



A dual-pathway neural architecture for specific temporal prediction



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ARTICLE INFO

Article history:

Received 7 January 2013
Received in revised form 19 July 2013
Accepted 15 August 2013

Keywords:

Prediction
Temporal processing
Cerebellum
Thalamus
Oscillation

ABSTRACT

Efficient behavior depends in part on the ability to predict the type and the timing of events in the environment. Specific temporal predictions require an internal representation of the temporal structure of events. Here we propose that temporal prediction recruits adaptive and non-adaptive oscillatory mechanisms involved in establishing such an internal representation. Partial structural and functional convergence of the underlying mechanisms allows speculation about an extended subcortico-cortical network. This network develops around a dual-pathway architecture, which establishes the basis for preparing the organism for perceptual integration, for the generation of specific temporal predictions, and for optimizing the brain's allocation of its limited resources. Key to these functions is rapid cerebellar transmission of an adaptively-filtered, event-based representation of temporal structure. Rapid cerebellar transmission engages a pathway comprising connections from early sensory processing stages to the cerebellum and from there to the thalamus, effectively bypassing more central stages of classical sensory pathways.

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1. Introduction

'Ready, set, go!' In the appropriate context, such a simple sequence of acoustic events evokes complex behavior. It prepares the organism to perform a specific type of action at a specific time. Ideally, this action is adequate to the goal and triggered in time, i.e. it is neither performed too early nor too late. These processes ultimately require predictive adaptation defined as the adjustment of overt and covert behavior to future events.

On the one hand, predictive adaptation may pertain to the form, or formal structure, of events (see [Glossary](#); [Fig. 1](#)), e.g. 'set' is associated with 'ready'. On the other hand, it may pertain to the temporal structure of events. The latter is twofold: (i) 'set' will follow 'ready',

or (ii) the temporal relation of 'ready' and 'set' will approximate the temporal relation of 'set' and 'go'. Both render predictive adaptation a powerful mechanism in optimizing an individual's behavior beyond mere reaction. Accordingly, a predictive bias is increasingly recognized as fundamental to brain function ([Bar, 2007](#); [Bubic et al., 2010](#); [Friston, 2005](#)). From this perspective, the brain is a constructive organ that predicts environmental demands in order to efficiently deploy its limited resources ([Engel et al., 2001](#); [Friston, 2012](#); [Raichle, 2010](#)).

The above example suggests that formal and temporal structure are conceptually independent, but may interact to optimize adaptive behavior. To this end, the predictive mechanism has to adjust to novel situations and events in real time and it has to be able to infer future events from perceived regularity in formal and temporal structure. Predictive adaptation is probably most efficient when it pertains to a specific point in time. Such specific temporal prediction needs to be distinguished from temporal order, which does

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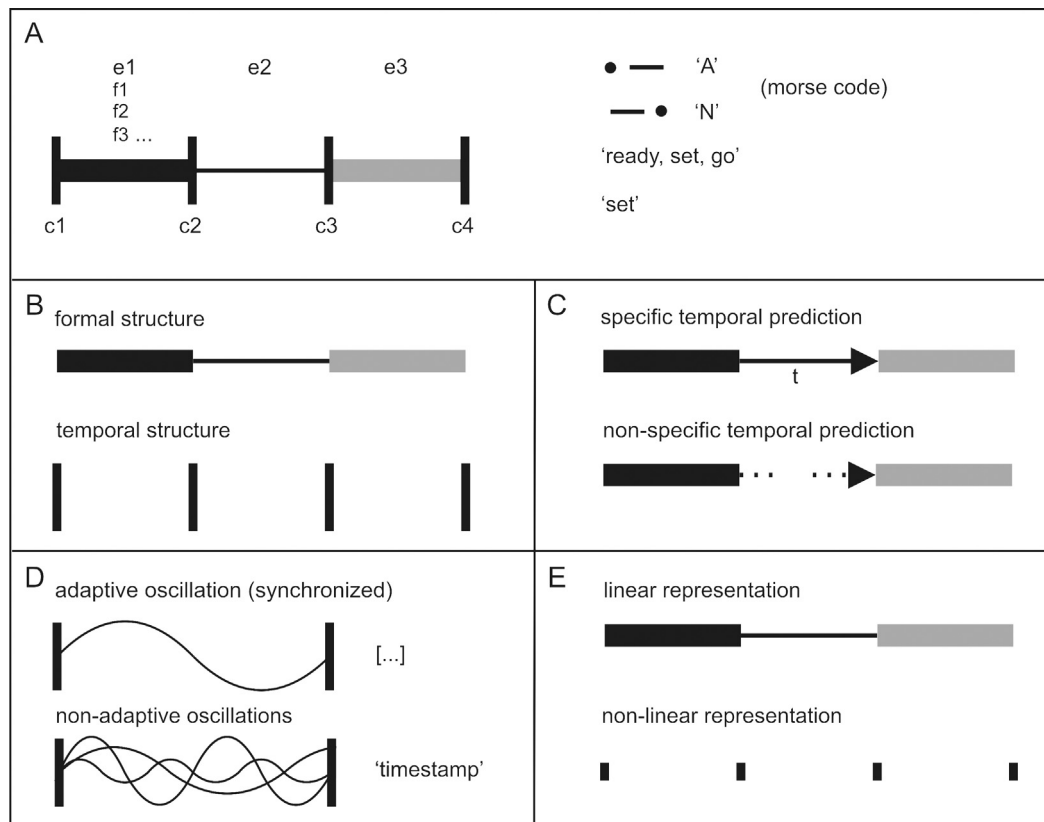


Fig. 1. Type and timing of events. (A), (B) Dynamic signals imply interplay of persistence and change, expressed in the concepts of succession (two events are perceived as different) and duration (the interval between two events; [Fraisse, 1984](#)). Events (e) can be described in terms of their formal structure (consisting of a set of features (f) which allow for their identification). Changes (c) in formal structure generate the temporal structure of successive events. For example, in morse-code, the alternation of gap events with short and long events with a temporal relation of 1:1:3 is used to encode messages. Successive events may develop on different time-scales in parallel, e.g., 'ready, set, go' but also 'set' instantiate three successive events, albeit with differing temporal structure. (C) Predictions concerning successive events can be temporally specific if the temporal relation between events is known (t), or non-specific, if the temporal relation between events is unknown, with several variants of uncertainty implied in neuropsychological contexts ([Kahneman and Tversky, 1982](#)). Specific temporal prediction may be more efficient on particular time-scales, while it may be irrelevant on others. In order to obtain knowledge about temporal structure and to use this information to optimize behavior, it is necessary to generate some internal representation of temporal structure. (D) Dynamic attending theory ([Large and Jones, 1999](#)) suggests that the allocation of attention can be modeled as an adaptive oscillatory process. Phase- and period adjustment of this oscillation based on the temporal relation between two events provides the opportunity to predictively focus attention. The striatal beat frequency model ([Matell and Meck, 2004](#)) proposes that the activity of nonadaptive oscillations (following an initial phase reset) provides a 'timestamp' for a specific interval (coincidence detection). Such an explicit encoding of intervals allows for evaluation and storage of temporal structure as a potential basis for predictive adaptation. (E) Linear representations (reflecting more continuous sampling of a dynamic signal) may be necessary to unambiguously identify an event, whereas a non-linear representation may provide an unambiguous representation of temporal structure.

not automatically suggest temporal specificity. Crucially, specific temporal prediction implies some form of an adequate neural representation of temporal structure and temporal relations. However, it is still unclear how precisely the brain deals with this task. The issue is further aggravated by the fact that different mechanisms may contribute to one and the same goal: the ability to exploit temporal structure to generate temporal predictions to optimize adaptive behavior. This ability most likely arises from the interaction of different functions and different brain areas, which may demand a revision of classical concepts starting with primary sensory processing and extending to higher level cognitive processes in order to explain the phenomenon.

2. Representations of temporal structure

One possibility to represent temporal structure is via synchronization, defined as coupling between different oscillations that start to oscillate with a common frequency ([Pikovsky et al., 2001](#); [Fig. 1](#)). Oscillations occur naturally in neurons and in neuronal populations. Since oscillations imply repetitive behavior, they are useful for temporal prediction (the 'when' aspect of events)—in

principle independent of formal prediction (the 'what' aspect of events; [Buzsáki and Draguhn, 2004](#)).

Limited cognitive resources such as attention and memory are associated with neural oscillations across different frequency bands ([Jensen et al., 2007](#)). These constructs interact and overlap ([Awh et al., 2006](#); [Gazzaley and Nobre, 2011](#)) and partly determine the quality of other cognitive operations. For example, attention enforces rhythmic shifting of neuronal excitability, thereby amplifying responses to events in a stimulus stream ([Lakatos et al., 2008](#); [Schroeder et al., 2008](#)). In other words, enhanced responses to attended events result from the alignment of high-excitability oscillation phases that are phase-locked to temporal structure ([Schroeder and Lakatos, 2008](#)). This view is also central to the *entrainment hypothesis* put forward in *Dynamic Attending Theory* (DAT; [Jones, 1976](#); [Large and Jones, 1999](#)). According to DAT, the allocation of attention proceeds in a stimulus-driven, oscillatory fashion. Adjusting the phase and the period of an adaptive oscillation ([McAuley, 1995](#)) establishes a synchronized, future-oriented attending mode if the temporal structure of the environment is 'coherent' (non-arbitrary). This stands in contrast to an analytic attending mode that is employed if temporal structure is incoherent ([Jones and Boltz, 1989](#)). DAT thus provides a framework for

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