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Research report

Spontaneous, synchronized, and corrective timing behavior in cerebellar lesion patients

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HIGHLIGHTS

- Cerebellar patients and controls performed self-paced and paced sensorimotor tasks.
- The results confirm a temporal processing dysfunction in cerebellar lesion patients.
- Lesions increase asynchronies, decrease tempo sensitivity, impair error correction.
- The results are compatible with a sensory predictive account of cerebellar function.

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ABSTRACT

To successfully navigate through and interact with a dynamic environment it is necessary to acquire and use adequate temporal information to guide behavior. Apart from several areas in the cerebral cortex and cortico-striatal networks, the cerebellum has been proposed to engage in the processing of temporal information. Damage to the cerebellum can impair precise event-based temporal processing in motor and non-motor behavior. To further substantiate cerebellar contributions to temporal processing and to explore its specific role in adapting to a dynamic environment, we investigated sensorimotor temporal processing in ten patients with cerebellar lesions and a corresponding number of healthy matched controls. Experimental tasks included simple self-paced repetitive finger-tapping (spontaneous motor tempo), temporally non-adaptive (isochronous pacing) and adaptive (tempo-changing pacing) sensorimotor synchronization with auditory sequences (synchronization-continuation tapping), and a perceptual tempo judgment. The results indicate that patients' performance diverges systematically from controls on several measures. Cerebellar patients demonstrate more variable self-paced tapping, larger negative asynchronies when synchronizing with isochronous pacing sequences, altered automatic error correction responses to tempo changes (phase correction), and decreased perceptual sensitivity to these perturbations, especially for small accelerations. These findings confirm imprecise temporal processing in cerebellar patients, and hint at a specific impairment in the tens-of-milliseconds range preceding critical events, in line with a temporally predictive account of cerebellar function. Moreover, this cerebellar profile complements previous findings concerning dysfunctional temporal processing in basal ganglia patients assessed with the same experimental setup, suggesting structural and functional differentiation within an integrative temporal processing network.

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1. Introduction

Reciprocal polysynaptic connections between the cerebellum, thalamus, cerebral cortex, and subcortical areas establish the structural basis for functional interactions, and an active role of the cerebellum in motor and non-motor behavior [1–6]. A common denominator in cerebellar function across these domains is *temporal processing*, conceived as the ability to encode, decode, and evaluate the temporal structure of sensory and sensorimotor

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events. In addition to the basal ganglia, prefrontal-, and supplementary motor areas, the cerebellum is among the brain regions consistently associated with temporal processing [7–11]. More specifically, the *cerebellar timing hypothesis* suggests that the cerebellum generates a precise internal representation of the temporal relation between salient events in the subsecond range [12–14].

Another denominator in cerebellar function is a conglomerate of related functions, namely the interplay of preparation, prediction, and attention, conceived as a dynamic process of constant adaptation to internal and external variation [15]. Cerebellar circuitry involved in predicting sensory consequences of action ("forward-modelling" [16]) has been suggested to generate a temporal signal, which, potentially in concert with pre-supplementary motor cortices, guides sensory prediction and the temporal orienting of attention [17]. This mechanism is reminiscent of a more general concept of attention and the allocation of attention in time as formulated in the framework of *dynamic attending theory* [18]. This theory considers naturally occurring internal variations (fluctuations) of attention directly sensitive to the temporal structure of external stimulation. Modelled as a complex of adaptive oscillations (attending rhythms), these fluctuations may establish a stimulus-driven, synchronized attending mode, which allows prediction of the temporal locus of future events. From this perspective, the temporal structure of events determines efficient allocation of attention and thereby the quality of integrated percepts [18].

The question arises whether the precise representation of event timing, forward-modelling, and the efficient allocation of attention converge into a generalizable function in behavior that requires or at least benefits from real-time prediction [19,20]. This assumption is essentially a variant of the idea that the cerebellum contributes to precise sensory discrimination and integration, and controls the acquisition of sensory data to increase the efficiency of processing in cerebral cortex [21]. These cerebellar contributions to temporal aspects of behavior are perhaps most evident (but not limited to) tasks, in which sensory processing concurs in conjunction with movement [22,23]. Notwithstanding functional specialization within specific cerebellar subregions, the cerebellum as a whole may thus instantiate a sensorimotor structure, which modulates activity in cerebral cortex to optimize behavior in terms of temporal precision and coherence, synchronization, and temporal prediction as facets of ongoing interactions with a dynamic environment. On this account, damage to the cerebellum should reduce the efficiency of these operations, leading to suboptimal temporal precision, which may cascade into a broad range of motor and non-motor behaviors.

In the current study, we compared the performance of patients with cerebellar lesions and healthy controls in a set of sensorimotor tasks that require a relatively high degree of temporal precision. Self-paced generation of temporal regularity (spontaneous motor tempo, SMT), paced synchronization and unpaced reproduction, as well as adaptation and perceptual sensitivity to tempo changes were assessed using previously established adaptive finger-tapping paradigms in combination with a modelling approach that has been shown to differentiate between automatic and attention-dependent forms of error correction in adaptive sensorimotor synchronization [24,25]. Firstly, we expected patients' performance to diverge systematically from controls in all domains tested: spontaneous, paced, and perceptual behaviour, and to exhibit a profile of dysfunctions that would be compatible with the proposed role of the cerebellum in precise subsecond temporal processing in production and perception as suggested by the *cerebellar timing hypothesis*. Secondly, based on the current modelling approach we also expected this profile to reflect dysfunctional automatic mechanisms, thus differing from the previously obtained profile of basal ganglia patients, who demonstrated dysfunctional attention-dependent error correction in adaptive sensorimotor synchronization [25]. The emergence of such a pattern would substantiate the notion of cerebellum and basal ganglia as nodes within an integrative temporal processing network, and specify this global function on the basis of a differential engagement of attention.

2. Material and methods

2.1. Participants

10 chronic-stage right-handed patients with cerebellar lesions (mean age: 45.0, SD: 14.0, range: 25–70 years; 3 women) and 10 healthy matched controls (mean age: 46.8, SD: 13.1 years) participated in the experiment (Table 1, Fig. 1). All participants provided informed written consent with the study. Individual control-patient pairings were matched in terms of handedness, gender, age (+/− 2 years), and education (in years). None of the participants had professional musical expertise. Both groups were recruited via databases at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. None of the participants had prior experience with finger-tapping in an experimental setup. The study was conducted in accordance with the World Medical Association Declaration of Helsinki and was approved by the ethics committee of the University of Leipzig.

2.2. Structural magnetic resonance imaging

High-resolution T1-weighted magnetic resonance scans were obtained for each patient on Bruker BioSpin (BioSpin GmbH, Rheinstetten, Germany) or Siemens TrioTim (Siemens Healthcare, Erlangen, Germany) magnetic resonance systems at 3 T using a 32-channel phased-array head array coil and an MP-RAGE sequence [26]. The resulting images were segmented and spatially normalized to Montreal Neurological Institute (MNI) space by means of a unified segmentation approach [27] in *SPM* (SPM8, Wellcome Department of Imaging Neuroscience, London, http://www.fil.ion.

Table 1
Patient characteristics. Abbreviations: cen. = center of mass (stereotactic coordinates provided by MRIcron), hem. = hemisphere, l = left, r = right, m/f = male or female, vol. = lesion volume in cc.

no.	m/f	age	vol.	cen. (x,y,z)	hem.	aetiology
1	m	25	48.0	77,38,35	l,r	arteriovenous malformation, intracranial haemorrhage
2	m	30	30.1	52,53,46	l	superior cerebellar artery aneurysm, intracranial haemorrhage
3	m	45	4.9	84,64,47	l,r	basilar artery aneurysm, superior cerebellar artery infarction
4	m	70	1.6	63,31,35	l	posterior inferior cerebellar artery infarction
5	m	59	7.1	89,37,26	r	posterior inferior cerebellar artery infarction
6	f	38	0.3	121,48,27	r	posterior inferior cerebellar artery infarction
7	f	45	7.9	62,41,24	l,r	posterior inferior cerebellar artery infarction
8	m	55	14.5	57,40,24	l	posterior inferior cerebellar artery infarction
9	f	33	8.8	84,49,37	r	medulloblastoma resection
10	m	50	2.4	88,52,15	r	posterior inferior cerebellar artery infarction

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