[Editorial] More than the sum of its parts: perception and neuronal underpinnings of sequence processing

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More than the Sum of its Parts: Perception and Neuronal Underpinnings of Sequence Processing

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Making sense of the world requires that we recognise and track temporal structure in the unfolding sensory input. The physical nature of objects, animate or not, introduces patterned, often predictable signals that sensory systems have evolved to exploit. Such temporal structure can be used to distinguish independent objects, decode their identity and meaning, track and predict their evolution across time, and rapidly respond to unexpected events.

It would be conceivable that sensory systems simply process each successive snippet of sequential information independently. However, there is ample evidence that this is not the case. An early example was drawn from musical melodies, which were observed to retain their identity in spite of various manipulations in the notes, such as multiplying the frequency of each note by a common factor (von Ehrenfels, 1937). This example of invariance of the melody's identity beyond the properties of each single element was advocated to be "Gestalt", a property of the whole that was more than the sum of its parts. This is obviously not restricted to music: the sound of a single footstep in isolation is meaningless, but a sequence of these sounds contains information about its agent's identity, direction, speed, posture and intentionality, and even the nature of the surface being walked on (Bregman, 1990). In vision, biological motion can be suggested by motion sequences of a few dots (Johansson, 1973). In touch, contact with an object elicits a sequence of skin vibrations whose temporal structure provides information about object texture and motion (Weber et al., 2013).

Perhaps as a result, it seems that brains fundamentally understand the world in terms of its temporal structure. How this occurs – how our perceptual experience of sequential stimuli is underpinned by neuronal activity – is the theme of this Special Issue. Its constituent papers ask basic questions such as: What makes any sensory sequence more than the sum of its parts? How are sequence-specific processes reflected in the ensuing patterns of neural activity?

A possible impediment to satisfactorily answering such deep questions is that, historically, the study of different aspects of sequence processing has occurred in relative isolation, from low-level mechanisms of perception to higher-level cognition. Even within the perceptual realm, approaches to the study of sequence processing have involved separate modalities, timescales, model systems, and levels of description. Whether common principles apply has therefore been hard to ascertain (Dehaene et al., 2015; Paton and Buonomano, 2018). Yet identifying and analysing such principles would be crucial, just to cite one instance, to the ongoing enterprise that seeks to understand the brain as a general statistical learning machine and explain perception as a process of context-driven inference (Friston, 2005; Bastos et al, 2012; Clark, 2013; Hohwy, 2013; Rao & Ballard, 1999).

The present Special Issue is an attempt to establish bridges between levels of investigation, sensory modalities, and temporal granularity, in order to address the emerging hypothesis that different forms of sequence processing are intertwined in their computational implementation and perhaps their neural substrates.

Sequence processing has been most explicitly investigated in the sense of hearing, perhaps following von Ehrenfels's impetus but also because of the fundamental reliance of auditory signals on patterning across time (Griffiths and Warren, 2004). In this issue, the auditory modality is covered by several contributions. Rajendran et al review the neurophysiology of rhythm perception –including beat and timing– using responses to music as a test case for general principles of temporal processing. Gandras et al demonstrate electrophysiological signatures of how the brain parses ambiguous speech sequences into representations of concurrent speakers, in a busy acoustic scene. Demany and Semal review work on "frequency shift detectors", the sequence-specific mechanisms which are hypothesized to underlie implicit binding over time of successive sounds into perceptual streams. Todd et al show a curious phenomenon in the learning of patterning in sound sequences, in which initial uncertainty ("first impressions") fundamentally conditions the later perception of sound novelty.

In general, the concept of surprise or prediction error is a key element in theories of predictive coding. Much of the work addressing prediction errors has been carried out in the auditory modality, due to the availability of powerful paradigms such as the mismatch negativity (Naatanen et al, 2007). But is there sufficient evidence that the auditory system implements predictive coding? Heilbron and Chait ask this provocative question in their review.

The effects of expectation are also prominent in visuomotor learning, where Heideman et al show that temporal expectation facilitates (i.e. makes for a more agile) motor response during learning of visual-motor sequences. Oculomotor learning is also the subject of Gonzalez and Burke's study, which identifies brain areas that respond during production of short and long ocular pursuit sequences.

In the tactile modality, Saal et al highlight how sequential representations of sensory objects –in this case, temporal patterns of spikes in fingertip primary afferents– can be invariant to physical contingency –here, contact force– thus allowing the emergence of a robust percept.

Finally, a series of contributions demonstrate fundamental similarities in sensitivity to sequence structure across modalities and species. Working in macaques and humans, Milne et al show similar capacities for statistical learning of "artificial grammars" (Wilson et al., 2017) in the auditory and visual modalities. Kang et al highlight how the rapid incidental learning of repeated random patterns transfers across auditory, visual and tactile modalities. Masquelier proposes a model showing that spike-timing dependent plasticity, a general form of synaptic plasticity, allows neurons to become sensitive to input patterns that last longer than the neuron's membrane integration timescale. Aizenman et al find that enhanced capacities for recognising auditory patterning, acquired through training in musicians, also boost visual performance. Kondo et al report that the binding of sequential events in both hearing and vision are similarly affected by aging and by biochemical depletion. A review by Himberger et al compellingly identifies a hierarchy of core computational principles for temporal processing across cortex, which could underlie these similarities across modalities.

To summarize, it seems obvious but still worth remembering that temporal patterning is inherent to the structure of the natural world and, thus inevitably, also to the operation of the brain. Sequential processing encompasses the representation of sensory stimuli, the dynamic flow of information across the brain, the production and control of series of actions, and the storage and online retrieval of information in memory. We believe that considering all of these aspects together rather than separately will lead to significant advances in understanding perception and core principles of brain function. The present conjunction of papers identifies multiple commonalities, across levels of investigation, which we hope will prompt further enquiry into these fundamental organizational principles.

References

Bastos AM, Usrey WM, Adams RA, Mangun GR, Fries P, Friston KJ (2012), Canonical microcircuits for predictive coding. Neuron 76: 695–711.

Bregman AS (1990), Auditory Scene Analysis: The Perceptual Organization of Sound. Cambridge, MA: Bradford Books, MIT Press.

Chambers C, Akram S, Adam V, Pelofi C, Sahani M, Shamma S, Pressnitzer D (2017), Prior context in audition informs binding and shapes simple features. Nature Communications 8: 15027.

Clark A (2013), Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behav Brain Sci 36: 181–204.

Dehaene S, Meyniel F, Wacongne C, Wang L, Pallier C (2015), The neural representation of sequences: From transition probabilities to algebraic patterns and linguistic trees. Neuron 88: 2-19.

Ehrenfels von C (1937), On Gestalt-qualities. Psychological Review 44:521–524.

Friston K (2005), A theory of cortical responses. Philos Trans R Soc Lond B Biol Sci 360: 815–36.

Griffiths TD, Warren JD (2004), What is an auditory object? Nat Rev Neurosci 5: 887-92.

Hohwy J (2013), The predictive mind. Oxford: Oxford University Press.

Johansson G (1973), Visual perception of biological motion and a model for its analysis. Percept Psychophys 14: 201–211.

Näätänen R, Paavilainen P, Rinne T, Alho K (2007), The mismatch negativity (MMN) in basic research of central auditory processing: a review. Clin Neurophysiol 118: 2544–90.

Paton JJ, Buonomano DV (2018), The neural basis of timing: Distributed mechanisms for diverse functions. Neuron 98: 687-705.

Rao RPN, Ballard DH (1999), Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nat Neurosci 2: 79–87.

Weber AI, Saal HP, Lieber JD, Cheng JW, Manfredi LR, Dammann JF, 3rd, Bensmaia SJ (2013), Spatial and temporal codes mediate the tactile perception of natural textures. Proc Natl Acad Sci U S A 110: 17107-12.

Wilson B, Marslen-Wilson WD, Petkov CI (2017), Conserved sequence processing in primate frontal cortex. Trends Neurosci 40: 72-82.