Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Behavioral Sciences

# The neural architecture of prediction over a continuum of spatiotemporal scales

Michael T Gravina and Per B Sederberg

Theories of time and space in memory have traditionally focused on their role in dividing experience into discrete episodes, despite the arbitrary nature of these divisions. We offer an alternative characterization that focuses on the fundamentally *predictive* role of perception and memory. In this account, perceptual hierarchies in sensory cortex detect patterns of feature-change across a logarithmic continuum of scales in time and space, which allows them to efficiently converge on nuanced, yet short-range, predictions of the present situation. Time and space emerge from this continuum as representations of feature-distance that provide a measure of the relevance of non-simultaneous experiences, allowing for long-range associations, mental time-travel, and predictions that go far beyond the immediate moment. This reframing of the nature and role of time and space in memory has implications for both the interpretation of existing findings and the design of future experiments.

**Address**
Department of Psychology, The Ohio State University, USA

Corresponding author: Sederberg, Per B (sederberg.1@osu.edu)

**Current Opinion in Behavioral Sciences** 2017, **17**:194–202

This review comes from a themed issue on **Memory in time and space**

Edited by **Lila Davachi** and **Neil Burgess**

**http://dx.doi.org/10.1016/j.cobeha.2017.09.001**

## Introduction

Humans are drawn to strict divisions and clear categories, which help us to simplify the otherwise intractable complexities we encounter in the world. Yet these same simplifying constructs may become a stumbling block to true comprehension when they impoverish *meaningful* complexity. A foundational concept in the field of memory is the categorical distinction between episodic and semantic memory [1]. However, the very notion of an episodic memory presupposes that an experience is bound to a specific time and space to produce discrete 'episodes' [2]. This distinction rests on deeper assumptions that 'time' and 'space' actually *exist* in the brain as representational scaffolds onto which experience can be bound. Moreover, the temporal and spatial components of episodic memory are frequently treated in isolation [3], even though it has not been firmly established that they are meaningfully separable.

We argue here that the apparent division of experience into discrete episodes is actually an over-simplification within the basic mechanisms of perception and memory. The flow of experience is continuous across temporal and spatial scales, from milliseconds to decades, and from millimeters to hundreds of kilometers. Given the need to adapt predictively across this full continuum of scales, the basic representations of our experience, and our episodic memories for that experience, must also span this continuum. This proposition does not imply that there are no meaningful boundaries in our experience (see [4] for discussion), but only that the establishment of a spectrum of spatiotemporal scales necessarily precedes, and provides the fundamental substrate for, the definition and identification of such boundaries.

In discussing this idea we also challenge the current discourse on representation in hierarchical sensory cortical streams, such as the ventral temporal stream, in order to move away from models of discrete regional specialization toward a continuous spectrum of scale-sensitivities. Finally, we position the neural representations of time and space as emergent, rather than elemental, properties in the brain, founded on a gradient of experiential scales established in the architecture of the medial temporal lobe.

To ground this proposal, we must first discuss how our senses and all layers of perceptual processing are basically change-detectors operating on continuous streams of low-level features. From this starting point, we must solve the evolutionary challenge of preparing adaptively for the future by making predictions on these feature-changes. Detailing how we accomplish this *efficiently* will lead us to the alternate memory paradigms that we champion here.

## Prediction machines

### The function of perception is to predict changes in sensory streams

We are accustomed to think of the brain primarily as a device for recognizing and responding to the higher-level wholes of exogenous experience: not only object recognition [5], but also recognition of scenes, events, and the subjectively 'real' dimensions of time and space. In this framework, sensory processing streams in cortex are conceptualized as hierarchies of distinct processing centers, each of which responds to a discrete higher-order category. For example, observations that anatomical loci in the ventral temporal cortex respond to specific visual categories (e.g., lateral occipital cortex, LOC, for objects [6], parahippocampal place area, PPA, for scenes [7], among others) have been taken as evidence that the primary role of these loci is to *represent* those categories [8].

But a living organism does not have direct access to any of these complex structures in its environment. It must extract them from experience mediated entirely by the streams it receives through its sensory receptors, each of which conveys only the intensity of a simple sensory *feature*, like the luminance of light or the pressure of dermal contact, as it varies continuously over time. Thus, at the input level, neither category, nor time, nor space, nor any of the other high-level ‘bins’ of content exist to the brain, only the content itself (a set of continuous, single-feature inputs). Furthermore, as we argue below, recognizing high-level phenomena is not even perception’s fundamental *objective*, but is rather an instrumental byproduct of a living system’s attempt to predict relevant fluctuations in these sensory streams in an energy-efficient manner.

The evolutionary fitness of a living system depends on its ability to efficiently reduce its entropy through interactions with its environment. Even though the universe exhibits a global trend toward increasing entropy, a living system can maintain or even reduce its own entropy, and therefore persist and propagate in the face of constant, disordering external perturbations, by identifying and exploiting *likely* environmental changes. In other words, they can proactively adapt themselves to survive energetic fluctuations from the environment, thereby *correlating* their own behavior with the environment [9–11]. Thus, the environment can be thought of as a state machine, and the organism’s principal adaptive challenge is to infer and encode that state machine’s transition probability structure, using its set of sensory feature inputs as the only available proxy for learning those states and transitions [12]. The resulting correlation between information stored in the system and probabilistically likely regularities in the environment can be considered the rudiment of memory that is harnessed by a living system to guide behavior.

So the primary function of perception is not actually to represent familiar categories of *content*, but rather to register and predict *changes* in that content. This accords well with the established principle that repetitive content is disregarded through neural habituation, with the retained information representing only the change from what was predicted [13]. Thus, every aspect of the architecture of our sensory processing must ultimately serve to *predict the future of a continuous stream of sensory features based on changes it has observed in that stream in the past.*

## Perceptual cortex differentiates scales, not categories

We therefore have reason to doubt the characterization of perceptual hierarchies as chains of loci representing discrete categories and properties. To the extent perceptual hierarchies do construct discrete representations of higher-order categories, we hold that it is likely only a mechanism in service of *prediction* of feature changes across a *continuum of scales*. In this view, each interval along the continuum of perceptual processing in the ventral temporal stream and medial temporal lobe is simply specialized for learning the patterns of feature-change that occur over a particular interval of temporal and, as we will argue below, spatial scales [14–17].

Take, for example, an office. An office is not a discrete whole, but rather a collection of objects (e.g., walls, floor, computer, coffee mug, desk, chairs, bookshelves, among others). Neurally, an office as a whole tends to activate scene-sensitive regions such as PPA, while its constituents activate object-sensitive regions such as LOC. We assert that this difference in selectivity stems from the duration of time over which each region integrates the continuum of scales to register behaviorally-relevant changes in sensory features.

The behavioral significance of timescale can be easily illustrated in the office example depicted in Figure 1. The timescale over which our senses stably interact with individual objects, such as a coffee mug, is short; our eyes, as they make numerous saccades around the area, only process the mug for a matter of partial or full seconds, and our hands typically manipulate the mug for similar periods. On these short timescales, in which we must predictively guide our interactions with individual objects, it is necessary to maximally distinguish between, say, the cup and a stapler, hence the regional specialization of LOC for representing and detecting changes in patterns on this scale. By contrast, we may remain in the general office environment from several full minutes up to several hours, and even as the constituent objects repeatedly pass in and out of perception on their smaller timescales, we must integrate over all those features to extract a stable, longer-lasting context from the scene as a whole. In this latter case we would want to maximally distinguish this office scene context from others, such as a supermarket, a street corner, or a beach [18•]. This idea of a continuum of representational scales is shared by other recent work on Temporal Receptive Windows (TRWs) for representing narratives, whereby regions that integrate over large TRWs have highly divergent representations when individuals interpret narratives that differ in only a few words on a finer scale, but where those small