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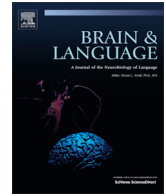
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Contributions of cerebellar event-based temporal processing and preparatory function to speech perception



Michael Schwartz¹, Sonja A. Kotz^{*,1}

School of Psychological Sciences, University of Manchester, Manchester, United Kingdom

Dept. of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

Faculty of Psychology and Neuroscience, Dept. of Neuropsychology and Psychopharmacology, Maastricht University, Maastricht, The Netherlands

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ABSTRACT

The role of the cerebellum in the anatomical and functional architecture of the brain is a matter of ongoing debate. We propose that cerebellar temporal processing contributes to speech perception on a number of accounts: *temporally precise cerebellar encoding* and rapid transmission of an event-based representation of the temporal structure of the speech signal serves to *prepare areas in the cerebral cortex* for the subsequent perceptual integration of sensory information. As speech dynamically evolves in time this fundamental preparatory function may extend its scope to the predictive allocation of attention in time and supports the fine-tuning of temporally specific models of the environment. In this framework, an oscillatory account considering a range of frequencies may best serve the linking of the temporal and speech processing systems. Lastly, the concerted action of these processes may not only advance predictive adaptation to basic auditory dynamics but optimize the perceptual integration of speech.

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1. Introduction

Recent interest and substantial progress in our understanding of cerebellar contributions to neurocognitive processes beyond the motor domain has been summarized in a comprehensive body of work (Baumann et al., 2014; Koziol et al., 2014; Manto et al., 2012; Mariën et al., 2014). It is important to note that a broad range of functions ascribed to the cerebellum is paralleled by increasingly detailed knowledge about its structural connectivity, which, in turn, allows speculation about complex cerebello-cortical and cerebello-subcortical interactions (Akkal, Dum, & Strick, 2007; Bernard et al., 2013; Bostan, Dum, & Strick, 2013; Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011; Chen, Fremont, Arteaga-Bracho, & Khodakhah, 2014; Strick, Dum, & Fiez, 2009). However, these empirical findings and theoretical frameworks tend to compete against a prevailing notion of the cerebellum as a genuine motor structure. In this aspect, cerebellar research is reminiscent of research in the language domain with a strong dichotomy of Broca's and Wernicke's area and their association with language production and perception. However, cerebellar

activity is found in the absence of movement, for example, in response to auditory stimulation including spoken language (Ackermann, 2008; Ackermann & Hertrich, 2000; Lockwood et al., 1999; Petacchi, Laird, Fox, & Bower, 2005). Accordingly, cerebellar contributions to language in general, and speech in particular, have been one of the major foci in the recent scientific discussion (for reviews see Mariën et al., 2014; Murdoch, 2010).

In the following, we will outline a proposal along these lines and discuss how specific contributions of the cerebellum regarding temporal and preparatory function may integrate into our understanding of speech perception. This proposal builds on the notion that the classical distinction of linguistic competence ("knowledge of a language") and linguistic performance ("actual use of a language"; Chomsky, 1965) is fundamental to our understanding of the cerebellar contributions to speech perception. Successful linguistic performance needs to be conceived as our capacity to use linguistic rules and constraints but requires, at the same time, that we cope with contextual variation, errors, memory limitations, and shifts of attention in concrete communicative settings (see for initial thoughts Chomsky, 1965). In line with such thinking we suggest that the cerebellum contributes to all of the latter aspects in speech perception. In particular, we will focus on two aspects: (i) the role of the cerebellum in temporal processing and "the preparation in advance of sensory events" (Courchesne & Allen, 1997; Ivry & Schlerf, 2008) and (ii) cerebellar connections to temporal and frontal cortices and how these connections may be reflected

* Corresponding author at: Faculty of Psychology and Neuroscience, Dept. of Neuropsychology and Psychopharmacology, P.O. Box 616, 6200 MD Maastricht, The Netherlands.

E-mail address: sonja.kotz@maastrichtuniversity.nl (S.A. Kotz).

¹ The authors contributed equally to this work.

by oscillatory activity. We acknowledge that a comprehensive account of cerebellar contributions to speech and language function will ultimately have to consider cerebellar subregions and their connections to temporo-parietal areas. However, we conceive the current opinion as a thought experiment that motivates why considering the contribution of these two aspects is essential in speech perception, thereby extending our earlier work on non-speech and speech specific auditory processing (Kotz & Schwartze, 2010; Schwartze & Kotz, 2013; Schwartze, Tavano, Schröger, & Kotz, 2012).

2. Dynamics in speech and speech perception

Speech serves the communication of meaning. This purpose is achieved by means of (neuro-) physiological processes that engage in the production and perception of speech, one of the most complex time-varying signals. In speech perception, the auditory system integrates sound features over multiple time-scales, ranging from tenths of a second (a few Hz) to milliseconds (kHz) (Rosen, 1992; Shamma, 2003). The dynamic and fleeting nature of the signal implies that speech perception involves some form of synchronization between a speaker and the decoding capacity of a listener (Greenberg, Carvey, Hitchcock, & Chang, 2003). Even though the speech signal is complex and our cognitive resources are limited, speech perception is a remarkably robust phenomenon. Consequently, speech perception must make opportunistic use of all types of information that are conveyed by the signal, including temporal information. In other words, the temporal structure of the signal may constitute a relevant source of information in its own right. Accordingly, domain-general dedicated processes specialized in the processing of temporal information may optimize general auditory processing and speech perception. A listener's ability to make use of the temporal structure of a dynamic signal may hence, in part, be responsible for qualitative differences in speech perception.

3. Cerebellar temporal processing and preparatory function

The cerebellum is among the brain regions that are most consistently associated with dedicated temporal processing, apart from the basal ganglia, the supplementary motor area, and prefrontal areas (Buhusi & Meck, 2005; Coull, Cheng, & Meck, 2011; Ivry & Schlerf, 2008; Wiener, Turkeltaub, & Coslett, 2010). The notion of *dedicated* temporal processing essentially implies a modular clock-like system that is specialized for representing temporal inter-event-relationships (Ivry & Schlerf, 2008). Accordingly, the *cerebellar timing hypothesis* suggests that the cerebellum establishes a precise representation of the temporal relation of salient events in the subsecond range (Ivry, 1996; Ivry & Schlerf, 2008; Spencer & Ivry, 2013; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). This event-based, short-range, and potentially also automatic cerebellar temporal processing system works in parallel with another dedicated system. This second system builds on oscillatory mechanisms in cortico-striato-thalamo-cortical circuits and performs interval-based, longer-range, and attention-dependent temporal processing (Buhusi & Meck, 2005).

Next to dedicated event-based temporal processing, the cerebellum has been associated with the complex interplay of attention, prediction, and preparation (Courchesne & Allen, 1997). The *cerebellar preparatory function* has been described as a domain-general process, in which the cerebellum predicts the internal conditions that are required for a particular mental or motor operation (including sensory, memory, attention, and speech-related operations) and prepares these conditions for operations in the respective neural systems (Courchesne & Allen, 1997). Critically, this preparatory

function is conceived as a dynamic process of constant adaptation to internal and external variation, which entails rapid, effortless, and accurate shifting of attention (Courchesne & Allen, 1997). Regarding attention, a conceptually similar perspective has been proposed in the *dynamic attending theory* (Large & Jones, 1999). According to this theory, inevitable fluctuations of attention are susceptible to the temporal structure of dynamic stimulation. A synchronized stimulus-driven attending mode may be established via the entrainment of adaptive neural “attention” oscillations to the temporal structure of the input, which may, in turn, prepare the organism for the perceptual integration of salient events.

Direct links between the proposed roles of the cerebellum in dedicated temporal processing, preparatory function, and the efficient allocation of attention in time may factor into a more general cerebellar role in guiding behavior that involves real-time prediction (Manto et al., 2012). An adequately precise representation of the temporal structure of successive events generated by the cerebellum and transmitted to cortical target areas via the thalamus may promote temporally specific predictions about the future course of events and allow more efficient preparation for subsequent “information acquisition and analysis” (e.g., by optimal positioning of sensory receptors, modulation of cerebral blood flow, enhanced neural signal-to-noise ratio and responsiveness in target areas including the thalamus; Courchesne & Allen, 1997). However, in the context of speech perception, a number of immediate questions arise from this proposal such as: Which type(s) of “speech events” may trigger dedicated cerebellar temporal processing? How does auditory information reach the cerebellum in the first place, and where does it go from there? What is known about oscillatory activity at the level of the cerebellum and how may this activity relate to the expanding literature on the role of cortical oscillations in dynamic attending and speech perception?

4. Auditory events and oscillatory dynamics

To approach these questions, it seems necessary to detail the notion of “event-based temporal structure.” Conceptually speaking, events may be conceived as arising from perceived changes in sensory input. Events thus stand in opposition to duration, i.e., the absence of change. Sensory systems, and the auditory system in particular, respond to signal properties that change as a function of time (Kluender, Coady, & Kieft, 2003). The cerebellum receives auditory input not only from temporal areas but also via its connections to the cerebellum-like dorsal cochlear nucleus during early stages of auditory processing (Huang, Liu, & Huang, 1982; Petacchi et al., 2005). Differential sensitivity of these early processing stages to signal changes (e.g., contrasts in loudness) may result in an adaptively filtered input representation, which preserves particularly salient events such as signal onsets and offsets and steeply rising spectral edges, while it suppresses other information (Schwartze & Kotz, 2013). This would facilitate the extraction of a discrete (non-linear) event-based representation of temporal structure from the ongoing speech signal. The proposed function of the cerebellum in dedicated temporal processing may thus guarantee temporally precise encoding and rapid transmission of the temporal locus of these events to cortical targets via the thalamus, thereby triggering preparatory processes in these areas. Dual-mode response characteristics of thalamic neurons may amplify this cerebellar “clock” signal by firing in a “burst-mode” to evoke more reliable postsynaptic responses effectively instantiating a “wake-up-call” to cortical targets (Sherman, 2001). Once they reach the cortex, the successive signals may guarantee temporal precision and specificity in compliance with the cerebellar preparatory function. Moreover, they may trigger adaptive attention oscillations and/or oscillatory mechanisms implicated in

attention-dependent temporal processing in cortico-striato-thalamo-cortical circuits (Fig. 1). Ultimately, this mechanism may play a role in optimizing the allocation of attention in time and support the perceptual integration or “bridging” of spatially distributed memory representations into a temporally coherent gestalt in frontal areas (Fuster, 1995). In speech perception, the respective memory representations, stored in the middle temporal gyrus and angular gyrus, may be transmitted to these frontal areas via white matter pathways for sentence construction and sentence comprehension, i.e., syntactic and semantic operations (Friederici, 2009; Rilling et al., 2008).

So far, our proposal provides partial answers to the questions about the general characteristics and the flow of auditory information to and from the cerebellar temporal processing system. In the following, we will substantiate this perspective on the basis of converging aspects in cerebellar and cortical oscillatory activity, thereby linking the current proposal to recent discussions about the role of neural oscillations in speech processing.

5. Oscillatory activity and cerebello-cortical interactions

Cerebellar encoding of event-based temporal structure and the thalamic amplification of this event-based stimulus representation may be limited to rates between 1 and 10 Hz (delta-to-theta range), with optimal thalamic responses obtained at about 4 Hz, reminiscent of the natural frequency of mandibular cycles generated during speech production (Giraud et al., 2007; MacNeilage & Davis, 2001; Sherman & Guillery, 2006). Electrophysiological studies in rats suggest that auditory evoked responses rapidly decay with stimulation rates >10 Hz (Lorenzo, Velluti, Crispino, & Velluti, 1977), which may, to some extent, reflect the coherence in cerebello-thalamo-frontal networks that is restricted to the theta (5–10 Hz) frequency range (Watson, Becker, Apps, & Jones, 2014). The total number of cochlear nucleus cells, which could transmit the adaptively filtered input representation to the cerebellum, is probably small but they may influence a vast number of Purkinje cells if they innervate the cerebellum via mossy fibers (Huang et al., 1982). In turn, afferent mossy fiber activity may be controlled by cerebellar Golgi cells, which display theta-frequency pacemaking behavior but are also optimally sensitive to theta-frequency input, responding with fast, intense, and precise bursts followed by a pause (Solinas et al., 2007). This mechanism may ensure that successive events evoke reliable and temporally distinct clock signals. Critically, Golgi cell activity in response to repetitive theta-frequency stimulation is “anticipated, intensified, and made more precise” (Solinas et al., 2007). The result of this combined effort may be the transmission of a temporally specific and increasingly precise theta-range signal to the thalamus and from there to frontal targets in preparation for the subsequent perceptual integration of memory representations retrieved from temporal areas into a temporally coherent gestalt (see Table 1).

In speech, 1–10 Hz activity corresponds to a range that overlaps with the syllabic level, and more specifically, with the succession of syllabic nuclei, which may instantiate the successive “signposts,” i.e., particularly salient events in the speech signal, which partly determine the overall quality of speech perception (Greenberg, 2006). However, thalamic cells in the classic ascending auditory pathway convey input at considerably higher frequencies. While the potential differential origin of the driving input is diffuse in surface recordings, events in the 1–10 Hz range and at higher frequencies are associated with different functions in speech perception. Theta oscillations (about 4–8 Hz) may instantiate a “master,” which tracks the temporal structure of syllabic input (“theta-syllable”), whereas higher frequencies (>25 Hz) are considered instrumental during memory access (Ghitza, 2012, 2013; Pelle & Davis,

2012). Furthermore, at this cortical processing level, the basic dissociation of slower and faster range oscillatory activity is also reflected in the differential oscillatory activity obtained from the right (3–6 Hz, the “dominant syllabic rate”) and left hemisphere (28–40 Hz, associated with perceptual sensitivity to acoustic correlates of tongue movements produced during articulation that allow discrimination between consonant families; Giraud et al., 2007).

Much less is known about the preceding processing stages of ascending auditory pathways and how they may influence the cortical “outcome.” However, as shown in cats, activity of thalamo-cortical cells in the gamma range is modulated by input from the cerebellum (deZeeuw, Hoebeek, & Schonewille, 2008; D’Angelo et al., 2009). This mechanism offers a potential explanation for cerebellar influence and interaction with the information flow of the classical auditory pathway at the level of the thalamus. In other words, ongoing cortical activity in the 1–10 Hz range may in part be determined by the modulation of thalamic activity in response to the event-based representation of temporal structure provided by the cerebellum. In a similar vein, cerebellar activity in speech processing with stimulation rates >4 Hz, is predominantly right-lateralized and may reflect an interaction of the respective cerebellar and cortical areas, e.g., in right-cerebellar-left-frontal loops and vice versa (Ackermann, Mathiak, & Riecker, 2007; Ackermann et al., 2001; Callan, Kawato, Parsons, & Turner, 2007). Activity in higher frequency ranges and induced activity (10–30 Hz and 40 Hz, respectively) has been suggested to reflect cerebello-cortical connectivity and frequency-specific coupling (Dalal, Ospino, Bertrand, & Jerbi, 2013; Pastor, Vidaurre, Fernández-Seara, Villanueva, & Friston, 2008). It is important to note that the ongoing oscillatory activity observed in speech perception may reflect both bottom-up and top-down processes mediated via pathways ascending from and descending to the cerebellum. Accordingly, it is unclear if interactions of activity in the theta range and higher frequency activity occur at the level of the cerebellum, the thalamus, or in cortical areas. Several functional implications depend on an answer to this question such as: Is the cerebellar temporal processing system directly involved in the encoding of temporal parameters at the phonemic level (Ackermann et al., 2007) or does the temporal precision of event-based temporal processing at the syllabic level indirectly modulate the quality of phonemic processing in cortical targets (a temporally specific variant of the cerebellar preparatory function)? Yet, oscillatory activity in the range of frequencies considered being central for cortical speech processing, might be influenced by the cerebellum. Generally speaking, higher-frequency cerebellar activity may interact with theta-range oscillations serving to implement a “temporal coding scheme,” which allows fast processing and serves learning-dependent timing in response to unexpected events and memory retrieval (deZeeuw et al., 2008). A similar type of interaction may be necessary to achieve the temporal resolution that ensures maximal temporal precision within the cerebellar temporal processing system, i.e. the precise sampling of the temporal locus of event rates in the theta range by oscillations operating at considerably higher frequencies (up to 260 Hz; deZeeuw et al., 2008).

6. Conclusions and future directions

Taken together, we suggest that linking the proposed roles of the cerebellum in dedicated temporal processing and preparatory function on the basis of oscillatory activity is key to a better understanding of the cerebellar contributions to speech perception. However, next to the functions discussed so far, one of the most important questions concerns the role of the cerebellum in sensorimotor internal (forward) modeling (Ramnani, 2006; Wolpert, Miall, & Kawato, 1998): We know that the cerebellum contributes

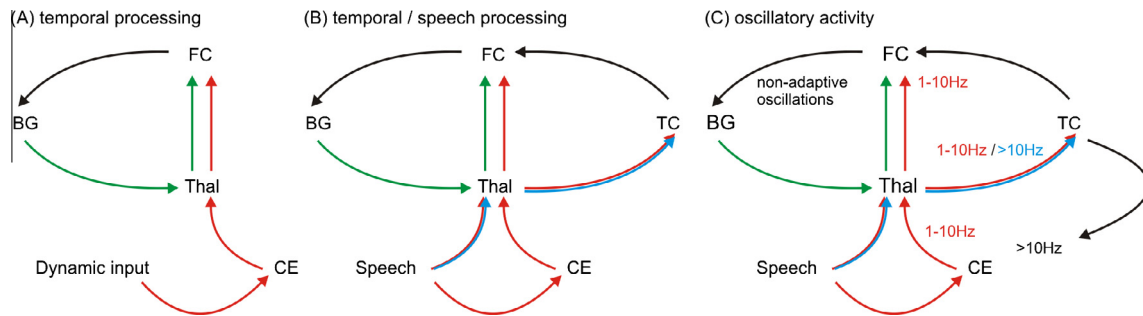


Fig. 1. Structural and functional embedding of the cerebellum into dedicated temporal processing and speech perception on the basis of oscillatory mechanisms. (A) The cerebellum (CE) receives input from early sensory auditory processing stages and encodes a precise event-based representation of the temporal structure of this input (red). This representation is rapidly transmitted to frontal (FC) cortices via the thalamus (Thal) and triggers adaptive and/or non-adaptive oscillatory mechanisms. Adaptive oscillations have been discussed as guiding the stimulus-driven allocation of attention in time, whereas ensembles of non-adaptive oscillations are integral to interval-based temporal processing, which engages the basal ganglia (BG) and associated cortico-striato-thalamo-cortical circuits (green). Both mechanisms may contribute to the optimal adaptation of the organism to dynamic environmental input and the efficient allocation of attention in time (B) The speech signal constitutes a highly complex dynamic input. It conveys events spread over different time-scales, including slower (red; e.g., syllable level) and faster dynamics (blue; e.g., phoneme level). In speech perception, a sufficiently detailed internal representation of this complex signal is conveyed to temporal cortices (TC), where it serves to establish and access memory representations. In parallel, rapid transmission of the cerebellar event-based representation of the temporal structure of the same input guides attention in time and prepares FC for the perceptual integration of elements retrieved from memory (C). Convergence of oscillatory activity at cerebellar, thalamic, and cortical levels may reflect ongoing interaction between temporal processing mechanisms and speech perception on the basis of cerebello-cortical and cortico-cerebellar connections. Activity in the 1–10 Hz range may reflect event-based temporal processing triggered by salient speech events at the syllabic level, whereas higher frequencies convey information critical to memory-related processes and cortico-cerebellar communication. Cerebellar activity in considerably higher frequency ranges may provide the temporal resolution that is necessary for a precise representation of the temporal structure of successive events. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Proposed function of oscillatory activity in selected frequency ranges.

Range	Location	Function
1–10 Hz	Cerebellum	Precise encoding of non-linear (event-based) stimulus representation
1–10 Hz (4 Hz)	Thalamus/frontal cortex	Transmission and amplification of non-linear stimulus representation; “wake-up-call”
1–10 Hz	Temporal cortex	Tracking of syllable structure
1–10 Hz	Frontal cortex	Stimulus-driven attending; attention-dependent temporal processing
>25 Hz	Thalamus/temporal cortex	Encoding of linear (continuous) stimulus representation; establishment of memory representations and memory access
>25 Hz (40 Hz)	Cerebellum/temporal cortex	Cortico-cerebellar communication; memory
High frequency	Cerebellum	Temporal precision

to this type of modeling, but does it extend to sensory processing, and, consequently to speech perception? These domains may converge in aspects such as the detection of a discrepancy (error) between the modeled (predicted) and the actual sensory information, the adaptation to (learning) of new information, and in the updating of a generalized “mental model” of the environment (Kotz, Stockert, & Schwartze, 2014). However, whether (i) these are genuine aspects of cerebellar function or (ii) they rely on the cerebello-cortical interplay, and (iii) they interact with dedicated temporal processing remains to be determined. Although the current proposal offers several potential venues for a functional and structural embedding of the cerebellum and cerebellar event-based temporal processing into auditory processing in general and speech perception in particular, the current proposition serves as a starting point for further investigations exploring it.

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