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The Neural Representation of Sequences: From Transition Probabilities to Algebraic Patterns and Linguistic Trees

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A sequence of images, sounds, or words can be stored at several levels of detail, from specific items and their timing to abstract structure. We propose a taxonomy of five distinct cerebral mechanisms for sequence coding: transitions and timing knowledge, chunking, ordinal knowledge, algebraic patterns, and nested tree structures. In each case, we review the available experimental paradigms and list the behavioral and neural signatures of the systems involved. Tree structures require a specific recursive neural code, as yet unidentified by electrophysiology, possibly unique to humans, and which may explain the singularity of human language and cognition.

As early as the 1950s, the problem of serial order was identified by Karl Lashley as one of the pressing questions that behavioral and neural sciences should address (Lashley, 1951). The problem can be stated succinctly: how does the brain encode temporal sequences of items, such that this knowledge can be used to retrieve a sequence from memory, recognize it, anticipate on forthcoming items, and generalize this knowledge to novel sequences with a similar structure?

Lashley noted that language perception and production, but also bird song or rat spatial navigation behavior, presented special problems for the then-dominant view of associative chains. Humans and other animals do not simply associate each successive item with the next one at a particular delay, but they also grasp abstract multi-item sequential structures. This faculty is most evident in human language: even a single word such as "inexplicably" may consist in a nested structure of morphemes [[in-[explic-able]]-ly].

Sixty years of linguistic analysis have confirmed that an accurate representation of language requires the postulation of nested tree structures (Chomsky, 1956). In parallel, behavioral and neurophysiological analyses of much simpler paradigms, involving for instance sequences of tones or gestures, have revealed a rich array of responses that go way beyond the simple associative chain (Restle, 1970; Restle and Brown, 1970). The purpose of the present article is to review those behavioral and neural findings and to provide a minimal taxonomy of brain mechanisms that any accurate model of sequence processing should emulate. We argue that there is evidence for a minimum of five distinct systems capable of representing sequence knowledge at increasing degrees of abstraction (Figure 1):

- Transition and timing knowledge: knowledge of the transitions from one item to the next (i.e., the identity and

approximate timing of the next item relative to the preceding ones).
- Chunking: the grouping of several contiguous items into a single unit that can be manipulated as a whole at the next hierarchical level.
- Ordinal knowledge: knowledge of which item comes first, which comes second, and so on, independently of their timing.
- Algebraic patterns: abstract schemas that capture the sequential regularities underlying a sequence of items; for instance, the word "cocolith" comprises twice the same syllable followed by a different one (AAB pattern).
- Nested tree structures generated by symbolic rules: at this level, characteristic of human languages, a sequence can be "parsed" according to abstract grammatical rules into a set of groupings, possibly embedded within each other, forming a nested structure of arbitrary depth, and possibly involving the recursive use of the same elements at multiple levels; an example is the parsing of the mathematical equation $a + b \sin \omega t$ as a nested set of parentheses $(a+(b (\sin (\omega t))))$ or, equivalently, a tree structure:

$$a+b \sin \omega t$$

Transition and Timing Knowledge

Many animal species are able to represent the time intervals between sensory or motor events and use these temporal representations in simple computations. An excellent example is provided by a temporal choice task that has been used to probe temporal and probabilistic calculations in mice and humans (Balci et al., 2009; Kheifets and Gallistel, 2012). On each trial,
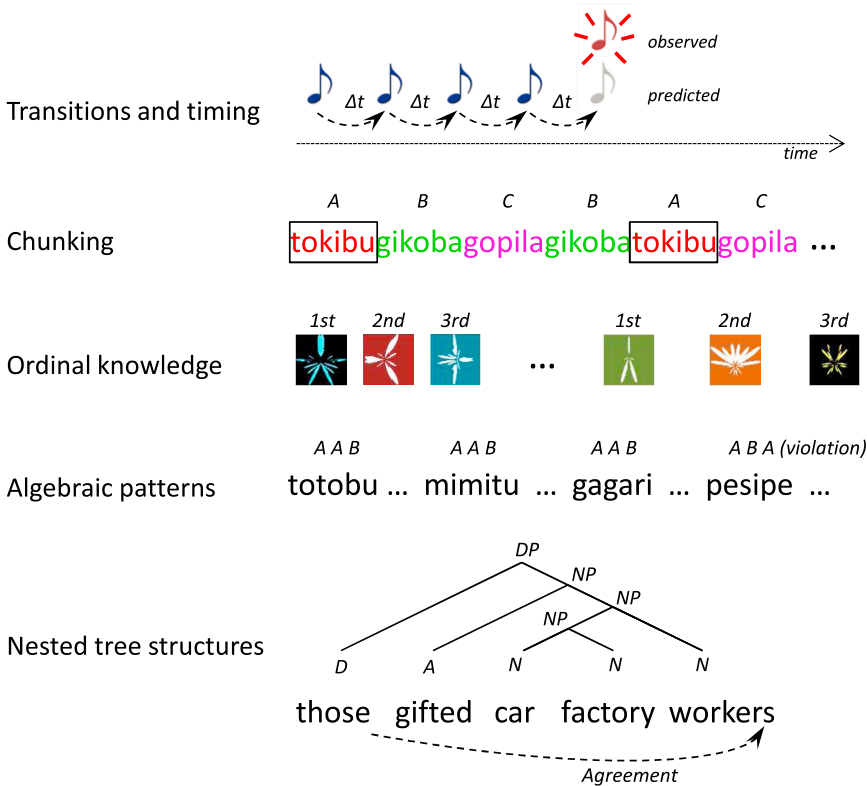
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Transitions and timing

Chunking

Ordinal knowledge

Algebraic patterns

Nested tree structures

Figure 1. Illustration of the Proposed Taxonomy of Sequence Knowledge
According to our proposal, incoming sequences can be encoded internally at one of five possible levels of abstraction: (1) transitions between specific items at a specific time delay; (2) a sequence of "chunks," for instance reproducible words within a stream of syllables; (3) an ordered list, with explicit knowledge of which item comes first, second, third…; (4) an algebraic pattern such *AAB*, indicating that the first two items are identical while the third is different; and (5) a tree structure, with constituents nested inside other constituents, as observed in human languages.

one of two events may occur: either, 3 s after trial initiation, a left lever press is rewarded or, 9 s after trial initiation, a right lever press is rewarded. Participants quickly learn to adjust their anticipations, first turning to the left lever, then if nothing occurs, switching to the right lever. The results show that mice and humans carefully and near-optimally adjust the duration after which they switch levers, taking into account both the imposed temporal delays and the internal and external uncertainties over which event is most likely. Because the behavioral switches occur after a roughly fixed delay, which is not cued by any sensory event, it implies that the organism must maintain an internal representation of elapsed time and base its decisions on a comparison of elapsed and memorized times of expected events. This and many other similar paradigms imply that time is one of the dimensions over which animals may compute (Gallistel, 1990).

A characteristic signature of this representation is its approximate nature, subject to scalar variability, also termed Weber's law (Gibbon, 1977; Gibbon et al., 1997): the imprecision (standard deviation) with which a delay is encoded is directly proportional to its duration, such that increasingly longer delays are represented with proportionally larger variability.

It is likely that, whenever we hear a sequence of stimuli $X_{1..n}$, their transitions $X_i \rightarrow X_{i+1}$ and corresponding time delays are automatically and unconsciously registered, and that such knowledge of temporal delays therefore constitutes a first level at which incoming sequences are internally represented. The main paradigm that has been used to demonstrate this is the auditory oddball paradigm, in which a reproducible series of auditory stimuli is presented at regular intervals (Figure 2A). Crucially,

when one of the stimuli is unexpectedly replaced by another one, the brain emits a mismatch response (MMR) (i.e., an activation increasing with the degree of mismatch between the expected and obtained stimuli) (Garrido et al., 2009). Most strikingly, a similar brain response is observed when the expected stimulus is omitted, peaking roughly at the time when the stimulus should have occurred (Raij et al., 1997; Wacongne et al., 2011). Such omission signals, which have been traced back to auditory cortices, incontrovertibly demonstrate that sensory circuits can internalize the timing of a regular sequence and generate an endogenous response in the absence of any sensory input, purely in anticipation of an expected event. Variations in stimulus onset asynchrony indicate that this capacity to store temporal intervals operates up to delays of 2–5 s, with a decreasing amplitude and an increasing temporal dilution compatible with scalar variability (Mäntysalo and Näätänen, 1987; Pegado et al., 2010).

Another remarkable characteristic of temporal sequence encoding is its automaticity. MMR responses continue to be emitted even of the absence of attention, awareness of changes, or even of any consciousness, as during coma, vegetative state, or when falling sleep (Bekinschtein et al., 2009; Strauss et al., 2015). In spite of this automaticity, MMR studies have revealed that auditory sequences are internally stored with a great variety of details. Changing the presence, pitch, identity, intensity, or duration of the expected stimuli all lead to MMRs localized to distinct sites in primary and secondary auditory cortices as well as prefrontal cortex (PFC) (e.g., Giard et al., 1995). Precisely timed neuronal responses, including mismatch and omission responses, have also been observed in many other modalities, e.g., with visual stimuli in early visual cortex (Gavornik and Bear, 2014; Namboodiri et al., 2015) and inferotemporal cortex (Meyer and Olson, 2011; Meyer et al., 2014), with action sequences in premotor cortex and basal ganglia (Bartolo et al., 2014; Crowe et al., 2014; Mello et al., 2015; Merchant et al., 2011), and with anticipated reward in dopamine neurons (Fiorillo et al., 2008). It is therefore likely that the neural mechanisms for encoding temporal knowledge are replicated in several brain circuits that operate automatically and in parallel to each other.