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Cerebellar vermis plays a causal role in visual motion discrimination

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ABSTRACT

Cerebellar patients have been found to show deficits in visual motion discrimination, suggesting that the cerebellum may play a role in visual sensory processing beyond mediating motor control. Here we show that triple-pulse online transcranial magnetic stimulation (TMS) over cerebellar vermis but not over the cerebellar hemispheres significantly impaired motion discrimination. Critically, the interference caused by vermis TMS on motion discrimination did not depend on an indirect effect of TMS over nearby visual areas, as demonstrated by a control experiment in which TMS over V1 but not over cerebellar vermis significantly impaired orientation discrimination. These findings demonstrate the causal role of the cerebellar vermis in visual motion processing in neurologically normal participants.

1. Introduction

The cerebellum has been suggested to play a critical role in sensory processing, beyond being involved in motor control (Bower, 1997; D'Angelo & Casali, 2012; Manto et al., 2012). Specifically, psychophysical studies with cerebellar patients have demonstrated the functional significance of this region in motion perception independent from actual movements (Baumann & Mattingley, 2010; Jokisch, Troje, Koch, Schwarz, & Daum, 2005; Nawrot & Rizzo, 1995, 1998; Thier, Haarmeier, Treue, & Barash, 1999). Both in acute and chronic post-ictus phases, cerebellar patients with lesions in midline structures have deficits in motion discrimination, which was not the case when lesions were restricted to the cerebellar hemispheres (Nawrot & Rizzo, 1995, 1998). The performance deficits, which occurred even though cortical processing was intact, were neither due to aberrant eye movements nor an indirect consequence of motor deficits (Ivry & Diener, 1991;

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Nawrot & Rizzo, 1995, 1998; Thier et al., 1999). However, lateral parts of the cerebellum have also been associated with deficits in motion discrimination (Jokisch et al., 2005); thus, the localization of cerebellar areas controlling motion discrimination remains unclear.

Neuroimaging evidence on the role of the cerebellum in motion discrimination is also somewhat conflicting. In positron emission tomography (PET) studies, Dupont, Orban, De Bruyn, Verbruggen, and Mortelmans (1994) found vermal activity in response to a moving dot pattern, and Barbur, Watson, Frackowiak, and Zeki (1993) reported such activity in a blindsight patient with a unilateral lesion in V1. However, using functional magnetic resonance imaging (fMRI) Baumann and Mattingley (2010) observed a complex pattern of activation in the cerebellar hemispheres, which was correlated with both auditory and visual motion signal strength.

Here we attempted to resolve this controversy by the use of brain stimulation in neurologically healthy volunteers in three different experiments. Brain stimulation can shed light on the causal role of the targeted brain regions in mediating specific perceptual functions, thus overcoming the correlational nature of neuroimaging and the poor focality of brain lesions. In the first two experiments online transcranial magnetic stimulation (TMS) was applied either over the cerebellar vermis (Experiment 1) or over the left and right cerebellar hemispheres (Experiment 2), while participants performed a visual motion discrimination task. In order to rule out effects due to nonspecific effects of TMS (e.g., tapping sensation, auditory distraction) or to spread of stimulation from the cerebellar vermis to the adjacent visual cortex, in Experiment 3 TMS was applied during a visual orientation discrimination task, which is known to causally involve the early visual cortex but not cerebellum (e.g., Neary, Anand, & Hotson, 2005 for previous TMS evidence using orientation discrimination).

2. Experiments 1 and 2: motion discrimination

2.1. Methods

2.1.1. Participants

Twelve healthy volunteers (10 F, mean age: 21.58 ys, SD: 1.0, range: 20–23) took part in Experiment 1 and twelve healthy volunteers (11 F, mean age: 22.17 ys, SD: 2.2, range: 20–27), none of whom had participated in Experiment 1, took part in Experiment 2. All participants were right-handed (Oldfield, 1971) and had normal or corrected to normal vision. Prior to the experiment, each participant filled in a questionnaire (translated and adapted from Rossi, Hallett, Rossini, & Pascual-Leone, 2011) to evaluate compatibility with TMS. None of the volunteers had a history of neurological disorders or brain trauma or family history of epilepsy. Written informed consent was obtained from all participants before the experiment. The protocol was approved by the local ethical committee and participants were treated in accordance with the Declaration of Helsinki.

2.1.2. Visual stimuli

All stimuli were presented centrally on a 17″ TFT-LCD computer monitor (screen resolution: 1440*900 pixels; refresh rate: 75 Hz). Stimuli consisted of 100 white dots (one pixel each), placed at random positions within an imaginary square that subtended $4.3^\circ \times 4.3^\circ$ of visual angle. The coherent dots were moving either to the right or left within the virtual square on a black background at a speed of 1 pixel per frame (at 2.15 deg/sec); noise dots changed direction randomly at every screen refresh. Each trial began with a fixation cross appearing in the middle of the screen for an interval comprised between 2600 and 2800 msec, followed by a blank screen for 500 msec, after which the stimulus appeared. Stimulus duration was between 40 and 67 msec, depending on participant's ability (see thresholding procedure below). After response, the next trial started. An example of experimental trial is shown in Fig. 1. Participants were required to report whether the visual stimulus moved to the left or right by left/right key presses using their right index and middle finger. Response speed was stressed in addition to accuracy.

2.1.3. Thresholding

Prior to the experiment, each participant underwent a thresholding procedure to determine the ratio of coherent moving dots and the number of frames (frame duration: 13 msec) necessary to obtain a stable performance around 75% accuracy. This was achieved by running a block in which motion coherence (i.e., the amount of dots moving coherently either to the left or right) ranged from 40% to 90% in steps of 10% with six levels. In this block, the motion stimulus contained five frames (with 20 trials per level with the method of

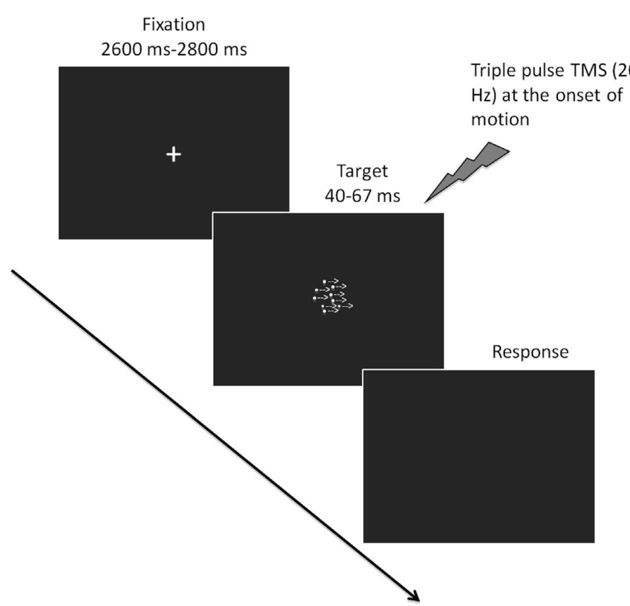

Fig. 1 – The timeline of an experimental trial in the motion discrimination task. In experiment 1, TMS was applied over the cerebellar vermis and the primary visual area (V1). In experiment 2, TMS was applied over the cerebellar left and right hemisphere. In both experiments, sham TMS (control condition) was also applied over the targeted sites in addition to a No TMS condition.

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