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

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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.

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, & Stick, 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

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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, & Kiefte, 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