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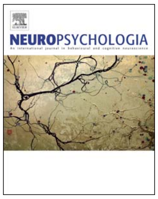

Cerebellar contribution to spatial realignment: A tDCS study during multiple-step prism adaptation

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ABSTRACT

Several processes are devoted to error reduction in response to a visual displacement, such as the one induced by wedge prisms. Strategic calibration and spatial realignment contribute to the iteratively process that allows a progressive adjustment of motor commands to reduce the magnitude of errors. Isolating the specific contributions to motor behaviour coming from these distinct processes is not possible using traditional single-step Prism Adaptation (PA), where participants are directly exposed to full prismatic shift. Here, we selectively investigated the effect of realignment on motor behaviour by means of a PA paradigm (the multiple-step PA) that allows to elude the development of strategic calibration. We tested for a specific cerebellar contribution to realignment by means of transcranial Direct Current Stimulation (tDCS) in healthy subjects. Confirming and expanding previous imaging and stimulation results, our study causally demonstrates cerebellar involvement in spatial realignment. Additionally, our results point to a possible contribution of the cerebellum in automatic online control. The role of a cortico-cerebellar network accounting for this results and possible clinical applications are proposed and discussed.

1. Introduction

Prism Adaptation (PA) is a behavioural technique allowing to trigger and to easily study short-term visuo-motor plasticity. PA is classically assessed in pointing tasks to visual targets while participants wear prism glasses shifting the visual field rightward or leftward. As the direct effect of the optical shift participants show a deviation of their movement endpoints toward the virtual position of the target (terminal error), i.e. in the direction of the optical shift. This pointing bias is progressively compensated for through successive trials (error correction/adaptation). More surprisingly, once glasses are removed participants make pointing errors in the direction opposite to the visual displacement (after-effect; Redding et al., 2005). This compensatory after-effect demonstrates the occurrence of adaptation and allows to quantify its magnitude.

Several mechanisms can contribute to error compensation during exposure to a visual distortion (Weiner et al., 1983; Redding and Wallace, 2002, 2006; Redding et al., 2005; Rossetti et al., 1993; O'Shea et al., 2014; Pisella et al., 2006). First, visual feedback allowing to rapidly update and modify ongoing actions, i.e. online control, contributes to reduce terminal error just like in every aiming movement (Pélisson et al., 1986; Prablanc and Martin, 1992; Pisella et al., 2000). This online error reduction mechanism is especially at work during the first trials of prism exposure, i.e. when on-flight errors are substantial (O'Shea et al., 2014). Visual feedback enables corrective corrections even when prisms are worn by the subjects (O'Shea et al., 2014). Strategic calibration or recalibration, a strategic process of error correction, may also participate in compensating for the terminal error particularly during early trials (e.g. pointing off the visible target or creating a virtual target; Weiner et al., 1983; Redding et al., 2005). This process makes use of the measure of terminal errors to update the aiming direction for the next movement (Rossetti et al., 1993; O'Shea et al., 2014). Spatial realignment, or "true adaptation" (Weiner et al., 1983), an automatic and unconscious process of movement correction further compensates the optical shift. The specific feature of spatial realignment is that it develops progressively over numerous trials of prism exposure (Inoue et al., 2015). Accordingly, it also needs time to resolve when the optical shift is removed. Crucially, spatial realignment is the component that gives rise to the after-effect by means of a deep process of re-mapping of spatial maps (Redding et al., 2005; O'Shea et al., 2014). All three compensatory mechanisms rely on error processing at an implicit or explicit level but they are likely to operate at

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different anatomo-functional circuits.

Neural correlates underlying these mechanisms have been investigated by several neuroimaging studies (Clower et al., 1996; Danckert et al., 2008; Luauté et al., 2009; Chapman et al., 2010; Kuper et al., 2014), but the discrepancy between the results obtained with brain imaging is best illustrated by comparing Luauté et al. (2009) to Kuper et al. (2014). The former study suggested a correlation between recalibration and the activity of the posterior parietal cortex on one hand, and spatial realignment and the activity of the cerebellum on the other. Indeed, during rightward prism exposure, Luauté et al. (2009) reported increased activation within a network of areas including the left parieto-occipital sulcus and the left anterior intraparietal sulcus, compatible with a role of these structures in adjusting movement plans. These areas would participate to successful correction during the first trials of prism exposure through feedforward use of error in the subsequent trial and hence would contribute to the strategic component of PA (i.e. recalibration; Luauté et al., 2009). In addition, Luauté et al. (2009) also observed a later increasing activity in the right cerebellum during exposure to prism suggesting that the cerebellum is involved in the slow and automatic process necessary to fully adapt to the optical shift and in the development of the after-effect (i.e. spatial realignment). The finding of an activation of the posterior cerebellar cortex and of the ventro-caudal dentate nucleus was also reported in the latter neuroimaging experiment, i.e. Kuper et al. (2014), who however observed such an activation pattern both during the first and late phases of prism exposure, suggesting that the cerebellum would be involved in both recalibration and spatial realignment. Consistent with Kuper et al.'s findings (2014), in a study using transcranial Direct Current Stimulation (tDCS), Panico et al. (2016) observed that interfering with cerebellar activity during PA can impair healthy participants' performance during all phases of the experimental procedure. The findings reported by Kuper et al. (2014) and Panico et al. (2016) converge in suggesting that the cerebellum contributes to several reactions triggered by active prism exposure. By contrast, lesion studies suggest that the cerebellum is specifically involved in spatial realignment (Weiner et al., 1983; Pisella et al., 2005). Taken altogether, the precise contribution of the initial and late cerebellar activation during PA remains to be elucidated. It is possible to interpret this activation as the result of the involvement of the cerebellum in *online control*, *recalibration* or *spatial realignment*. It is indeed possible that these processes, although different in nature, depend on common cerebellar functions.

The traditional single-step PA used in previous imaging and stimulation studies (e.g., Panico et al., 2016), in which participants are directly exposed to the full prismatic shift, does not allow disentangling the contribution of these processes. In fact, recalibration and spatial realignment are only distinguished on the basis of time. Recalibration is ascribed to early trials and spatial realignment to later trials of prism exposure (Rossetti et al., 1993) but the number of trials involving recalibration is undetermined. Moreover, error correction achieved by online control cannot clearly be distinguished by error compensation achieved by means of recalibration. To untangle the knot, it would be necessary to assess the effect of interference over the cerebellum in experimental conditions where one of these processes is completely eluded. The multiple-step exposure to wedge prisms (Michel et al., 2007), which keeps participants unaware of the optical deviation by means of progressive stepwise increases from a no-shift condition to the full prism displacement, permits the specific observation of spatial realignment. Since participants are not aware of the progressive displacement of the visual field, they are not in the position of using strategic processes for error correction (i.e., recalibration), and they should only make use of spatial realignment to durably compensate for errors. In addition, online control remains at work during the initial trial of exposure, i.e. when visual error signals enable in-flight motor control.

The aim of this work was to isolate and describe the processes contributing to error correction, adaptation and after-effect development during Prism Adaptation and to specifically test whether spatial realignment depends on cerebellar functioning. The possible contribution of cerebellar structures to online control during PA will be easier to disentangle from true adaptation as it contributes only to very initial trials, whereas realignment gives rise to after-effects. Transcranial Direct Current Stimulation (tDCS) was delivered during multiple-step exposure to wedge prisms. We hypothesize that inhibitory functional stimulation of the cerebellum should interfere with adaptation and magnitude of after-effect (the direct outcome of realignment), due to interfered spatial realignment. No effect of stimulation was expected on recalibration as it should be totally eluded by the current experimental procedure.

2. Materials and method

2.1. Participants and experimental design

Thirty-two right-handed university students (average age = 21.92, SD = 2.48, 20 females) voluntarily participated to this study. Participants had normal or corrected-to-normal vision and no contraindications to tDCS. They were naïve to the purposes of the study and they were included only if they had not previously participated to PA experiments and had no knowledge about PA.

Participants were informed that tDCS was used to evaluate the role of specific brain regions during a visuo-motor task, and gave their written informed consent to take part in the experiment.

Participants were randomly divided in two stimulation groups: 16 participants were assigned to the cathodal tDCS Group (ctDCS), while 16 participants were assigned to the Sham Group. The procedure was in agreement with 1975 Helsinki Declaration and was approved by the Local Ethic Committee.

2.2. transcranial direct current stimulation

A battery-driven, constant current stimulator (BrainSTIM, EMS Medical, Italy) was used to deliver stimulation using a pair of 5 × 5 cm surface saline-soaked sponge electrodes at a constant current of 2.0 mA. tDCS was delivered exclusively during the Exposure phase with a maximum time of stimulation set at 20 min to comply with safety guidelines (Nietzsche et al., 2003; Iyer et al., 2005). We decided to exclude data from participants who did not complete the Exposure phase within the maximum stimulation time. The cathodal electrode was placed over the right cerebellum, 1 cm below and 4 cm right to the inion, while anodal electrode was placed over the right deltoid muscle. This montage was preferred to other head montages (for a review: van Dun et al., 2016) since it was shown to efficiently interfere with PA (Panico et al., 2016) and because we wanted to ensure selective stimulation of the right cerebellum. Moreover, the need to regularly change prism glasses did not allow to place the reference electrode on the buccinator muscle or the supraorbital area as in other experiments (e.g. Galea et al., 2011; Grimaldi and Manto, 2013; O'Shea et al., 2017, Panico et al., 2017). Stimulation was delivered over the right cerebellum, since participants had to use their right hand to perform the task (Schlerf et al., 2014; Pisella et al., 2005). Sham stimulation was performed in the same way as active stimulation but the stimulator was turned off after 30 s. This procedure ensured that participants felt the same itching sensation at the beginning of tDCS as participants assigned to the experimental group, and were thus blinded for the stimulation condition they had been assigned to (Gandiga et al., 2006).

2.3. Experimental Procedure

Fig. 1 illustrates the experimental procedure of this study. A pointing task was performed on a touch-sensitive screen before wearing prisms (Pre), during multiple-step exposure to wedge prisms (Exposure), and after Exposure (three phases: Post 1; Deadaptation; Post