The Neural Basis of Behavioral Sequences in Cortical and Subcortical Circuits

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Summary

Sequences of actions and experiences are a central part of daily life in many species. Sequences consist of a set of ordered steps with a distinct beginning and end. They are defined by the serial order and relationships between items, though not necessarily by precise timing intervals. Sequences can be composed from a wide range of elements, including motor actions, perceptual experiences, memories, complex behaviors, or abstract goals. However, despite this variation, different types of sequences may share common features in neural coding. Examining the neural responses that support sequences is important not only for understanding the sequential behavior in daily life but also for investigating the array of diseases and disorders that impact sequential processes and the impact of therapeutics used to treat them. Research into the neural coding of sequences can be organized into the following broad categories: responses to ordinal position, coding of adjacency and inter-item relationships, boundary responses, and gestalt coding (representation of the sequence as a whole). These features of sequence coding have been linked to changes in firing rate patterns and neuronal oscillations across a range of cortical and subcortical brain areas and may be integrated in the lateral prefrontal cortex. Identification of these coding schemes has laid out an outline for understanding how sequences are represented at a neural level. Expanding from this work, future research faces fundamental questions about how these coding schemes are linked together to generate the complex range of sequential processes that influence cognition and behavior across animal species.

Keywords: monkey, rodent, electrophysiology, behavioral sequence, serial order, neural coding

Subjects: Cognitive Neuroscience, Motor Systems, Sensory Systems

Introduction

What is a Sequence?

Because humans and animals exist in time, nearly all processes can be considered sequential. A sequence, specifically, is defined by progression through a series of ordered steps with a beginning and an end. The timing of sequential items can be fixed or flexible and internally or externally determined. In this framework, each sequence item is defined not only by a particular stimulus or action but by its serial position. An item that is correct in one position can be an error if it deviates from the set order. Thus, the relational structure of serial items is the organizing principle of sequences.

There are many different types of sequences. They can be broadly grouped into perceptual (e.g., the order of visual objects), motor (e.g., playing the piano), and abstract (e.g., multiply and divide before adding and subtracting). Several reviews have discussed these and other categories of sequences (Dehaene et al., 2015; Desrochers & McKim, 2019; Desrochers et al., 2016). In contrast, this article focuses on the neural mechanisms that underlie sequences, largely remaining agnostic to specific sequence types in order to focus on commonalities in neural coding. Similarly, this article does not attempt to strictly parcellate the observations of particular neural codes to particular regions in the brain. Electrophysiology, the technique most referenced here, is by definition limited to areas that have been targeted for recording. A broader, simultaneous field of view is necessary to make definitive statements about what codes are specialized for each region under each set of sequential conditions and these data are understandably rare.

Why Are Sequences Important?

Given the variety of sequence types and relevant brain regions, why is it important to examine the neural codes associated with sequences overall? Nearly all of daily life can be parsed into sequences. Making your morning coffee is an abstract task sequence (e.g., grind beans, add water, start machine, drink coffee) that supervises many motoric subsequences (e.g., scoop, stir, pour). It doesn't take much for the control of these sequences to break down. Alcohol and drugs of abuse, aging, psychiatric disorders, head injury, and many diseases all disrupt sequences, often to the point where normal activities of daily life are no longer possible (Desrochers & McKim, 2019). For example, driving, a highly skilled sequential set of actions, can be disastrous under the influence of alcohol. Similarly, seemingly simple sequences, like cooking, can become problematic for aging relatives, especially when a pot is forgotten on the stove. These deficits can often be very specific. Patients with damage to the frontal lobes may perform well on standard, laboratory-based tests of executive function but are unable to live independently because they cannot complete sequences such as preparing meals for themselves (Eslinger & Damasio, 1985; Shallice & Burgess, 1991).

Many treatments for sequential disorders involve altering brain function. For this reason, among others, it is fundamental to understand the neural mechanisms that underlie these conditions and their treatments. Such treatments can be pharmacological or involve brain stimulation (both invasive and noninvasive). For example, obsessive-compulsive disorder (OCD) is often associated with repetitive, ritualistic behaviors where patients can become stuck in a "loop." In these loops, a behavior or thought pattern must be repeated and other activities neglected—for example, going back and forth through a doorway until the transition feels "just right." These ritualistic patterns of behavior can be conceptualized as sequences. When OCD is resistant to pharmacological intervention, treatment often includes noninvasive transcranial magnetic stimulation (TMS) or invasive deep brain stimulation (DBS) (for reviews, see Fitzsimmons et al., 2022; Mar-Barrutia et al., 2021). While these treatments are often successful, there is very little understanding of their specific neural mechanism of action. Fully understanding these and other treatments that affect the brain requires a precise understanding of the neural coding that underlies sequences.

This article describes the neural responses that reflect key features of sequences, including ordinal position, interitem relationships, boundaries, and gestalt structure. It focuses primarily on spiking activity but also considers the potential role of oscillations in encoding the structure of sequences across time. Disambiguating these codes is the key first step to understanding how they may (or may not) work together to code the wide array of sequential processes across multiple brain areas. Building from this framework, future research has the opportunity to further specify and investigate the interrelation of these sequential codes to understand their strengths and limitations in constructing the complex behaviors that characterize daily life.

Structural Organization of Sequences

Sequences are constructed by combining individual elements into an ordered structure. Each element can be defined by its ordinal position in the sequence (ordinal coding) and by its relationship with other items (relational coding). For example, in the sequence [*red, blue, yellow, green*], the element *blue* can be described as the second item in the sequence and as the item that comes after *red* and before *yellow*. Notably, relational codes can vary in their complexity, from pairwise associations between adjacent items to extended relationships across multiple sequence elements. More complex relative coding schemes may be particularly important for abstract or "algebraic" sequences, which are defined by a pattern of relationships across items rather than specific stimuli or actions (Dehaene et al., 2015). The nature of sequence coding in the brain depends on how ordinal and relational codes interact, what types of relational structure can be encoded, and how each type of coding constrains sequence representations in different conditions. Theoretical and behavioral evidence suggest that both ordinal and relational coding are used to represent sequence structure but many of the details are still being understood.

Early sequence learning research suggested that sequence representations relied on an ordinal code, where elements were learned based on their position in the sequence. This view contrasted the hypothesis that sequence learning arose from chaining together pairs of adjacent elements, a type of relational representation (Primoff, 1938; Young, 1962). Humans learned new sequences more quickly if the elements were drawn from previously learned sequences but only if the ordinal position of those elements was kept the same (Ebenholtz, 1963; Young, 1962). These findings, later replicated in monkeys (Chen et al., 1997), suggested that item–position associations were a cue for learning and remembering sequences. Conversely, evidence did not support the idea that stronger associations formed between pairs of adjacent items after sequence learning (Ebenholtz, 1963; Young, 1962) or that interitem associations predicted errors on sequence tasks (Conrad, 1965; Henson et al., 1996). Taken together, these findings challenged the idea that sequences were constructed from a chain of item-to-item associations and shifted focus toward an ordinal account for sequence representation.

While these experiments illustrated the importance of ordinal coding, it cannot fully account for sequence representation on its own. Theoretical and experimental evidence support this view. Conceptually, ordinal coding relies on stable associations between specific items and specific sequence positions. If there is only one sequence to consider, each ordinal position can be uniquely associated with one item. However, when multiple sequences are encoded, a single

ordinal position corresponds to different items in different sequences and no longer provides a unique cue (figure 1A). To distinguish multiple sequences, ordinal coding must be combined with item-to-item or item-to-sequence associations. Importantly, these associations are not limited to pairwise relationships between adjacent items. Like ordinal coding, adjacency can only account for sequence representation in a limited set of cases—in particular, when a given item is always followed by the same subsequent item. If an item appears multiple times in the sequence and is followed by different items, or if the sequence is defined by a more abstract pattern across elements, representations must account for extended relationships across positions (figure 1B).

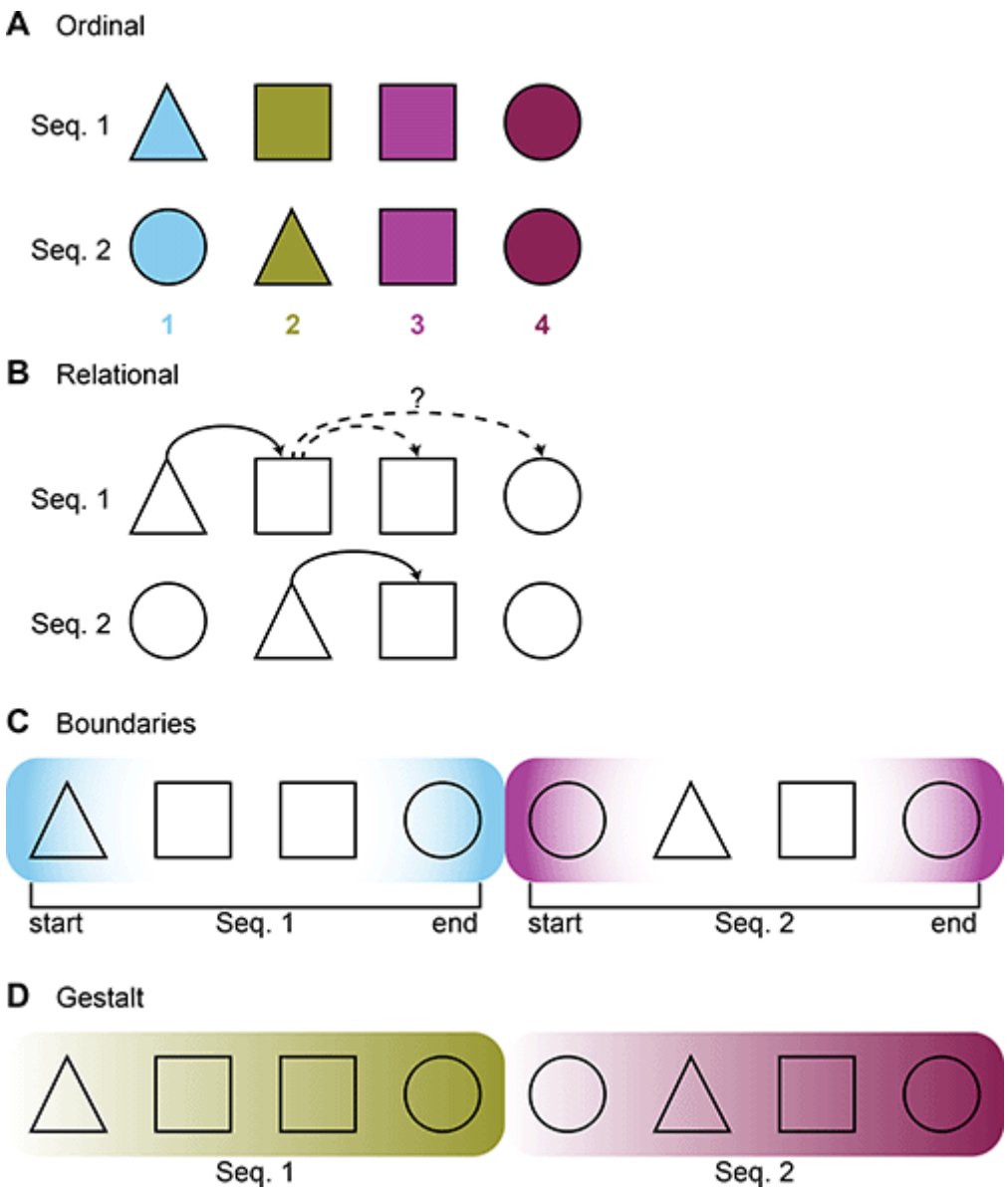

Figure 1. Schematic of neural coding categories. (A) Ordinal codes associate items with serial position in the sequence. Pure ordinal coding functions well to uniquely locate items within sequences but may break down across sequences, as knowing the ordinal position will not uniquely disambiguate sequence 1 from sequence 2. (B) Relational codes can contribute context to what comes before and after a particular item in the sequence. However, a pure relational code will break down when context is similar across positions or sequences. For example, knowing the current item is square can imply that either square or circle comes next, depending on sequence identity and

ordinal position. (C) Boundary coding can disambiguate when sequences begin and end, especially when they follow each other. Item identity alone is often not sufficient to identify these boundaries. For example, in the sequences illustrated, triangle would not uniquely indicate the beginning of a sequence, nor would circle uniquely indicate the end. (D) Gestalt coding, either at specific time points or as a time-varying signal throughout sequences, may provide unique context throughout the sequence and augment other types of codes. Such a code must be selective for each sequence.

Experimental evidence suggests that ordinal coding may scaffold sequence organization, with temporal context and other relational structure building from there. In sequence memory tasks, the pattern of errors can inform which codes are in use. Misidentifying an item as in-sequence if it occurs at the correct ordinal position in a different sequence indicates the use of an ordinal code. Monkeys display this pattern of errors (Orlov et al., 2000) and learn ordinal position more quickly than item–item associations. However, if an exclusively ordinal code were used, then behavioral performance would be at chance for incorrect items with the correct ordinal position. This is not the case. This and other behavioral evidence suggest that a relational code is also used (Allen et al., 2014; Long & Kahana, 2019; Orlov et al., 2000; Reeders et al., 2021). A prime candidate for such a relational code is temporal context coding, in which each event is linked to contextual state (Howard & Kahana, 2002). In the temporal context model, nearby sequence items share a more similar context, a direct consequence of the gradual way that neural activity evolves. This feature allows the context during one event to serve as an automatic cue for the next but it also makes it more difficult to distinguish their activity patterns, contributing to memory errors. Human and rat behavior on a sequence monitoring task is consistent with this prediction (Allen et al., 2014; Reeders et al., 2021) and simultaneously shows the pattern of errors discussed for ordinal coding. Therefore, these experiments provide behavioral evidence for the concurrent use of ordinal and temporal context codes.

Notably, while both ordinality and temporal context appear involved in sequence coding, these schemes have divergent strengths. Ordinal coding provides a simple framework that can be applied to a wide range of sequence structures and modalities. Its modularity may make it easier to recombine items into new sequences and distinguish different sequence steps. In contrast, temporal context codes provide a continuous, gradually varying map of interitem relationships between the set of items that make up a sequence. This type of representation may be ideal for constructing abstract feature spaces and extrapolating the relationships within them (Rueckemann et al., 2021). Investigating the interactions between these complementary systems will be a valuable path for understanding sequence processing.

The evidence that ordinal and relational codes contribute to sequence representation raises the question of how these codes are implemented at the neural level. Neural recordings across a variety of brain regions have been used to examine sequences of stimuli and actions. These experiments have identified a wide variety of sequence-related responses, including responses to ordinal position, pairs of adjacent items, sequence progression, and the sequence pattern as a whole (Barone & Joseph, 1989; Berdyyeva & Olson, 2010; Naya & Suzuki, 2011; Nieder et al., 2006; Shima & Tanji, 2000; Shima et al., 2007). While most experiments have not explicitly aimed to distinguish ordinal and relational coding directly, their results show how serial order, interitem

relationships, and sequence structure affect neural responses during sequential tasks. These findings provide a basis for understanding the key features of sequence processing and the neural processes that mediate them.

Neural Encoding of Ordinal Position

Ordinal position has likely been the most studied aspect of sequence coding at the neural level. Neural responses to ordinal position have primarily been studied in motor sequences and serial order memory. These two types of sequence processing have generally been investigated separately, leaving an open question of whether they draw on related neural mechanisms. Nevertheless, it is worth noting that many motor sequence tasks include a working memory component and have identified ordinal coding in neurons in both delay and execution phases of the task. For example, some of the earliest evidence of ordinal selectivity was found in dorsolateral prefrontal cortex (DLPFC) during both the instruction and sequence execution phases of a cued sequential reaching task (Barone & Joseph, 1989). These results imply that serial order representations may partially overlap across different cognitive and behavioral conditions.

In the context of motor sequences, a promising candidate for ordinal position coding is the activation of rank-order-selective neurons (Salinas, 2009). Rank-order-selective neurons have been identified in a variety of regions, including the supplementary motor area (SMA), pre-SMA, supplementary eye field (SEF), lateral prefrontal cortex (LPFC), and the basal ganglia (Averbeck et al., 2006; Berdyyeva & Olson, 2009, 2010; Isoda & Tanji, 2003; Kermadi & Joseph, 1995; Mushiake & Strick, 1995; Ninokura et al., 2004; Shima & Tanji, 2000). These neurons respond at specific time points in a motor sequence and generally align with a particular sequence step, e.g., the second item in a three-item sequence, rather than the continuous passage of time (Berdyyeva & Olson, 2010). Rank-selective neurons can be active during sequence planning as well as execution and in some cases may respond to multiple ordinal positions (Shima & Tanji, 2000) but their selectivity for serial position remains consistent across different movements, sequences, and task conditions (Berdyyeva & Olson, 2009, 2010; Ninokura et al., 2004; Shima & Tanji, 2000). Berdyyeva and Olson (2010) found that rank-selective neurons in pre-SMA, SMA, and SEF maintain their rank preference across object-based and direction-based saccade tasks, suggesting a relatively abstract order code. Yet while ordinal selectivity is stable, some rank-selective neurons respond more strongly to specific sequence patterns or motor actions (Berdyyeva & Olson, 2010; Isoda & Tanji, 2003; Kermadi & Joseph, 1995; Shima & Tanji, 2000). These neurons respond at the same ordinal position in different sequences, but with a varying magnitude (Salinas, 2009). Taken together, these results suggest that ordinal coding is a fundamental aspect of sequence representations but is intertwined with information about interitem relationships and the sequence identity as a whole.

Causal manipulations and computational modeling suggest that rank-selective responses may play a functional role in generating sequences. Transient inactivation of either SMA or pre-SMA impairs the ability to learn new motor sequences or execute known sequences from memory (Nakamura et al., 1999; Shima & Tanji, 1998). Similarly, microstimulation of SEF disrupts the order of saccade sequences but not the memory of target locations, suggesting a specific role in

the ordinal structure of actions (Histed & Miller, 2006). Complementing these findings, modeling work shows that a network of rank-selective neurons can flexibly learn and execute multiple motor sequences with minimal practice (Salinas, 2009). In this model, sequence identity modulates the output of rank-selective neurons, making it possible to encode multiple sequences in the same network. This modulation effectively unpacks the sequence into its individual components through gain-modulated connections from rank-selective neurons to motor-related outputs. Further, because each motor output receives input from a wide range of rank-selective neurons, the network can improve performance on specific sequences with only minor changes to synaptic weights, suggesting a potential mechanism for rapidly learning new sequences or adapting to changing environments.

Modulated rank-order coding offers a promising mechanistic account of sequence generation, but there are a few caveats to consider. First, in its current form, the model does not account for parallel processing of adjacent sequence items, which has been observed in several motor sequence tasks (Averbeck et al., 2002; Basu et al., 2021; Becker & Jürgens, 1979; Bhutani et al., 2013; McPeek et al., 2000; Zimnik & Churchland, 2021). Parallel processing occurs when planning for an upcoming action in a sequence overlaps with planning or execution of the previous item. This overlap was first observed for pairs of saccades (Becker & Jürgens, 1979) but can also occur during other types of highly learned motor sequences (Zimnik & Churchland, 2021). Parallel processing appears to reflect the overlap of independent action plans rather than the fusion of multiple actions into a new hybrid structure (Zimnik & Churchland, 2021). In principle, rank-order coding models can account for these overlapping action plans by allowing a sequence item to activate before the previous step is complete. However, alternate models have also been proposed to explain sequence generation from parallel action plans. When multiple action plans are represented simultaneously, each sequence item can be chosen by competition between each action plan, a process known as competitive queuing (Bullock, 2004; Rhodes et al., 2004). In this framework, serial order is coded implicitly in the relative activation of plans rather than an explicit ordinal position code. The role of these different models of sequence generation in different behavioral contexts merits further exploration, particularly in tasks where multiple models may apply.

In addition to this caveat, it is not clear whether rank-order-selective neurons could play an analogous role in other, nonmotor sequential tasks. While similar mechanisms might be used to recall learned sequences or predict future events, the Salinas (2009) model is unlikely to account for sequential structure during working memory. Serial order working memory relies on the ability to build a representation of a sequence as it is presented in real time and maintain that information over a short delay. In contrast, motor sequence learning involves constructing templates for each sequence and storing them over an extended period of time.

Serial working memory can arise from ordinal coding of item–position associations but it requires a slightly different model of inputs and outputs. One potential solution draws on two types of ordinal coding observed in tasks that require serial working memory. First, neurons frequently respond to a combination of item identity and ordinal position during sequential tasks, a phenomenon known as “conjunctive coding.” For example, many neurons in perirhinal cortex and ventral LPFC respond preferentially to specific combinations of ordinal position and item

identity during a serial order working memory task (Naya & Suzuki, 2011; Naya et al., 2017). Second, neurons in the intraparietal sulcus (IPS) respond to a specific ordinal number during a serial numerosity task (Nieder et al., 2006). Other work suggests that this ordinal response also occurs for motor actions (Sawamura et al., 2002), nonnumeric sequences (Fias et al., 2007), and multiple stimulus modalities (Nieder, 2012), hinting at a generalized code for ordinal position. Based on these observations, Botvinick and Watanabe (2007) constructed a model of serial order working memory that takes ordinal numerosity and item identity as inputs for each point in the sequence. These inputs are integrated using gain modulation, leading to conjunctive item–position responses that can be used to extract the serial order of inputs. Thus, electrophysiological and computational studies support the idea that serial working memory requires a combination of item and position information at the cellular level.

Despite differences in proposed neural mechanisms, motor sequences and serial memory may have underlying sequence coding similarities. Both behaviors require a stable representation of sequence order that can be later reproduced, the ability to distinguish current from prior sequences, and an overarching serial structure to encode item information. The LPFC is one potential site for task-general sequence processing. Item–order associations and other sequence-related responses have been observed in this region in both serial working memory and motor sequence tasks (Barone & Joseph, 1989; Naya et al., 2017; Ninokura et al., 2004). General sequence-related responses may also exist in the IPS, which shows responses to ordinal numerosity in both perceptual and motor tasks (Nieder et al., 2006; Sawamura et al., 2002). Notably, inactivating this region impairs monkeys' ability to shift between actions after a set number of movements, suggesting that these responses play an important role in tracking serial position in ongoing sequences (Sawamura et al., 2010). Comparisons of neural activity across different sequential tasks in these areas and other regions will be important for distinguishing task-specific processing from general mechanisms for sequence coding.

In addition to these questions, investigations of ordinal coding will also benefit from an increasing focus on sequence coding at a population level. The mechanisms discussed thus far have focused on the responses of single or small groups of neurons. However, computations in the brain are not the product of single neuron activity, but patterns and transformation across populations. Interest in analyzing activity across neural ensembles as a whole has been supported by improved techniques for measuring activity simultaneously across neurons. These approaches may be particularly important in areas like LPFC, where neural responses are frequently modulated by multiple variables in a wide variety of tasks (Rigotti et al., 2013).

Two studies provide particular insight about sequence representation in LPFC at the population level. The first highlights the fact that ordinal position codes can be distributed across neuronal populations (Chiang et al., 2022). In a self-guided saccade task, information about serial position was dispersed more widely across neurons during more consistent sequences. Further, responses to adjacent sequence items overlapped, raising the possibility that these overlapping response patterns might provide information about both the sequence position and its relation to past and future steps (Conen & Desrochers, 2022). The second study used calcium imaging to measure the activity in large subpopulations of LPFC neurons during a cued motor sequence task (Xie et al., 2022). They found a modular representation of ordinal position at the population level,

characterized by the observation that activity across the population varied in nearly independent ways for each ordinal position (i.e., orthogonal dimensions of encoding). Within each ordinal position, responses to target positions have a consistent relational structure that parallels the spatial relationship of targets.

These results support the idea that ordinal position is an organizing principle for sequence representation in primates, and raise intriguing questions for future work. Many of these questions will be important to answer at both the single-neuron and population levels. Specifically, it will be valuable to investigate how neural responses vary with the length and complexity of sequences, how ordinal codes interact with relational structures, and how the structure of ordinal codes varies across task demands and brain regions. Answering these questions will be a fundamental step toward understanding the basic principles that underlie sequence processing in neural circuits.

Adjacency and Relational Codes

Responses to sequence items have mostly been studied in terms of ordinal position, but behavioral evidence indicates that sequence coding uses a combination of ordinal and relational codes (Allen et al., 2014; Petkov & ten Cate, 2020). Identifying relational codes can be challenging, since it relies on neural responses to particular combinations of items rather than a single item or sequence position. Additionally, experiments are often not designed to distinguish ordinal and relational structure. For example, when a limited number of fixed sequences are used, it is difficult to separate responses to particular item pairs from responses to the overall sequence pattern or item-in-position codes. Further, when neurons are modulated by both serial order and sequence structure, they are often primarily interpreted as serial order responses, without specifying how particular combinations of sequence elements influence their activity. The rank-order-selective responses discussed in "Neural Encoding of Ordinal Position" exemplify this tendency. Nevertheless, despite these factors, clear item-to-item associations have been identified in several sequential tasks.

The simplest examples of relational coding are adjacency-based responses. Barone and Joseph (1989) identified a range of context-dependent responses in the lateral prefrontal cortex (LPFC) during a motor sequence task, including neurons that responded to a particular target only when it was immediately preceded or followed by another specific target. Similarly, neurons in the supplementary motor area (SMA) and pre-SMA respond in the intervals between specific pairs of actions, regardless of their ordinal position (Shima & Tanji, 2000; Tanji & Shima, 1994). Adjacency-based responses such as these could be used for linking subsequent sequence steps, letting the execution of one item trigger preparation for the next (Tanji, 2001). These responses and more complex relational codes may be important to building associations across items in a sequence and defining the sequence structure as a whole.

Beyond adjacency, the distinction between ordinal and relational coding has been examined most explicitly through work on temporal context in sequence memory. Conceptually, temporal context combines ordinal and associative information into a general context code. Timing,

sequence position, and the pattern of past and future items all contribute to the context associated with each item (Howard & Kahana, 2002; Long & Kahana, 2019). At the neuronal level, the temporal context model predicts that items near each other in the sequence should have more similar response patterns than more temporally separated items. Consistent with this prediction, research in rats has found that neural ensembles in hippocampus had more similar response patterns to odors presented close to each other in a learned sequence (Shahbaba et al., 2022). Importantly, this similarity reflects activity patterns across neurons rather than in single cells. It is difficult to assess what leads to this relational similarity between items. Connecting these neural responses to results at a behavioral level will be necessary to determine which aspects of temporally drifting signals reflect a relational code with a functional role in sequences.

In summary, both behavioral and physiological evidence suggest that adjacency and relational codes are an important, and likely underspecified, part of sequence processing. Thus far, such codes are often observed in the same brain areas and local cellular regions as ordinal codes, though only rarely in the same neurons (Shima & Tanji, 2000). This observation underscores the importance of further research into adjacency and relational codes and how they interact with other features of sequence coding.

Boundaries

Ordinal and relational coding reflect the structure within a sequence but leave an important question: how does the brain indicate when a sequence begins and ends? One potential answer lies in the neural activity that is prominent at the boundaries of a sequence (figure 1C). This activity may mark the start and stop of sequences and reflect changes in information processing involved in sequence initiation and termination.

Difficulty beginning sequences of behaviors may indicate that a specific neural code controls such initiations. Some of the first insights into the neural origins of these signals came from studying Parkinson's disease. In addition to general slowness, motor deficits in Parkinson's disease are often characterized by difficulty initiating sequences of movements, such as walking. Though there is debate in the field, patients with Parkinson's disease may also have behavioral deficits when performing implicitly learned laboratory-based sequential tasks (for review, see Ruitenberg et al., 2015). Because Parkinson's disease is primarily caused by degeneration of the dopamine containing cells that project to the striatum of the basal ganglia, the striatum is a logical place to examine for sequence-initiation signals.

Early work identified the striatum as key to performing natural sequences of movements in both monkeys and rodents (rats: Aldridge & Berridge, 1998; Berridge & Whishaw, 1992; Pellis et al., 1993; monkeys: van den Bercken & Cools, 1982). Further, the dorsolateral striatum (DLS) in rodents (similar to the putamen in primates; Graybiel, 2008) was specifically shown to be necessary for sequence learning (Yin, 2010). This finding and similar ones have been followed up by many other studies investigating the correspondence between reinforcement learning and neural responses in the striatum (for reviews, see Dezfouli & Balleine, 2012; Niv, 2007; Smith &

Graybiel, 2014). Since most studies examining these variables have not focused on sequences (with some exceptions, which are noted), this article will not include an in-depth discussion of reinforcement learning variables in the striatum.

What neural code in the striatum could underlie its role in sequence initiation? As rodents complete the sequence of movements required to run a maze, one of the most salient features of striatal activity is that it occurs primarily at the beginning and end of that sequence to "bracket" the task (Barnes et al., 2005; Jin & Costa, 2010; Jin et al., 2014; Jog et al., 1999; Smith & Graybiel, 2013). Task-bracketing striatal activity develops over the same time course that animals learn to perform the sequential task automatically, suggesting a role for this activity in the learning and execution of these sequences. This sequence-bracketing activity is not limited to rodents or maze tasks, as it has been observed in monkeys performing sequential eye movement tasks as well (Desrochers et al., 2015; Fujii & Graybiel, 2003, 2005). These results suggest that task-bracketing neural activity in the striatum may be a dominant neural mechanism marking the beginnings and ends of sequences as they are learned.

The question then arises, what information does this bracketing activity encode? Limited evidence suggests that these signals provide motivation and evaluation information for the executed sequence. When rodents perform maze tasks automatically, inhibiting activity in the DLS precisely at the sequence start leads to dramatically decreased vigor (Crego et al., 2020). Striatal activity at the end of naturalistic sequences of eye movements in monkeys provides information about the cost (i.e., total distance) and benefit (i.e., whether or not reward was earned) (Desrochers et al., 2015). Notably, these cost signals may shape the animal's trial-by-trial behavior via reinforcement learning (Desrochers et al., 2010), suggesting that reinforcement learning signals can be applied to sequence learning not just as rewards but also costs. Work in rodents supports these findings, as end activity primarily reflects the previously rewarded location, rather than the upcoming location to be rewarded (Cunningham et al., 2021). Additionally, the ability to decode activity at the start and end of a sequence is diminished when it was not correctly completed, suggesting a relationship with motivation (Vandaele et al., 2021). Together, these studies suggest that sequence-bracketing activity reflects motivation at the beginning of sequences and evaluation at the end.

Most studies in this section have focused on task-bracketing activity in the striatum. Similar responses likely also exist in other sequence-related areas of the brain. One study observed such signals in the prefrontal cortex of monkeys performing a sequence saccade task (Fujii & Graybiel, 2003). The final phasic signal could not be explained by the anticipation of rewards or the turning off of stimuli, suggesting a true sequence end marker. Sequence-bracketing signals have not been studied in depth outside of the striatum, presenting an important avenue for future investigation.

Gestalt

Thus far, this article has discussed potential neural codes for different segments of a sequence (the "interior" steps and boundaries). In contrast, some representations of sequences do not reflect constituent parts, but the "gestalt," whole sequence (figure 1D). These responses must be

selective for specific, complete sequence patterns, though they may occur either throughout the sequence or during particular events. As described in the rest of this section, this type of gestalt coding has been found in both cortical and subcortical structures.

Perhaps the first activity that could be considered a gestalt sequence response was in cortical neurons that were selective for a particular item only when it was part of a specific sequence. During a spatial sequencing task, some cellular responses to specific sequence elements in the monkey LPFC, SMA, and premotor cortex depended on the sequences as a whole (Barone & Joseph, 1989; Mushiake et al., 1991). Similar coding, where responses to particular stimuli depend on the sequential context, have been observed in other brain areas, such as the SEF (Lu et al., 2002), and other tasks, such as more abstract motor sequences (Shima et al., 2007) and vibrotactile tasks (Rossi-Pool et al., 2016). Responses to the entire sequence have also been observed when a particular sequential rule is established (e.g., same, same, same, different) and then broken. Deviant responses, which theoretically would not exist without a representation of the sequence as a whole, have been observed in a variety of cortical and subcortical areas associated with sequential processing, including the PFC, striatum, SMA, and anterior insular cortex (Wang et al., 2015). The existence of such sequence-specific selectivity raises interesting questions as to what purpose this activity has. It could be part of a larger schema to keep track of or plan sequential actions on a more abstract level than item-by-item, but further research is necessary to evaluate this hypothesis.

In addition to activity during the sequence, sequence-specific activity has been observed in the period before a sequence is executed. In a delayed sequential reaching task, activity in the LPFC retains information about the spatial location and order of the items that will be targeted (Funahashi et al., 1997). However, in this experiment it was difficult to separate sequential coding from planning, because upcoming sequential movements could be planned during the delay period. Subsequent studies found that delay activity reflects the order of future items even if the subsequent responses could not be planned or predicted (i.e., order was dictated by shape, rather than location) (Ninokura et al., 2003). These studies suggest that the LPFC tracks sequential patterns as part of a general coding scheme, not only for the purpose of planning movements.

The role of sequence-specific activity in the LPFC and other cortical areas may contrast with sequence-specific activity in subcortical regions. Subcortical sequence-specific activity may be more relevant for the ongoing execution of sequences than their tracking or planning. By example, sequence-related activity in the striatum is not limited to the boundary activity previously discussed. The activity of neurons in the DLS of rodents correlates with running speed, position, and time, indicating that variables relevant to ongoing sequence execution are encoded there (Rueda-Orozco & Robbe, 2015). To interpret the role of this activity, it is necessary to consider the unique structure of striatal circuitry (extensively reviewed elsewhere, e.g., Graybiel, 2000). The striatum receives midbrain dopamine input that can act on one of two main pathways: the “direct” pathway via D1 dopamine receptors and the “indirect” pathway via D2 receptors. Classically, the direct pathway was associated with the disinhibition (or permitting) of kinetic movement while the indirect pathway was associated with the inhibition of kinetic movement. The broad classification into these two pathways of activity raises questions about the dynamics during ongoing and temporally extended movements such as sequences.

Mounting evidence suggests that neurons from both pathways are necessary for ongoing sequence performance. Both direct and indirect pathway neuron activity were necessary to initiate lever press sequences in mice (Jin et al., 2014). Further, direct pathway neuronal activity was often sustained or increasing ("ramping") throughout sequences, suggesting a role in ongoing dynamics, while indirect pathway neurons were often suppressed. Additionally, progress through a sequence could be decoded from striatal ramping activity (Vandaele et al., 2021). Other studies supported the idea that both pathways were necessary not only for sequence initiation, but also performance (Tecuapetla et al., 2016). These findings have been extended to more natural sequences. In freely moving mice, behavioral "syllables" (sequences of movements such as rearing or sniffing) were uniquely identified by activity from both direct and indirect pathway neurons (Markowitz et al., 2018). Lesioning them produced deficits in both the ordering and frequency of these "syllables." This and other studies that inhibited the action of indirect pathway neurons in the DLS (Garr & Delamater, 2020) support a role for the striatum during sequences that are more automatic or habitual, but perhaps not in more goal-oriented sequential behaviors. Evidence also suggests that each pathway may have selective control over specific subsequence elements (Geddes et al., 2018). Future studies will be necessary to understand the potential interplay between cortical areas such as the LPFC and striatum during sequences.

Another neural phenomenon that may reflect entire sequences is neural "replay." Replay, often associated with memory of spatial sequences in the hippocampus, is when patterns of activity present during the execution of behaviors is recapitulated after those behaviors are complete, either during rest or sleep. These replay events can be "forward," i.e., in the same order as they were experienced, or "backward," i.e., in the reverse order. There are many thorough reviews on this topic (e.g., Foster, 2017; Momennejad, 2020; Olafsdottir et al., 2018; Roscow et al., 2021) and several findings are relevant to sequence coding.

Most studies of replay have been performed in rodents. The memories referenced are sequential in nature in that animals must complete a spatial navigation task that can be conceptualized as visiting a sequence of locations. Replay has been observed in the hippocampus, medial prefrontal cortex (MPFC), and other brain areas and is thought to play a role in memory consolidation (Euston et al., 2007). Even though replay is observed concurrently in the hippocampus and MPFC, replay is independent in these two areas (Kaefer et al., 2020). Replay in the MPFC reflects more general locations and is positively correlated with behavioral performance, suggesting that it might play a role in flexible behavior. This suggestion has been extended by work that may show a role for replay-like events ("preplay") in planning future events (Pfeiffer & Foster, 2013); however, there is debate in the field. Though evidence is limited, replay also occurs beyond spatial navigation in rodents. Using electroencephalography (EEG), replay has been observed in humans that reflects the content of memorized sequences of visual objects (Huang et al., 2018). Together these studies support a role for the organized playback of neural activity patterns in performing sequential behaviors.

In summary, there are several ways that neural activity encodes sequences as a unitary construct, including sequence-specific selectivity, unique representations of ongoing sequences, and replay events. How these coding schemes may or may not work together, and whether they apply across all types of sequences, remains open to further investigation.

Neural Oscillations and Sequence Structure

While the majority of this article focuses on neural spiking activity, oscillations in the local electromagnetic field may also provide a useful window into sequence processing. Oscillations arise from multiple processes that affect electric potential in neural tissue, including synaptic currents, intrinsic voltage-dependent currents, and synchronous activity across neurons (Buzsáki et al., 2012). While the role of oscillations in sequence coding is not yet clear, several factors suggest the value of investigating them. Sequences evolve over time and require some mechanism for organizing events into an extended temporal structure. Theoretical work suggests that oscillations may play a key role in this process, providing an ongoing signal for computing the timing and order of events (Gu et al., 2015; Pöppel, 1997; van Wassenhove, 2016). Supporting this idea, several studies indicate that oscillations may contribute to important aspects of sequence processing, including relative item order and boundary positions.

The strongest evidence that oscillations contribute to sequence processing comes from theoretical and experimental work on nested oscillations. Computational work has shown that interactions between theta and gamma oscillations can create the serial structure used for encoding and generating sequences (Fukai, 1999; Horn & Usher, 1991; Jensen et al., 1996; Lisman & Jensen, 2013). These models are based on the fact that gamma oscillations (30–80 Hz frequency) complete several cycles over the course of a single theta cycle (4–10 Hz). In this model, the set of neurons that fires during each gamma cycle corresponds to one sequence element. Over the course of a theta cycle, each element activates in turn, matching the order of the sequence. Taken together, this structured relationship between theta, gamma, and neural spiking integrates information about event identity, relative order, and the sequence structure as a whole.

Nested oscillation models draw on the idea of phase precession. Phase precession describes the observation that neurons in the hippocampus and connected regions tend to fire at progressively earlier points in the theta cycle as subjects navigate through a space or progress through a task (Jones & Wilson, 2005; O'Keefe & Recce, 1993; Qasim et al., 2021; Reddy et al., 2021; van der Meer & Redish, 2011). In conjunction with nested oscillations, phase precession offers a mechanism to track the current sequence position and predict what comes next. Each time sequence position progresses, responses to each item shift in the theta cycle, so that the current sequence position always corresponds to a specific phase. The order of upcoming items relative to the current position is also represented at consistent points in the theta cycle, forming a robust representation of relative order that could guide sequential planning or memory.

Experimental evidence suggests that phase precession may be important for sequential processing. Theta precession of hippocampal firing in CA1 is associated with the use of sequence-based rather than location-based strategy in navigational task, suggesting that this activity pattern may reflect the structure of serially ordered events rather than the general mechanism for associative coding (Cabral et al., 2014). The structure of events may drive theta phase precession, as it was better explained by changes in task epoch rather than by time or spatial distance in the rat basal forebrain (Tingley et al., 2018). The relationship to sequences is more explicit in a study

showing that hippocampal ensembles encoding a memorized sequence of odors reactivated sequentially over the course of the theta cycle (Shahbaba et al., 2022). Complementing animal studies, phase precession has also been observed during image sequence memory in humans, first using magnetoencephalography (MEG) (Heusser et al., 2016) and subsequently at the single neuron level (Reddy et al., 2021). Reddy et al. (2021) also showed that neurons associated with each item in a sequence activate in order over the course of a theta cycle, with the strongest activation for the item at the current sequence position. These results build on other work showing that theta oscillations are important to learning and remembering sequence order (Bahramisharif et al., 2018; Crivelli-Decker et al., 2018; Hsieh et al., 2011; Roberts et al., 2013) and support the idea that the theta cycle carries information about event order and item-to-item relationships during sequence processing. Together, these studies provide compelling evidence that dual oscillations operate in parallel with the firing rate codes to encode the relational structure of sequences.

While phase precession and nested oscillations have primarily been studied in the context of hippocampal theta oscillations, in principle they could provide a general mechanism for organizing sequential structures. One study of serial order memory in the LPFC provides tentative evidence that information about the first stimulus occurs at an earlier phase in local field oscillations than the second stimulus (Siegel et al., 2009). Beyond traditional sequence paradigms, work in the nematode model organism *Caenorhabditis elegans* (*C. elegans*) suggests that nested oscillations may provide a general mechanism for organizing behavior and cognition across different time scales (Kaplan et al., 2020). However, information about temporal order stored in theta-phase relationships is not exclusive to sequence memory or sequential behavior. Serial order structures may be relevant when there is no distinct beginning or end of a sequence. Notably, a neural mechanism to build relationships between subsequent events may also be vital for the construction of spatial and conceptual maps (Rueckemann et al., 2021). While a detailed discussion of cognitive maps is beyond the scope of this article, it is worth noting the potential bidirectional relationship between maps and sequences: a map can be used to generate a sequence and sequences can be used to define a map.

There are some limitations to theta–gamma coding of sequences. First, this coding scheme assumes that sequences have a fixed set of items in a set order. It is unclear whether it would generalize to cases where one or more items in a sequence can vary or where the sequence is defined by more abstract interitem relationships. Second, theta–gamma coding implies a limit to the number of items that can be linked in a sequence, since it is constrained by the number of gamma oscillations that fit in a single theta cycle. Past work suggests that this factor may contribute to working memory capacity limits (Jensen & Lisman, 1998; Kamiński et al., 2011; Lisman & Idiart, 1995), though this interpretation is still uncertain (Malenínská et al., 2021). In principle, representations that account for patterns and regularities in sequential structure could compensate for this constraint through computational compression (al Roumi et al., 2021; Planton et al., 2021), though this possibility remains to be tested at the neural level.

Other neural oscillations may reflect important aspects of sequence processing. However, relatively few studies have focused on oscillations during sequences and variability in tasks and methodologies makes it difficult to directly compare results across experiments. Nevertheless, a

few findings stand out. First, changes in oscillations occur around sequence boundaries. Decrements in globus pallidus beta oscillations develop at sequence boundaries over the course of motor learning and may be involved in binding sequence elements (Ruiz et al., 2014). Theta power in frontal areas also increases at the ends of sequences, as observed using electroencephalography (EEG) (Crivelli-Decker et al., 2018). These results complement the changes in neural firing rate discussed in "Boundaries," and may provide a window into changes in information processing that occur at these transition points. Understanding the functional role of this activity during sequential tasks will be an important question for future work.

In addition to these findings, several studies have linked changes in oscillations with sequence processing deficits in human disorders (Liu et al., 2020; Meissner et al., 2018; Perfetti et al., 2010; Zheng et al., 2021). Differences in alpha (8–12 Hz), beta (13–30 Hz), and theta (4–10 Hz) oscillations have been observed between patients with Parkinson's and healthy controls during motor sequence learning (Meissner et al., 2018; Perfetti et al., 2010). Similarly, deficits in short- and long-term memory of visual sequences in patients with schizophrenia were accompanied by changes in alpha, beta, and theta power relative to controls (Liu et al., 2020; Zheng et al., 2021). Theta power in particular appeared to be associated with order memory, suggesting differences in sequence-related processing (Liu et al., 2020). In contrast, reduced alpha power occurred during both item and order memory, suggesting a more generalized deficit. While more work is needed to clarify how different frequency bands relate to underlying changes in sequence processing, these studies demonstrate that oscillations can be a valuable tool for studying sequence processing deficits in human disorders.

Taken together, the existing research on oscillations in sequence processing is promising but should be interpreted cautiously. Commonalities are difficult to extract from a small array of studies that have examined oscillations across a variety of tasks, methodologies, and brain regions. Broadly, changes in oscillations are associated with sequence processing (Bahramisharif et al., 2018; Chao et al., 2018; Crivelli-Decker et al., 2018; Hosaka et al., 2016; Hsieh et al., 2011; Pollok et al., 2014; Roberts et al., 2013; Ruiz et al., 2014; Zhuang et al., 1997) but specific results vary across experiments. For example, beta oscillations in M1 are suppressed during motor sequence learning and this suppression correlates with reaction time (Pollok et al., 2014). In contrast, beta power in parietal and occipital regions increases over learning in a visual sequence memory task and higher beta power correlates with faster reaction times in that paradigm (Crivelli-Decker et al., 2018). It is not yet clear which factors contribute to the different oscillation patterns observed across tasks or how these patterns relate to sequence processing as a whole. Further research will be necessary to examine the potential relationships among sequences and oscillations across brain areas and relate them to a theoretical framework of sequence coding.

In sum, studies point to a potentially intriguing mechanism for the engagement of sequential tracking with oscillatory activity in theta. Using this mechanism, successive items or locations can be bound in time with specific neural dynamics. However, it is uncertain how universal this mechanism may be in other sequential tasks or brain areas or how it relates to other forms of sequence coding. Other studies point to interesting links between sequences and oscillations in a

range of frequency bands but findings are often inconsistent. Investigating how patterns of oscillation reflect shared aspects of sequence processing across tasks will be a profitable direction for understanding how sequential structure is encoded in the brain.

Conclusion

Sequences are essential to daily life yet our knowledge of the underlying neural mechanisms is limited. This fact is all the more striking when considering the array of conditions that may be thought of as a disruption to sequential processes. This article highlights several categories of sequential coding: ordinal, relational, boundary, gestalt, and oscillatory. Across these categories, the majority of studies have addressed ordinal coding but this fact should be interpreted with caution. Any single coding scheme does not exclude others and it is likely that multiple coding schemes coexist across and within individual brain areas and even neurons. Similarly, the majority of the studies discussed involve motor sequences. Though it is improbable that motor, nonmotor, and abstract (rule-based) sequences have fully independent coding mechanisms, it is likely that there are important adjustments to coding schemes specialized for different sequence types. The studies discussed are also limited in the species that are considered, with the majority of experiments conducted in monkeys or rodents. While sequences have been studied in humans, most of these experiments use techniques that cannot resolve the neural code on a precise spatiotemporal scale. These gaps in the literature point to the need for research to expand our understanding of sequential coding across brain areas, sequence types, and species.

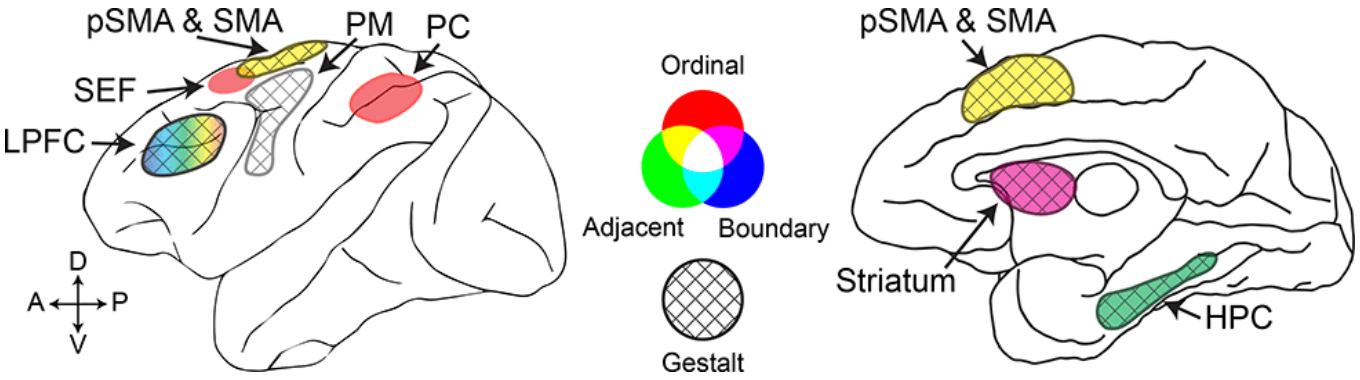

Figure 2. Schematic of macaque monkey brain areas involved in sequential coding. Left is a lateral view and right is a medial view. Note that all four types of sequential codes have been observed in the LPFC. A, anterior; P, posterior; D, dorsal; V, ventral. LPFC, lateral prefrontal cortex; SEF, supplementary eye fields; SMA, supplementary motor area; pSMA, pre-supplementary motor area; PM, premotor; PC, parietal cortex; HPC, hippocampus.

Despite these gaps in knowledge, a few commonalities can be extracted from the studies presented here (figure 2). First, the dorsolateral prefrontal cortex (DLPFC) in monkeys is a probable hub for sequential processing, as nearly all the presented codes can be found represented there. Other prefrontal cortical areas are likely more specialized for specific kinds of sequences (e.g., motor) or neural codes (e.g., ordinal). Division of labor in sequential processing may also be seen in the fact that the striatum is heavily involved in marking the beginnings and

ends of sequences. Aside from these observations, there are several brain areas that remain relatively unexplored or have been primarily studied to test a specific type of coding, such as the parietal cortex and hippocampus. Whether these and other areas specialize for a particular kind of sequential coding and how they interact in different behavioral contexts remain important open questions. Drawing these sequential connections, through the brain, space, and time, will be essential for furthering our understanding of behavioral structure in daily life.

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