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Research report

The cerebellum and visual perceptual learning: Evidence from a motion extrapolation task

Cristina Deluca [a,1], *Ashkan Golzar* [a,b,1], *Elisa Santandrea* [a,1], *Emanuele Lo Gerfo* [a], *Jana Estocinova* [a], *Giuseppe Moretto* [c], *Antonio Fiaschi* [a,d], *Marta Panzeri* [e], *Caterina Mariotti* [e], *Michele Tinazzi* [a,d] and *Leonardo Chelazzi* [a,d,*]

[a] *Department of Neurological and Movement Sciences, University of Verona, Italy*
[b] *Department of Physiology, McGill University, Montreal, Canada*
[c] *Neurology Unit, Borgo Trento Hospital, Verona, Italy*
[d] *National Institute of Neuroscience, Verona, Italy*
[e] *IRCSS Foundation Carlo Besta, Department of Genetics of Neurodegenerative and Metabolic Diseases, Milan, Italy*

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ABSTRACT

Visual perceptual learning is widely assumed to reflect plastic changes occurring along the cerebro-cortical visual pathways, including at the earliest stages of processing, though increasing evidence indicates that higher-level brain areas are also involved. Here we addressed the possibility that the cerebellum plays an important role in visual perceptual learning. Within the realm of motor control, the cerebellum supports learning of new skills and recalibration of motor commands when movement execution is consistently perturbed (adaptation). Growing evidence indicates that the cerebellum is also involved in cognition and mediates forms of cognitive learning. Therefore, the obvious question arises whether the cerebellum might play a similar role in learning and adaptation within the perceptual domain. We explored a possible deficit in visual perceptual learning (and adaptation) in patients with cerebellar damage using variants of a novel motion extrapolation, psychophysical paradigm. Compared to their age- and gender-matched controls, patients with focal damage to the posterior (but not the anterior) cerebellum showed strongly diminished learning, in terms of both rate and amount of improvement over time. Consistent with a double-dissociation pattern, patients with focal damage to the anterior cerebellum instead showed more severe clinical motor deficits, indicative of a distinct role of the anterior cerebellum in the motor domain. The collected evidence demonstrates that a pure form of slow-incremental visual perceptual learning is crucially dependent on the intact cerebellum, bearing the notion that the human cerebellum acts as a learning device for motor, cognitive and perceptual functions. We interpret the deficit in terms of an inability to fine-tune predictive models of the incoming flow of visual perceptual input over

* *Corresponding author*. Department of Neurological and Movement Sciences, Section of Physiology and Psychology, University of Verona, Strada Le Grazie 8, 37134 Verona, Italy.
E-mail address: leonardo.chelazzi@univr.it (L. Chelazzi).

[1] The first three authors (C.D., A.G., and E.S.) contributed equally to this work.

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time. Moreover, our results suggest a strong dissociation between the role of different portions of the cerebellum in motor versus non-motor functions, with only the posterior lobe being responsible for learning in the perceptual domain.

1. Introduction

Perception of the visual world is adjusted (fine-tuned) by experience – known as visual *perceptual learning*, which can be defined as the improvement in detecting and discriminating low-level or more complex features of the visual input as a result of extended practice with a specific set of stimuli and task (Ahissar, Nahum, Nelken, & Hochstein, 2009; Byers & Serences, 2012; Censor, Sagi, & Cohen, 2012; Dosher & Lu, 2009; Fahle, 2009; Gilbert, Li, & Piech, 2009; Lu, Hua, Huang, Zhou, & Dosher, 2011; Roelfsema, van Ooyen, & Watanabe, 2010; Sasaki, Nanez, & Watanabe, 2010). Although the understanding of perceptual learning phenomena and the underlying neural mechanisms is far from complete, a long tradition of research in the field has focused on plastic changes occurring along the cerebro-cortical pathways, including at the earliest stages of processing, though increasing evidence indicates that higher-level brain areas are involved as well (Ahissar et al., 2009; Byers & Serences, 2012; Fahle, 2009; Gilbert et al., 2009; Lu et al., 2011; Roelfsema et al., 2010; Sasaki et al., 2010). So far the possibility that the cerebellum contributes significantly to perceptual learning has never been addressed.

It is instead solidly established that the cerebellum is critical for motor control, supporting smoothly unfolding and precise movements (Dow & Moruzzi, 1958; Rothwell, 1994, chap. 10, pp. 387–445). This role is largely mediated by a key contribution of cerebellar mechanisms to various forms of motor learning (Blazquez, Hirata, & Highstein, 2004; Doyon, 1997; Imamizu et al., 2000; Ioffe, Chernikova, & Ustinova, 2007; Krakauer & Shadmehr, 2006; Manto et al., 2012; Smith & Shadmehr, 2005; Thach, 1998) and adaptation (Bastian, 2008; Golla et al., 2008; Manto et al., 2012; Prsa & Thier, 2011; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007; Werner, Bock, & Timmann, 2009), which allow the system to acquire new skills and re-calibrate motor commands when movements become inaccurate as a result of consistent perturbations. The latter notion, initially formulated in theoretical, computational terms on the basis of the available knowledge at the time (Albus, 1971; Marr, 1969), has subsequently been supported by a vast array of converging empirical observations (e.g., Ito, 2006). Moreover, different forms of plasticity within the cerebellar circuitry have been hypothesized to mediate this role (e.g., Carey, 2011; Gao, van Beugen, & De Zeeuw, 2012; Lamont & Weber, 2012).

More recently, numerous findings have led to the emerging notion that the cerebellum is also involved in non-motor functions (e.g., Bellebaum & Daum, 2011; Bostan, Dum, & Strick, 2013; E, Chen, Ho, & Desmond, 2012; Ito, 2008; Leiner, Leiner, & Dow, 1989; Leiner, Leiner, & Dow, 1991; Schmahmann, 1998; Strick, Dum, & Fiez, 2009; Timmann & Daum, 2007; Timmann et al., 2010), including cognitive domains – such as language (Durisko & Fiez, 2010; Marvel & Desmond, 2010; Murdoch, 2010), executive control (Bellebaum & Daum, 2007), emotion (Strata, Scelfo, & Sacchetti, 2011; Timmann et al., 2010) and working memory (Ben-Yehudah, Guediche, & Fiez, 2007; Durisko & Fiez, 2010), sensory/perceptual domains (Bastian, 2011; Bhanpuri, Okamura, & Bastian, 2012; Molinari et al., 2008) and time processing (Bueti, Lasaponara, Cercignani, & Macaluso, 2012; Ivry & Spencer, 2004). This view of a more diverse role of the cerebellum fits well with the detailed description of widespread and bidirectional cerebro-cerebellar connections, which engage motor and non-motor areas of the cerebral cortex, including frontal, prefrontal, parietal and temporal territories (Bostan et al., 2013; Stoodley, 2012; Strick et al., 2009; Sultan et al., 2012).

Whether or not the cerebellum contributes significantly to non-motor functions, and especially the very nature of this putative contribution, is nevertheless still a matter of debate (e.g., Glickstein, 2007; Glickstein & Doron, 2008). Mainly based on the complex, often times subtle, and highly variable pattern of cognitive disturbances which can be detected in patients suffering from cerebellar damage, the proposal has been made that the cerebellum contributes to cognitive functions in a way similar to its role in the motor domain, allowing well-coordinated and smoothly unfolding, cognitive processes (Schmahmann, 1991; 1998). This has generated the idea that damage to the cerebellum leads to what has been termed "dysmetria of thought" (Schmahmann, 1991; 1998). Consistent with the view that the cerebellum exerts similar functions within the motor and the cognitive domain, the obvious prediction would be that the cerebellum mediates learning phenomena also within non-motor, cognitive functions, and within perception. Surprisingly, however, the claim that the human cerebellum plays a key role in learning within pure forms of perceptual processing has so far never been made (but see Section 4 for an analysis of related findings). It is noteworthy that in a number of recent, non-selected and highly authoritative review articles on perceptual learning, terms such as "cerebellum" or "cerebellar" do not appear a single time (Ahissar et al., 2009; Byers & Serences, 2012; Censor et al., 2012; Fahle, 2009; Gilbert et al., 2009; Lu et al., 2011; Roelfsema et al., 2010; Sasaki et al., 2010). Likewise, in a comparable number and type of review articles on cerebellar function, including in the cognitive domain, the term "perceptual learning" is again entirely absent (Bastian, 2011; Ito, 2008; Ramnani, 2006; Schmamann, 2010; Stoodley, 2012; Strick et al., 2009). Similarly, no mention to a possible role of the cerebellum in "perceptual learning" can be found in a comprehensive Special Issue addressing the cerebellar contribution to non-motor functions, which appeared