We argue that the brain, at least in some cases, computes using *functions* describing information over some continuum (Figure 1a). Consider some function f defining a scalar value in the external world over some domain x, $f(x)$, for instance, in vision the pattern of light in a greyscale image as a function of retinal position. We will write $f(x_o)$ to refer to the value at a single position and understand $f(x)$ to mean the brightness over all possible positions. The activity of neurons along the retina along the retinal surface estimates this function. To distinguish the brain's internal estimate from the actual function in the world, we will write $\tilde{f}(\overset{*}{x})$ to describe the activity over a population of neurons. The value at a particular location $\tilde{f}(\overset{*}{x}_o)$ corresponds to the activation of the receptor that is indexed to the physical location x_o. We understand $\tilde{f}(\overset{*}{x})$ to mean the activation of all the receptors
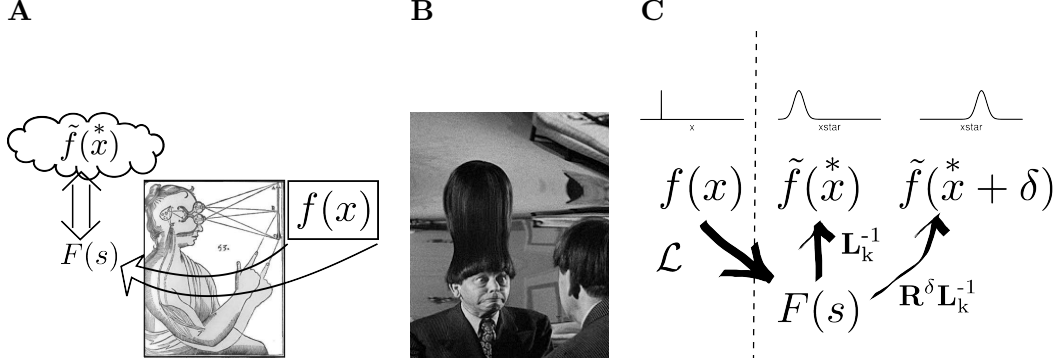
Figure 1. **Encoding functions in the Laplace domain. A.** The brain tries to estimate functions $f(x)$ out in the world. The brain's estimate of this function is denoted $\tilde{f}(\overset{*}{x})$. In many cases, it is not practical to directly compute $\tilde{f}(\overset{*}{x})$. Instead the brain first estimates the Laplace transform of $f(x)$, $F(s)$ and then constructs $\tilde{f}(\overset{*}{x})$ by inverting the transform *via* an inverse transform operator $\mathbf{L}_k^{-1}$. Both $\tilde{f}(\overset{*}{x})$ and $F(s)$ correspond to firing rate across many neurons indexed by $\overset{*}{x}$ or s as appropriate. We assume the population is very large so we can think of $\overset{*}{x}$ and s as effectively continuous. **B.** The Laplace transform of a function is analogous to a reflection in a fun-house mirror. Like the reflection, the transform of a function need not superficially resemble the original image. However, each unique image causes a unique reflection. This means that given a particular reflection, and knowledge of the distortion introduced by the mirror, one could reconstruct the particular image associated with the particular reflection. Similarly, each function specifies a unique transform, one can in principle reconstruct the original function from its transform. **C.** Data-independent operators to compute with functions in the Laplace domain. The world, left of the dashed line, contains some function, $f(x)$. The Laplace operator $\mathcal{L}$, is used to generate the Laplace transform of the function $F(s)$ in the brain. Approximately inverting the transform, *via* an operator $\mathbf{L}_k^{-1}$ generates an internal estimate of the external function, $\tilde{f}(\overset{*}{x})$. Note that there is some "blur" in this estimate of the true function. Data-independent operators are necessary for symbolic computation. Many such operators can be efficiently implemented in the Laplace domain. Here we illustrate a translation operator. Although the world has provided $f(x)$, we want to compute a translated version of the function $f(x + \delta)$. We can rcompute the Laplace transform of $f(x + \delta)$ by operating on $F(s)$ with an operator $\mathbf{R}^\delta$ such that $\mathbf{R}^\delta F(s)$ is the transform of $f(x + \delta)$. Now, applying the inverse operator we can obtain an approximation of $f(x + \delta)$, $\tilde{f}(\overset{*}{x} + \delta) = \mathbf{L}_k^{-1}\mathbf{R}^\delta F(s)$. Note that the translation operator $\mathbf{R}$ is independent of the data—it works equally well on any function. Moreover, in the case of translation, $\mathbf{R}$ is particularly simple—just a diagonal matrix—enabling efficient computation of translation. Other data-independent operators have a simple form in the Laplace domain.

over all their locations. The continuous parameters associated with each neuron, $\overset{*}{x}$ maps onto the continuum of x, enabling the population to distinguish many different functions $f(x)$. We can understand the particular shape of the receptive fields as basis functions over the domain x. We will assume that the number of receptors is very large and the distance between their centers is small so that we can think of $\tilde{f}(\overset{*}{x})$ as if it was a function over a continuous variable. Note that the density of receptors need not be constant in different regions of x.

If we cannot directly place a receptor at a particular physical location x_o, how can we estimate functions over variables such as time or allocentric position, or location within an abstract conceptual space? We hypothesize (Shankar & Howard, 2010, 2012; Howard et al., 2014) that as an intermediate step in estimating $\tilde{f}(\overset{*}{x})$ the brain could construct the Laplace transform of $f(x)$ over another population of neurons. We describe this situation notationally as $F(s) = \mathcal{L}f(x)$. Analogous to the way in which $\tilde{f}(\overset{*}{x})$ corresponds to the activity of many neurons indexed by their value of $\overset{*}{x}$, $F(s)$ is understandable as a particular pattern of activity over a population of neurons, each indexed by a continuous parameter s. Rather than receptive fields that tile x, neurons in $F(s)$ have receptive fields that fall off exponentially like e^{-sx}.

The insight that $F(s)$ is the Laplace transform of $f(x)$ is very powerful—it means that knowing $F(s)$ is enough to specify $f(x)$. Because neurons in $F(s)$ do not have receptive fields centered on a particular value of x, it is not necessarily intuitive to visualize the connection between f and F. In this sense, the Laplace transform of a function is something like the reflection in a funhouse mirror (Fig. 1B). We can construct $\tilde{f}(\overset{*}{x})$ by inverting the transform: $\tilde{f}(\overset{*}{x}) = \mathbf{L}_\mathrm{k}^{-1}F(s)$. Here $\mathbf{L}_\mathrm{k}^{-1}$ is a feedforward operator that approximates the inverse Laplace transform (Shankar & Howard, 2012; Liu, Tiganj, Hasselmo, & Howard, 2019). Of course the inverse cannot be precise—with a finite number of neurons we cannot reconstruct the potentially infinite amount of information in a continuous function (Appendix 2). However, it can be shown (Shankar & Howard, 2012) that the properties of $\mathbf{L}_\mathrm{k}^{-1}$ blur $\tilde{f}$ such that the width of each receptive field in $\tilde{f}$ is a constant fraction of $\overset{*}{x}$. This is closely analogous to the finding that the size of receptive fields in the visual system grows proportional to the distance from the fovea.

One of the reasons the Laplace transform is so widely used in engineering and data processing applications is because one can efficiently implement data-independent operations on functions in the Laplace domain. That is, suppose one wants to perform an operation on some function f. In many cases, it is is more computationally efficient computational to construct $F = \mathcal{L}f$, apply the appropriate operator in the Laplace domain to F and then take the inverse to get the desired answer. Figure 1C provides a schematic for how this could work for function translation—constructing $f(x + \delta)$ from $f(x)$. Efficient Laplace domain methods exist for many unary operators that take in one function f, such as translation, computing the mean or moments of the distribution or taking derivatives. Moreover, there are also methods for binary operations that compare two functions f and g to one another, such as convolution and cross-correlation. Thus, if the brain had access to both Laplace transforms it could in principle take advantage of some of this computational power to implement data-independent operations.

Coding for past events as a function of time in the brain

Memory, by definition, requires some record of the past. Psychologists have long appreciated that memory relies on an explicit record of what events happened when in the past (James, 1890; Brown, Neath, & Chater, 2007; Balsam & Gallistel, 2009). Computational neuroscientists have long proposed models with sequentially-activated neurons could represent past events (Tank & Hopfield, 1987; Grossberg & Merrill, 1992; Goldman, 2009). The observation that memory is less precise for less recent events has led to the proposal that this record of the past is compressed, such that the time at which recent events occurred has better resolution than events further in the past (Fig. 2A). This compression is analogous to the compression of the visual system where regions of visual space near the fovea have a much greater resolution than regions further from the fovea (Howard, 2018).

More formally, at time t the brain tries to estimate the objective past leading up to the present $f(\tau)$. In this formulation, τ runs from zero to infinity with zero corresponding to the moment in the immediate past at time t. At each moment, we can understand the past as a function over the τ axis (Fig. 2A). This function $f(\tau)$ is estimated by a population of neurons that we write as $\tilde{f}(\overset{*}{\tau})$. Cognitive modeling and theoretical work (Shankar & Howard, 2012; Howard, Shankar, Aue, & Criss, 2015) has shown that this kind of representation can be used to construct detailed behavioral models of many memory tasks if the representation of the past is compressed. We first argue that hippocampal time cells have the properties predicted for $\tilde{f}(\overset{*}{\tau})$ and then review evidence suggesting that neurons in the entorhinal cortex of rodents and monkeys show properties consistent with the Laplace transform $F(s) = \mathcal{L}f(\tau)$.

Time cells in the hippocampus code for a compressed timeline of the recent past

Time cells in the hippocampus behave as if they have receptive fields organized in time (Figure 1C, (Pastalkova, Itskov, Amarasingham, & Buzsaki, 2008; MacDonald, Lepage, Eden, & Eichenbaum, 2011; Eichenbaum, 2014; Terada, Sakurai, Nakahara, & Fujisawa, 2017; Taxidis et al., 2018; Cruzado, Tiganj, Brincat, Miller, & Howard, 2019)). As a triggering event recedes into the past, the event first enters and then exits the "time field" of different time cells indexed by $\overset{*}{\tau}$. Because the time fields for different cells are centered on different $\overset{*}{\tau}$s, the population fires in sequence as the triggering event moves through the past. Hippocampal time cells have the computational properties one would expect of a compressed representation of what happened when as a function of past time. First, different external stimuli can trigger distinct sequences of hippocampal time cells (MacDonald et al., 2011; Terada et al., 2017; Taxidis et al., 2018; Cruzado et al., 2019), meaning that these populations carry information about what stimulus happened in the past. Second, hippocampal time cells show decreasing temporal accuracy further in the past. The number of cells with receptive fields around a particular value $\overset{*}{\tau}_o$ goes down as $\overset{*}{\tau}_o$ goes up. Moreover, the width of receptive fields go up with $\overset{*}{\tau}_o$ (Cruzado et al., 2019; Kraus, Robinson, White, Eichenbaum, & Hasselmo, 2013; Howard et al., 2014; Salz et al., 2016).
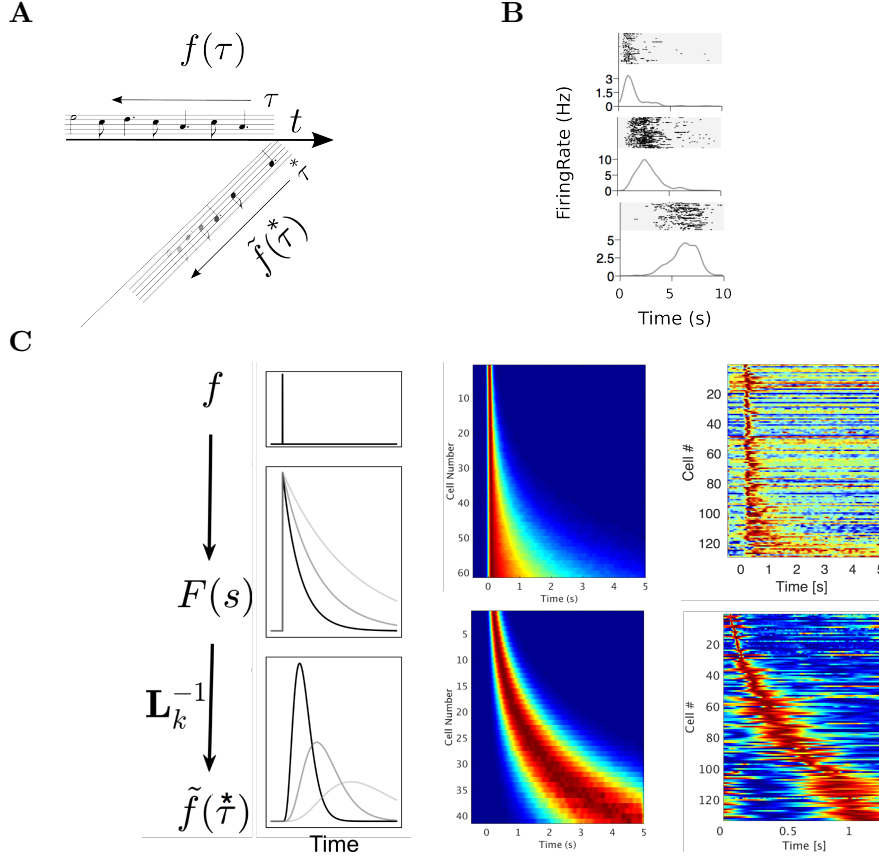
Figure 2. **A compressed timeline and its Laplace transform in hippocampus and entorhinal cortex. A.** Schematic for a compressed internal timeline. The horizontal line describes a sequence of distinct events, here a sequence of tones, in the external world. At a particular moment t, $f(\tau)$ describes the objective past leading up to the present, with $\tau = 0$ corresponding to the immediate past. At any moment $f(\tau)$ describes what event (i.e., which note) happened at each time τ in the past. One can imagine an internal estimate of the timeline leading up to the present $\tilde{f}(\overset{*}{\tau})$ (diagonal line). $\tilde{f}(\overset{*}{\tau})$ estimates what happened when in the past, but the internal time axis is compressed. This means that the time of occurence for past events is resolved with decreasing accuracy for events further in the past (note that spacing between the memory for notes further in the past is decreased). **B.** Hippocampal time cells have receptive fields in time. Each panel is a different neuron, with a series of rasters at the top and a smoothed peri-stimulus time histogram shown below. Time zero in this study is the beginning of the delay period of a memory experiment. Time cells fire when the triggering event is a certain time in the past. They can thus be understood as coding for a function over past time. Note that the cells that fire later have wider temporal receptive fields. This is general characteristic of hippocampal time cells and indicates less temporal resolution for events further in the past, consistent with a compressed representation in the brain. After MacDonald, et al., (2011). **C.** Left: Time courses for model units encoding the instantaneous input f, the Laplace transform of the past $F(s)$, and the inverse transform $\tilde{f}(\overset{*}{\tau})$. When the input was a time τ in the past, the neurons coding the Laplace transform are activated as $e^{-s\tau}$. Neurons in $F(s)$ activate at the same time after the input is presented and then decay exponentially at different rates in time as τ increases. Neurons coding for $\tilde{f}(\overset{*}{\tau})$ activate sequentially. Middle, Theoretical predictions for the two populations expressed as a heatmap. Right; Empirical heatmaps for units in macaque entorhinal cortex (top) and hippocampus (bottom). Data from Bright, et al., (2019) and Cruzado, et al., (2019).

Temporal context cells in entorhinal cortex code for the Laplace transform of a compressed timeline of the past.

Let us consider how we would identify neurons coding for the Laplace transform $F(s) = \mathcal{L}f(\tau)$. Cells coding the Laplace transform of a variable x should show receptive fields that fall off like e^{-sx}. A set of neurons coding the Laplace transform of past time τ should show receptive fields that go like $e^{-s\tau}$, with many different values of s across different neurons. If we think of the triggering stimulus as a delta function at time $t = 0$, it enters $f(\tau)$ at time t at $\tau = 0$. At time t after the triggering stimulus, the firing rates should change like e^{-st}. Observing the firing of a neuron with rate constant s, we should see it change shortly after the triggering stimulus, and then relax back to baseline exponentially in the time after the triggering stimulus. Cells with high values of s (corresponding to fast time constants) should relax quickly; cells with small values of s corresponding to slow time constants) should relax more slowly. We would expect a continuum of s values to describe the continuum of τ values. If the representation is compressed, we would see more neurons with fast decay rates than with slow decay rates. The grey lines in Figure 2C depicts how $F(s)$ and $\tilde{f}(\overset{*}{\tau})$ should behave in the time after a triggering stimulus for different values of s and $\overset{*}{\tau}$.

Recent evidence shows that cells in the entorhinal cortex contain temporal information, like hippocampal time cells, but with temporal receptive fields that are as we would expect from the Laplace transform (Figure 2C, (Bright et al., 2019)). These "temporal context cells" are analogous to findings from a rodent experiment recording from lateral entorhinal cortex (Tsao et al., 2018). In that study, neurons in the EC were perturbed by entry into an enclosure for a period of random foraging. Different neurons relaxed with a variety of rates, showing gradual decay over time scales of up to tens of minutes. Although there are thus far only two studies showing this phenomenon, the similarity of the qualitative properties of the neurons despite drastic changes in the methods of the two studies is striking. Appendix 1 discusses possible neurophysiological mechanisms to implement the Laplace transform and $\mathbf{L}_k^{-1}$ in neural circuits.

Time and memory outside the MTL

The entorhinal cortex and hippocampus are believed to be important in episodic memory. Computational modeling suggests that a representation like $\tilde{f}(\overset{*}{\tau})$ is also useful for other "kinds" of memory, including short-term working memory tasks, conditioning tasks, as well as interval timing tasks (Howard et al., 2015; Tiganj, Cruzado, & Howard, 2019). This suggests that other brain regions have access to representations like $\tilde{f}(\overset{*}{\tau})$. Indeed, time cells with more or less the same properties of hippocampal time cells have been observed in the striatum (Mello, Soares, & Paton, 2015; Akhlaghpour et al., 2016; Jin, Fujii, & Graybiel, 2009) medial prefrontal cortex (Tiganj, Shankar, & Howard, 2017), lateral prefrontal cortex (Tiganj, Cromer, Roy, Miller, & Howard, 2018; Cruzado et al., 2019) and dorsolateral prefrontal cortex (Jin et al., 2009). The fact that this kind of representation is so widespread suggests that many different types of memory utilize a compressed timeline of the past. Ramping neurons observed outside of the EC during memory and timing tasks (e.g., (Mita, Mushiake, Shima, Matsuzaka, & Tanji, 2009; Rossi-Pool et al., 2019; Zhang et al., 2019; Wang, Narain, Hosseini, & Jazayeri, 2018)) could also be manifestations of the

Laplace transform of the past, but this hypothesis has not thus far been explicitly tested.
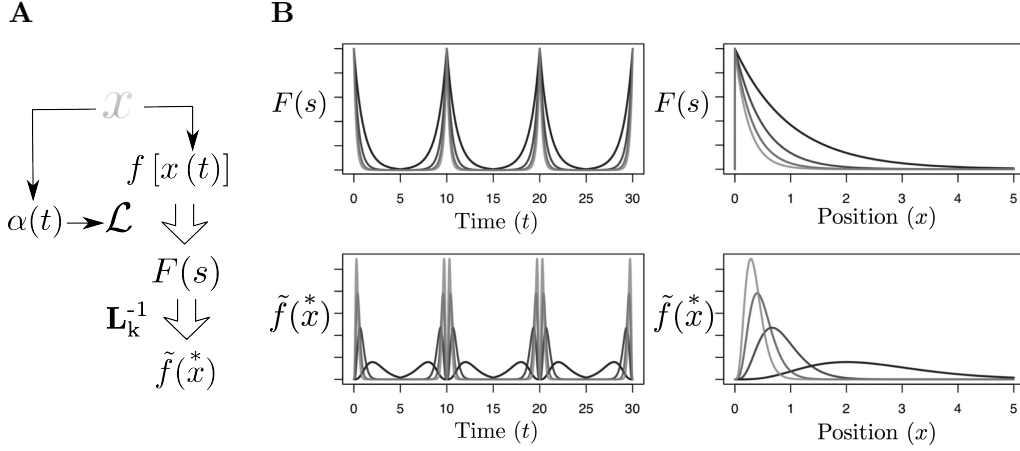
Compressed functions of other variables

A general framework for cognitive computation in the brain requires that representations of many different variables use the same "neural currency." The same formalism utilizing the Laplace transform and its inverse can give rise not only to functions over time but functions over many other variables as well. The basic idea (Appendix 2) is the equations implementing the Laplace transform of a function of time are modulated by the rate of change of some variable x. We refer to the modulation factor at time t as $\alpha(t)$. At the cellular level, $\alpha(t)$ is understandable as a gain factor that changes the slope of the f-i curve relating firing rate to input current. If all of the neurons participating in the transform are modulated at each moment by $\alpha(t) = dx/dt$, then $F(s)$ holds the transform with respect to x rather than time, $F(s) = \mathcal{L}f(x)$. When one inverts the transform, with $\mathbf{L}_k^{-1}$, this results in an estimate of the function of x, $\tilde{f}(\overset{*}{x}) = \mathbf{L}_k^{-1}F(s)$ (Figure 3A).

This strategy can be used to describe different kinds of functions by coding for different input stimuli—different "what" information—and choosing $\alpha(t)$ to be the rate of change of different variables. In this section, we discuss computational work representing compressed functions of variables other than time. For instance we will see that this approach can be used to compute functions coding for the relative spatial position of the wall of an enclosure, for past movements as a function of their position in the sequence or the amount of evidence accumulated for one of two alternatives in a simple decision-making task. The first subsection, entitled "Spatiotemporal trajectories in the medial temporal lobe," reviews evidence that transform/inverse pairs of representations can account for a "particle zoo" of functional cell types in the MTL during spatiotemporal navigation. In the next subsection, entitled "Accumulated evidence and decision-making," we describe a neural implementation of widely-used cognitive models for evidence accumulation models using transform/inverse pairs. Finally, in the last subsection, entitled "Cognitive models built entirely of transform/inverse pairs," we consider the possibility of cognitive models made entirely of transform/inverse pairs and how they could exploit computational properties of the Laplace domain for symbolic computation.

Spatiotemporal trajectories in the medial temporal lobe

It has long been suggested that the hippocampal place code is a special case of a more general form of representation coding for spatial, temporal and other more abstract relationships between events (O'Keefe & Nadel, 1978; Cohen & Eichenbaum, 1993; Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999; Hasselmo, 2012). A wide diversity of functional cell types that communicate information about kinematic variables have been reported in the hippocampus and related structures, including place cells, border cells, splitter cells, trajectory coding cells, speed cells, head direction cells and many more. Many of these functional cell types (the most notable exception being grid cells) can be understood as the Laplace transform of a function coding a spatiotemporal trajectory; others can be understood as an approximate inverse of a function. Moreover, these populations seem to come in pairs, with populations with properties like the Laplace transform in the entorhinal cortex and the populations with properties like the inverse in the hippocampus.

A

B

Figure 3. **Laplace domain code for space and other variables. A.** This computational framework can be used to construct compressed functions over any continuous variable, here denoted x, for which the brain has access to the time derivative. The gain of the neurons coding for the transform is dynamically set to $\alpha(t)$ (see Eq. 5 in Appendix 2). If $\alpha(t) = dx/dt$, the time derivative of x, then the transform is with respect to x instead of t. The inverse thus estimates $f(x)$ rather than $f(t)$. **B.** Schematic showing the activity of a population of cells coding for one-dimensional position from an environmental boundary. In this simulation, the landmark is at the left of a linear track (position zero). The animal moves at a constant speed to the other end of the track and is reflected back towards its initial starting point. The activity of populations of cells coding the Laplace transform ($F(s)$, top row) and the inverse transform ($\tilde{f}(\overset{*}{x})$, bottom) are shown as a function of time (left) and position (right) over three laps. Different values of s and $\overset{*}{x}$ are shown as different lines. As the animal moves away from the landmark, firing rates in the transform decay exponentially with different rates. When the animal reverses direction, these cells rise until the starting position is reached. The cells coding the inverse fire in sequence as the distance to the landmark grows and then fire in the reverse sequence as the agent approaches the landmark. When plotted as a function of position rather than time the cells in $F(s)$ show characteristic exponential receptive fields as a function of position and the cells in $\tilde{f}(\overset{*}{x})$ show circumscribed place fields.

Consider border cells in the medial entorhinal cortex (MEC) (Solstad, Boccara, Kropff, Moser, & Moser, 2008). Border cells fire maximally at a location close to the boundary of an environment with a particular orientation. Their firing rate decays monotonically with distance to the boundary. We saw earlier that temporal context cells in the entorhinal cortex are perturbed by a specific stimulus and then relax monotonically towards their baseline firing rate over time (Fig. 2C, (Tsao et al., 2018; Bright et al., 2019)). Temporal context cells code the Laplace transform of a function over time $F(s) = \mathcal{L}f(\tau)$. The Laplace transform of distance to the boundary $F(s) = \mathcal{L}f(x)$ would behave similarly, with exponentially-decaying receptive fields in space. As the animal moves away from a cell's preferred boundary, firing rate would decrease exponentially with distance; as the animal moved towards the boundary the firing rate would increase along the same curve describing the receptive field (Fig. 3B). This is possible because $\alpha(t)$ is the signed velocity in the direction of the boundary. If a population of border cells encodes the Laplace transform of distance to the boundaries, then across neurons there should be a wide variety spatial

receptive field sizes, and more neurons should have narrow spatial receptive fields than wide spatial receptive fields. The continuum of spatial locations should be mapped onto a continuum of values of s in the population of border cells.

By analogy to time cells, which have receptive fields in a circumscribed region of time since a triggering event, the inverse of border cells would generate a population of neurons with circumscribed receptive fields in space. Boundary vector cells (BVCs), observed within the subiculum, have just this property, with elongated firing fields that align with boundaries of an enclosure (Lever, Burton, Jeewajee, O'Keefe, & Burgess, 2009). In fact classical hippocampal place cells behave as if they are formed from conjunctions of BVCs (O'Keefe & Burgess, 1996; Barry et al., 2006). If BVCs and place cells are the result of an approximate inverse transform, they should have properties analogous to those observed for populations of time cells. BVCs should have more fields close to boundaries and the width of fields should increase with distance to the boundary.

This framework organizes other "cell types" in the MTL as well. Consider a population of cells coding for the sequence of movements leading up to the present position as a function of distance traveled. In words, this population codes for a function f that carries information like "I got here by travelling North for 2 cm; before that I moved West for 10 cm ..." In this case, the "what information" in the population would be head direction ("2 cm in the past I was facing North" or "8 cm in the past I was facing West"). In order to convey this information as a function of traveled distance, we would set $\alpha(t)$ to be speed (unsigned velocity in the direction of motion). Cells coding the Laplace transform of this kind of function would behave as "trajectory-dependent" or "retrospective coding" cells (Frank, Brown, & Wilson, 2000). Cells coding for the inverse transform would manifest as "splitter" cells that fire differentially on the central arm of a figure-8 maze during an alternation task depending on the past locations (Frank et al., 2000; Wood, Dudchenko, Robitsek, & Eichenbaum, 2000; Dudchenko & Wood, 2014) that have been observed in the entorhinal cortex and hippocampus.

Other functional cell types in the MEC can be understood as coding for spatiotemporal trajectories in the Laplace domain or approximating functions. When an animal pauses during a virtual navigation task, a population of MEC cells fire sequentially recording the amount of time since the animal ceased moving (Heys & Dombeck, 2018). Even speed cells, which are believed to map the animal's instantaneous speed onto their firing rate, actually filter speed as a function of time with a spectrum of time constants (Dannenberg, Kelley, Hoyland, Monaghan, & Hasselmo, 2019). This is consistent with the idea that speed cells in MEC are actually coding the Laplace transform of the history of speed in the time leading up to the present. The characteristic predictions from this theoretical approach are best evaluated at the level of populations and manifest largely as distributions of parameters.

Accumulated evidence and decision-making

In many simple decision-making experiments, noisy instantaneous evidence must be integrated over time in order to reach a confident decision. Decades of work in mathematical psychology has resulted in sophisticated computational models for simple evidence accumulation tasks (Luce, 1986; Smith & Ratcliff, 2004). The best known is the diffusion model (Ratcliff, 1978) (Figure 4). At each moment during the decision, the observer samples some evidence. The "particle's position" at any moment, X_t, describes the accumulated evidence
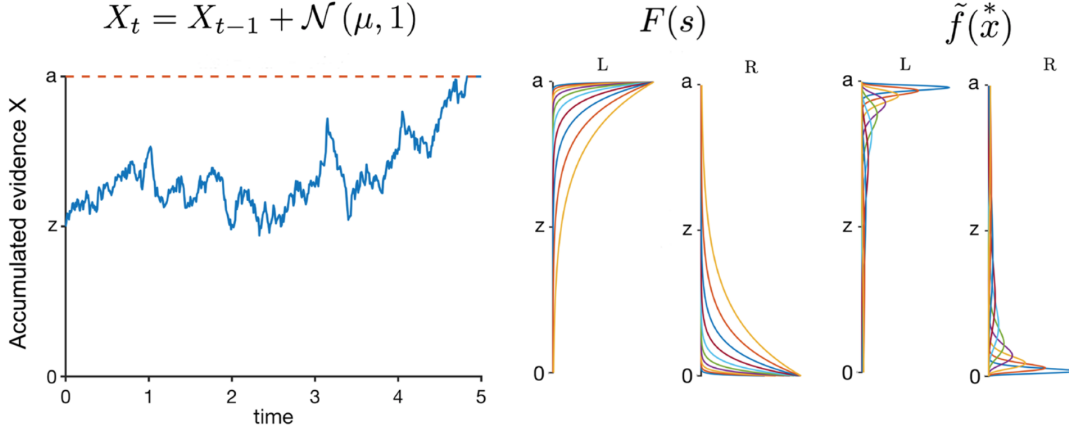
Figure 4. **A Laplace-domain implementation of the diffusion model for evidence accumulation.** The diffusion model describes the internal state while a decision is being made as a particle moving towards two absorbing boundaries, each corresponding to one of two possible decisions. At each moment of the decision, the position of the particle is a delta function located at a position X_t that starts at a position z and moves between the two boundaries. In the Laplace domain implementation of the diffusion model, two populations code for the distance to each of the two decision bounds. Cells coding for the Laplace transform of distance-to-bound, $F(s)$, will ramp their firing up (or down) as evidence accumulates. These cells have exponential receptive fields over the decision axis. Different populations code for each of the two boundaries. We distinguish the two populations as $F_L(s)$ and $F_R(s)$. Within each population, different neurons have different values of s. Cells coding for the inverse Laplace transform, $\tilde{f}(\overset{*}{x})$, have receptive fields that tile each decision axis. Within each population different cells have different receptive field centers. After Howard, et al., (2018).

for each alternative up to that point. This abstract model aligns to a strategy in which the starting position (usually referred to as z) is controlled by the decision-maker's prior expectations and the boundary separation (usually referred to as a) describes the degree of confidence the decision-maker requires before making a choice (Gold & Shadlen, 2007). We can understand the evidence at any moment t as a function $f(x)$ with a peak at a single value X_t. The time derivative of the position of the particle is just the instantaneous evidence sampled at time t.

With this understanding, it is straightforward to build a Laplace-domain model of the diffusion model by constructing two populations, one of which estimates the distance of X_t to the lower bound and one that estimates the distance to the upper bound. We will subscript the two populations such that $F_R(s)$ and $F_L(s)$ correspond to the Laplace transforms of these two functions and $\tilde{f}_R(\overset{*}{x})$ and $\tilde{f}_L(\overset{*}{x})$ correspond to the inverse transforms (Figure 4, (Howard, Luzardo, & Tiganj, 2018)). In the diffusion model evidence for one alternative reduces the evidence for the other alternative so $\alpha_L(t) = -\alpha_R(t)$. A decision is made when the "particle" reaches the smallest value of $\overset{*}{x}$ in one of the populations. Setting α_L and α_R to be non-zero and have the same sign effectively changes the decision bounds. Positive paired values of α have the effect of widening the decision bounds whereas negative paired values of α have the effect of collapsing the decision bounds enabling speeded

decisions (Palestro, Weichart, Sederberg, & Turner, 2018).

This Laplace-domain neural implementation of the diffusion model has at most subtle behavioral differences from the diffusion model. However, it is quite distinct from other neural implementations of evidence accumulation. Rather than assuming that the abstract decision variable x is carried by the average firing rate of many neurons (Zandbelt, Purcell, Palmeri, Logan, & Schall, 2014), the Laplace domain representation represents x as a distributed pattern of firing across many neurons indexed by their value of s. This population has receptive fields that are exponential curves in the decision variable, much like leaky integrator models for decision-making (Busemeyer & Townsend, 1993). This approach further predicts that there should be a heterogeneous distribution of s values across neurons, analogous to recent findings from rodent cortex (Koay, Thiberge, Brody, & Tank, 2019). It is precisely this heterogeneity across neurons—the fact that s forms a continuum—that allows the population to code the Laplace transform of accumulated evidence. The inverse transform leads to neurons with compact receptive fields along the decision axis, analogous to empirical findings from rodent posterior parietal cortex (Morcos & Harvey, 2016).

Cognitive models built entirely of transform/inverse pairs

We have seen evidence that memory—data represented as functions over time and space—and evidence accumulation—a function over position within a decision space—can both be represented with the same form of neural circuit for encoding the Laplace transform and inverse. Many detailed cognitive models of memory tasks include a memory component and an evidence accumulation component in describing behavioral data (Ratcliff, 1978; Nosofsky & Palmeri, 1998; Sederberg, Howard, & Kahana, 2008; Donkin & Nosofsky, 2012). Moreover, detailed models of evidence accumulation make use of memory for past outcomes to make sense of sequential dependencies in RTs (Kornblum, 1973) manifest as changes in bias, drift rate or boundary separation (Gold, Law, Connolly, & Bennur, 2008; Urai, De Gee, Tsetsos, & Donner, 2019). Neurally, reward history can be decoded from neural activity in several brain regions (Morcos & Harvey, 2016; Marcos et al., 2013). Bernacchia and colleagues (Bernacchia, Seo, Lee, & Wang, 2011) estimated the time scale over which cortical neurons were modulated by reward history and found a wide range of decay rates, very much consistent with the idea that the population contained information about the Laplace transform of the history of rewards.

This convergence between memory and evidence accumulation suggests the possibility that two interrelated systems using the same mathematical form interact with one another. That is, perhaps the same equations that govern memory for reward history over tens of minutes (Bernacchia et al., 2011) also govern the evolution of evidence between two decision bounds over the scale of less than a second (Koay et al., 2019). The reward history could be used to set the bias parameter of the evidence accumulator so that segment of the computational cognitive model could be built from the same form of equations. Cognitive architectures (Laird, 2012; J. R. Anderson, 2013) have long provided self-contained models for cognitive performance, with many interacting modules contributing to any particular task. Perhaps if the same neural circuit can be used for the evidence accumulation and working memory modules, one could use the same kind of canonical Laplace circuit to construct all (or most of) the modules needed to perform a complete task. A general cognitive computer built along these lines would require sequential operation of "cognitive programs"

operating on circuits representing information as functions. Evidence accumulation circuits, along with the property that $\alpha(t)$ can be externally set, could be used to implement conditional flow control of the sequence of operations. We discuss two additional considerations that suggest the Laplace domain could be well suited for a more general cognitive computer. First, it is mathematically straightforward to write out efficient data-independent operators using the Laplace representation. These can be understood as population-level modulations of circuits and, at least in the case of the translation operator—can lead to interesting connections to neurophysiology. Second, neural evidence suggests neural representations of sequences of motor actions can be understood as functions over planned future time. This suggests that other sequences—for instance sequences of cognitive operations—could also be constructed as functions over a planned future. These properties are necessary (but certainly not sufficient) to develop a general computing device to mimic human cognition (Gallistel & King, 2011). Early computational work has demonstrated the feasibility of this approach at least for a few simple laboratory memory tasks (Tiganj et al., 2019).

Efficient data-independent operators in the Laplace domain. The properties of the Laplace domain make it particularly well-suited for data-independent operations. Given data—in the form of functions represented as $F(s)/\tilde{f}(\overset{*}{x})$ pairs—these operators generate an appropriate answer for every possible function they could encounter. For instance, an addition operator should not need to know in advance what pair of numbers will be added together and should work effectively on numbers it has never experienced before. Properties of the Laplace domain provide efficient recipes for data-independent operators. We discuss several of these here.

The translation operator takes a function $f(x)$ and shifts it by some amount to $f(x + \delta)$. Consider how to implement translation of a function represented by a neural population $\tilde{f}(\overset{*}{x})$. We would need to transfer information from each cell $\overset{*}{x}_o$ to a translated cell $\overset{*}{x}_o + \delta$. This could be implemented *via* a functional connection between pairs of cells—i.e., a matrix of synaptic connections. However, because we do not know *a priori* what displacement δ will be required, to be useful for all possible translations this hypothesized circuit must connect every neuron in $\tilde{f}(\overset{*}{x})$ with every other neuron. Translation in the Laplace domain is computationally more simple. If $F(s)$ is the transform of $f(x)$, the transform of the translated function $f(x + \delta)$ is simply $e^{-s\delta}F(s)$. That is, the activity of each cell coding for the transform is multiplied by a number that depends on s and δ. There is no need for information to be exchanged *between* cells in F. To examine the translated function, we simply need to invert the transform with $\mathbf{L}_k^{-1}$ and obtain an estimate of $f(x + \delta)$.

Translation is potentially useful for many problems that arise in cognitive science. For instance, translating functions over time can be used to predict the future. A model implementing function translation to predict the future (Shankar, Singh, & Howard, 2016) can be mapped on to theta phase precession in the hippocampus and associated regions (van der Meer & Redish, 2011). The key neurobiological property necessary to implement translation in this model is the ability to dynamically modulate synaptic weights over the course of theta oscillations, a property that has been observed in field potential recordings (Wyble, Linster, & Hasselmo, 2000). Translation could also be useful in manipulating visual representations or generating planned movements in allocentric space (e.g., Johnson & Redish, 2007).

Translation by a specific amount is a unary operation. That is, translation takes in one piece of data—here a neural estimate of a function—and returns its answer. The Laplace domain provides efficient recipes for other data-independent unary operators—for instance estimating the moments of a distribution or the derivative of a function. A cognitive computing language would also requires binary operations. For instance, addition is a binary operator—it requires two pieces of information to return its answer. Consider what addition of two functions would mean computationally. Suppose we have two functions $f(x)$ and $g(x)$ representing two specific numbers x_f and x_g. We can imagine $f(x)$ as a flat function except for a peak at the value x_f and $g(x)$ as a flat except for a peak at x_g. What would we desire for a function representing the sum of these two numbers? Simply adding $f(x) + g(x)$ is clearly not what we want—this would give two peaks, one at x_f and the other at x_g, which is not understandable as a single number. A moments reflection shows that we would want the representation $[f + g][x]$to have a single peak at $x_f + x_g$. The *convolution* of two functions produces just this answer. The convolution of two functions is written $f \star g$. Much like translation, convolution performed directly on functions is computationally demanding. To directly convolve a population of cells $\tilde{f}$ and another population $\tilde{g}$ would require one to take the product of the activation of all possible pairs of cells and then sum the results, keeping separate the information about the difference in $\overset{*}{x}$ between them. While this is possible to compute it would require many connections and a relatively elaborate circuit. In contrast, convolution is much more simple in the Laplace domain. In particular, $\mathcal{L}[f \star g] = F(s)G(s)$. That is, to construct the transform of the convolution of two functions, we need only take the product of the transform of each of the functions at each s. To invert the transform and obtain a direct estimate of the answer, we would apply $\mathbf{L}_k^{-1}$ as $\mathbf{L}_k^{-1}F(s)G(s)$. A neural circuit implementing this mathematical operation would provide a sensible answer for any pair of numbers.

To subtract a pair of numbers, we need an operator that is the inverse of addition. The inverse to convolution is referred to as cross-correlation, $f \# g$. Like convolution, the Laplace transform of the cross-correlation of two functions is relatively simple: $\mathcal{L}[f \# g] = F(s)G(-s)$. Although there are certainly important problems to solve in constructing a detailed neural model of subtraction, existence of an inverse operator to addition eliminates a conceptual obstacle to constructing a number system: any pair of "numbers" (represented as functions over a popuation of neurons) could be combined to obtain a new "number." The compression of neural representations $\tilde{f}(\overset{*}{x})$ means that our estimate of number is not precise, but of course the brain's estimate of number is also imprecise (Gallistel & Gelman, 2000; Feigenson, Dehaene, & Spelke, 2004; Nieder & Dehaene, 2009). Notably, the quantitative form of compression of the brain's number system is believed to be similar to the compression of retinal coordinates in the cortex (Schwartz, 1977; Van Essen, Newsome, & Maunsell, 1984) and is at least roughly consistent with the form of compression of time shown by time cells. Moreover, a general subtraction operator could be used across many different cognitive domains.

Are planned actions represented using the Laplace domain?. In order to build "cognitive programs" it would be necessary to sequentially gate information in and out of memory and to and from the evidence accumulation circuit. Gating can in principle at least be implemented *via* oscillatory dynamics in the brain (Sherfey, Ardid, Miller, Hasselmo, & Kopell,

2019; Bhandari & Badre, 2018). But this still leaves the question of how the brain could construct plans for sequential application of various operations. Although little is known about neurophysiological signatures of sequential plans for abstract computations, there is a good deal of neurophysiological evidence about plans for sequential plans for motor operations. This literature is at least consistent with the idea that a these plans could be represented over planned future time.

Sequential plans of motor actions can be understood as a function describing what *will* happen when in the planned future. In a task where monkeys had to make a series of movements, recordings from the lateral PFC showed neurons that code for what motion an animal makes in sequence (Mushiake, Saito, Sakamoto, Itoyama, & Tanji, 2006). That is, the animal had to perform a series of movements, say moving a cursor LEFT-RIGHT-DOWN. As the sequence unfolded, cells fired conjunctively for specific movements (e.g., LEFT or DOWN) but only in specific positions in the sequence (e.g., first, second, or third). In much the same way a stimulus-specific time cell fires only when its preferred stimulus is in its temporal receptive field (Tiganj et al., 2018; Taxidis et al., 2018), these cells fire when their preferred movement occurs in their sequential receptive field. Notably, these populations in lPFC also fired in the moment before the sequence was initiated (Mushiake et al., 2006), but retaining the coding properties that will occur in the future movement. This pre-movement firing was as if the entire sequential plan was quickly loaded into memory prior to movement initiation. Smooth reaching movements also result in sequentially activated cells in motor cortex (Lebedev et al., 2019). The similarity to stimulus-specific time cells suggests that these neural populations could code for an estimate of a function of sequential actions.

By analogy to the Laplace transform of the past, cells coding the Laplace transform of planned future actions would manifest as cells that ramp *to* the time when an event will take place. Ramping neurons during movement preparation have been observed in prefrontal cortex cortices (Narayanan, 2016), including anterior lateral motor (ALM) cortex (Li, Daie, Svoboda, & Druckmann, 2016; Inagaki, Inagaki, Romani, & Svoboda, 2018; Svoboda & Li, 2018; Inagaki, Fontolan, Romani, & Svoboda, 2019). Neurons in ALM in particular can be used to decode what movement will occur and how far in the future (Li et al., 2016). Note that when s is small, an exponential function is approximately linear. If this ALM population codes for the Laplace transform of time until a planned movement, this predicts that different cells should ramp at a variety of rates.

Discussion

This paper pursues the hypothesis that the brain represents functions in the world as activity over populations of neurons. The parameters of the receptive fields of these neurons trace out a continuum and the brain uses two distinct forms of receptive fields. Exponential receptive fields enable a population to code for the Laplace transform of a function; circumscribed receptive fields enable a compressed estimate of the function itself. We reviewed evidence that the brain maintains both of these kinds of representation for functions over past time in the EC and hippocampus. Computationally, this approach can be used to estimate functions over many other variables. Considering spatial variables we can make sense of border cells, boundary vector cells and other functional cell types in the hippocampus and related regions. We reviewed computational work showing that widely-used cognitive models for evidence accumulation can be cast in this framework, making

distinctive neural predictions.

Computational neuroscience and cognition

As our ability to measure activity from large numbers of neurons grows, it will be increasingly necessary to have ways of understanding the collective behavior of large numbers of neurons (Yuste, 2015; Hasselmo, 2015). The basic unit of analysis we have argued for is not the neuron, but rather populations of neurons representing and manipulating continua. This is analogous to the approach taken in many fields of physics where it has long been appreciated that theories should describe phenomena at an appropriate level of detail (P. W. Anderson, 1972). For instance, fluid dynamics describes the flow of liquids not in terms of molecules but in terms of incompressible volume elements. To determine the flow of water in a pipe one does not need need to worry at all about chemistry. If we could measure the position of each individual water molecule during an experiment, we could evaluate the theory, but the theory would be equally correct no matter whether we understand the chemistry of water molecules or if the incompressible volume element was made of green cheese. A different theory would be required to understand why some liquids have different viscosity than others. Returning to neuroscience, if the approach in this paper has merit, it suggests a number of specific problems that are tractable in the context of computational neuroscience. How does a population of temporal context cells manage to have a specific distribution of time constants? How do neural circuits implement $\mathbf{L}_k^{-1}$? We discuss some possibilities in Appendix 1, but the larger point is that this approach segments the computational neuroscience of circuits of neurons from cognitive neuroscience. Understanding cognition starting from individual neurons is kind of like trying to understand the flow of water through a channel starting with a model of the Bohr atom.

If it is really the case that populations of neurons organize themselves to estimate continua, then this places constraints on the data analysis tools we use to study populations of neurons. Thus far, the strategy taken with time cells and temporal context cells has been to construct a hypothesis about the specific variable being represented and then estimate individual receptive fields to hopefully trace out a continuum of parameters across neurons corresponding to $\overset{*}{\tau}$ or s. This approach could in principle be applied piecemeal to problems in different brain regions, but there are significant challenges. First, even in the hippocampus, cells have receptive fields along more than one kind of variable. For instance, consider the situation when an animal is placed on a treadmill with varying speeds. Because the speed changes from trial to trial, the time since the run started is deconfounded from distance traveled. We would expect "time cells" to care only about time and "distance cells" to care about distance. However, all possible combinations of time and distance sensitivity are observed, with time cells and distance cells as special cases of a continuous mixture (Kraus et al., 2013; Howard & Eichenbaum, 2015). Second, our *a priori* hypotheses about what a specific population of cells codes for depend on prior work. A data-driven approach to neural data analysis would avoid these kinds of problems. However, widely used data-driven approaches can be ill-suited to discover continua. For instance, individual reaching movements generate sequences of activity in motor cortex strikingly similar to sequences of time cells (Lebedev et al., 2019). These sequences can be readily understood as cells tiling a continuum, $\tilde{f}(\overset{*}{x})$. But data-driven dimensionality reduction methods can identify rotational dynamics from the same kinds of data (Churchland et al., 2012; Aoi, Mante,

& Pillow, 2019). To overcome this problem will require data-driven tools that look for multidimensional continua in neural coding.

Computational models of natural and artificial cognition

Laboratory cognitive tasks allow us to study behavior in a quantitative way under tightly controlled circumstances. Although this approach is quite artificial relative to real-world cognition, it places strong constraints on computational models of behavior. However, recent work in mathematical psychology has shown that even very successful cognitive models cannot be uniquely identified using behavioral data alone (Jones & Dzhafarov, 2014). Joint modeling of neural and behavioral data is a promising avenue to constrain cognitive models (Turner, Sederberg, Brown, & Steyvers, 2013; Turner, Forstmann, Love, Palmeri, & Van Maanen, 2017; Palestro, Bahg, et al., 2018), but it does not solve the problem of determining whether a particular cognitive model is neurally plausible *a priori*. If we knew with certainty that populations of neurons really do represent continua *via* the Laplace transform and that those continua have a specific form of compression, this would place a strong constraint on detailed cognitive models of behavior.

If thoughts map onto functions, then thinking maps onto manipulating those functions. The Laplace domain provides recipes for data-independent operators that could be used to manipulate and compare functions—to think. As such, this way of viewing cognition and neurophysiology sidesteps many of the conceptual concerns that have traditionally dogged connectionist models and much of contemporary deep learning approaches.

Appendix 1: Possible neurophysiological mechanisms for the Laplace transform

There are three main requirements to implement the Laplace transform/inverse coding scheme for functions over arbitrary variables. First, the the Laplace transform requires that neurons have a wide range of functional time constants that are very large compared to membrane time constants. Second, to invert the Laplace transform it is necessary for a circuit to implement the $\mathbf{L}_k^{-1}$ operator. Third, to enable coding of the Laplace transform of functions other than time, it is necessary to manipulate the gain of neurons. This box sketches possible neurophysiological mechanisms for these three computational functions. There are almost certainly other possible mechanisms that could give rise to these properties and there is no guarrantee that, even assuming that different brain regions obey the same equations, that they are implemented using the same mechanisms in different regions.

Neurophysiological data indicates that neural circuits could implement the mechanisms of the Laplace transform. The real part of the Laplace transform corresponds to exponential decay with a spectrum of time constants. Recurrent network connections could generate slow time constants, but it is also possible that intracellular mechanisms contribute to exponential decay with a variety of time constants across cells. Intracellular recordings in cortical slice preparations show persistent firing over a range of time scales in the absence of synaptic input. For instance, spike frequency accommodation of neurons in piriform cortex shows a pattern of exponential decay over hundreds of milliseconds (Barkai & Hasselmo, 1994). In entorhinal cortex slice preparations show exponential decay in persistent firing rate over seconds (Tahvildari, Fransén, Alonso, & Hasselmo, 2007; Knauer, Jochems, Valero-Aracama, & Yoshida, 2013). At the upper limit, isolated neurons in slices from entorhinal (Egorov, Hamam, Fransén, Hasselmo, & Alonso, 2002) and perirhinal cortex (Navaroli, Zhao, Boguszewski, & Brown, 2011) integrate their inputs and maintain persistent firing for arbitrarily long periods of time. These cells show effectively infinite time constants in the absence of synaptic inputs. The decay in persistent firing can be modeled based on the properties of nonspecific calcium dependent cation current and calcium diffusion (Fransén, Tahvildari, Egorov, Hasselmo, & Alonso, 2006; Tiganj, Hasselmo, & Howard, 2015).

The entorhinal cortex provides input to the hippocampus, so that the population coding for $F(s)$ is one synapse away from the population coding for $\tilde{f}(\overset{*}{\tau})$. Because the equation $\tilde{f}(\overset{*}{\tau}) = \mathbf{L}_k^{-1} F(s)$ is mathematically true, there should be some way to understand the functional mapping between the regions as an approximate inverse Laplace transform $\mathbf{L}_k^{-1}$. The inverse Laplace transform requires combining the different exponential decay rates with different positive and negative values (Eq. 4, Appendix 2). The simplest way to think of this is subtraction of an exponential function with a faster decay from an exponential of the same starting value with slower decay. This will result in a function that peaks at a time point dependent upon the difference of the two time constants. If we multiplied both of the time constants by the same number, the difference would peak at a proportionally larger time. A biological detailed spiking model of the inverse Laplace transform (Liu et al., 2019) can be built from a series of additions and subtractions in which a particular time constant has subtractions from time constants close in value. These derivatives with respect to s (Eq. 4) are analogous to center-surround receptive fields (Marr & Hildreth, 1980), only in s rather than in retinal position. Methods for blind source separation including independent

component analysis and sparse coding have been shown to give rise to center-surround receptive fields in models of the visual system (Bell & Sejnowski, 1997; Olshausen & Field, 1996). Higher order derivatives could be implemented by placing center-surround circuits in series.

Generalizing the Laplace transform to dimensions other than time require a coordination of gain control of decay by factors such as running velocity to code spatial location. In at least some studies, spatial attention works to enhance the gain of receptive fields (McAdams & Maunsell, 1999; Maunsell & Treue, 2006). In slice preparations, gain can be controlled by the variability of synaptic inputs (Chance, Abbott, & Reyes, 2002) and computational studies have suggested a number of possible mechanisms (Silver, 2010), including active dendritic computation (Mehaffey, Doiron, Maler, & Turner, 2005; Poirazi, Brannon, & Mel, 2003), and neuromodulatory agents such as acetylcholine (Barkai & Hasselmo, 1994; Fransén et al., 2006).

Appendix 2: Mathematics of the Laplace transform

Consider a population of leaky integrators indexed by their rate parameter s. Each of the neurons in this population receive the same input $f(t)$ at each moment and update their firing rate as

$$\frac{dF(s)}{dt} = -sF(s) + f(t). \tag{1}$$

We understand $F(s)$ as describing the activity of a large number of neurons with many values of s. Note that Eq. 1 only requires information about f and F at the present moment. However, the solution to Eq. 1 gives the real Laplace transform of the entire function $f(\tau)$ running backwards from the present infinitely far in the past:

$$F(s) = \int_0^\infty f(\tau)e^{-s\tau}d\tau \tag{2}$$

where we understand $f(\tau)$ on the right hand side to be the series of inputs ordered from the present towards the past. That is, the $f(\tau)$ on the right hand side of Eq. 2 is related to $f(t)$ in Eq. 1 as $f(\tau) \equiv f(t - \tau)$. Another way to say this is that $F(s)$, the pattern of activity at time t, is the Laplace transform of the entire history of f leading up to the present.

The Post approximation (Post, 1930) provides a neurally-realistic method for approximately inverting the Laplace transform. This method allows us to take the set of cells coding for $F(s)$, each with a different value of s and map them onto a new population of cells that estimate the original function. We index those cells by a parameter $\overset{*}{\tau}$ and write $\tilde{f}(\overset{*}{\tau})$ to refer to the firing rate of the entire population. The approximation of $f(\tau)$ is computed as follows:

$$\tilde{f}(\overset{*}{\tau}) = \mathbf{L}_k^{-1}F(s) \tag{3}$$

$$= C_k s^{k+1}\frac{d^k}{ds^k}F(s) \tag{4}$$

The parameter k controls the precision of the approximation. Post proved that in the limit as $k \to \infty$, $\tilde{f}(\overset{*}{\tau}) = f(\tau)$. The internal estimate of past time $\overset{*}{\tau}$ is related to s as $\overset{*}{\tau} = k/s$. This means that $\overset{*}{\tau}$ is proportional to the time constant $1/s$. The value of $\overset{*}{\tau}$ has a physical meaning in that it gives the time lag at which each cell in $\tilde{f}$ would peak following a delta function input.

Equation 4 describes a mapping from a population of cells indexed by s to another population indexed by $\overset{*}{\tau}$. To understand the mechanism of the inverse operator, let's consider Eq. 4 from the perspective of a particular cell with a particular value $\overset{*}{\tau}_o$. The time dependence on the right hand side comes entirely from the derivative term—C_k is a constant that is the same for all cells and s^{k+1} is a scaling factor specific to the value of $\overset{*}{\tau}_o$. The derivative term says that the firing rate $\tilde{f}(\overset{*}{\tau}_o)$ is controlled by the kth derivative with respect to s in the neighborhood of a specific value of s, $s_o = k/\overset{*}{\tau}_o$. Computing the kth derivative requires comparing the firing rate other cells in the neighborhood of s_o (Shankar & Howard, 2013).

To generalize to functions over variables other than time, we allow the gain of all of the neurons coding for $F(s)$ to be modulated together by a time-dependent function $\alpha(t)$:

$$\frac{dF(s)}{dt} = \alpha(t)\left[-sF(s) + f(t)\right] \tag{5}$$

Note that if $\alpha(t) = 1$, this expression reduces to Eq. 1. Consider the situation where $f(t)$ is a delta function input at $t = 0$. This initializes the activation at 1 for all units. This is the Laplace transform of a delta function at $x = 0$. If, in the time after $t > 0$, we find $\alpha(t) = 1$, $F(s)$ at time t will code for the Laplace transform of the time since the delta function, $F(s) = e^{-st}$. However, if $\alpha(t)$ was some positive constant that was greater or less than one, α_o we would find $F(s) = e^{-s(\alpha_o t)}$. That is, changing α_o from 1 is equivalent to making time go faster or slower. If we found $F(s)$ in a state where $F(s) = e^{-sx}$ for some value of x, then we set α to some specific value α_o, we would find after some time displacement Δ_t that $F(s)$ is now

$$e^{-s\alpha_o \Delta_t} e^{-sx} = e^{-s(x + \alpha_o \Delta_t)}.$$

If we could arrange for α_o to be the rate of change of x during this interval, then our new value of $F(s) = e^{-s(x + \Delta_x)}$. Note that this is true whether Δ_x is positive or negative. This means that during an interval where $f(t) = 0$, if $\alpha(t) = dx/dt$ then $F(s)$ records the Laplace transform of $f(x)$ rather than $f(t)$.

Although there are many variables that could be productively represented in this way, there are two potentially important limitations to this approach. First, if $f(t)$ is to be non-zero, $f(t)$ must be an implicit function of x, $f[x(t)]$. This makes sense if $f(t)$ corresponds to, say, contact with a landmark in a spatial environment but can lead to complications in general. Second, significant problems arise when one attempts to use this approach to represent values of $x < 0$. To make this concrete, note that Eq. 5 works for both positive and negative rates of change—as we would expect in a spatial navigation task where the animal can move either to the left or to the right. Suppose one starts with $F(s) = e^{-s0}$; each cell at a high firing rate. If we set α to be α_o and evolve Eq. 5 for some time we find $F(s) = e^{-s\alpha_o \Delta_t}$. If α_o is positive, each of the cells decay from 1. However, if α_o is negative, the cells increase their firing rate exponentially from 1, growing without bound. Moreover, the inverse operator does not not behave well as x passes through zero.

Acknowledgments

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