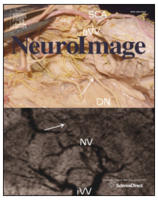
NeuroImage 124 (2016) 248–255

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Functional connectivity between the cerebrum and cerebellum in social cognition: A multi-study analysis☆

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ARTICLE INFO

Article history:
Received 8 June 2015
Accepted 1 September 2015
Available online 5 September 2015

Keywords:
Social cognition
Mentalizing
Cerebellum
Functional neuroimaging
Functional connectivity

ABSTRACT

This multi-study connectivity analysis explores the functional connectivity of the cerebellum with the cerebrum in social mentalizing, that is, understanding the mind of another person. The analysis covers 5 studies ($n = 92$) involving abstract and complex forms of social mentalizing such as (a) person and group impression formation based on behavioral descriptions and (b) constructing personal counterfactual events (i.e., how the past could have turned out better). The results suggest that cerebellar activity during these social processes reflects a domain-specific mentalizing functionality that is strongly connected with a corresponding mentalizing network in the cerebrum. A significant pattern of connectivity was found linking the dorsal medial prefrontal cortex (mPFC) and the right temporo-parietal junction (TPJ) with the right posterior cerebellum, and linking the latter with the left TPJ. In addition, in the cerebrum, further connectivity was found through links of the bilateral TPJ with the dorsal mPFC, orbitofrontal cortex and between right and left TPJ. The discussion centers on the role of these cerebro-cerebellar connections in matching external information from the cerebrum with internal predictions generated by the cerebellum. These internal predictions might involve the sequencing of the person's behaviors.

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Introduction

Social cognition is the capacity to infer the social purpose of the behaviors of other persons or the self (i.e., "body" reading) and their state of mind (i.e., "mind" reading or mentalizing). Although the focus of neuroscientific research during the last decade has been on the cerebrum and core areas that support social reasoning (for reviews, see Molenberghs et al., 2012; Schurz et al., 2014; Van Overwalle and Baetens, 2009; Van Overwalle, 2009) a potential role of the cerebellum has recently attracted increased attention. Van Overwalle et al. (2014) conducted a large-scale meta-analysis on social cognition and the cerebellum that included over 350 functional magnetic resonance imaging (fMRI) studies. They found robust clusters in the cerebellum that showed activity in about one third of the social-cognitive studies, and in about all studies that involved more complex and abstract social inferences (cf. Trope and Liberman, 2010). Abstract mentalizing involves, for instance, person judgments as opposed to visual descriptions of the same behaviors (e.g., respectively judging "why" versus "how" a person is reading a book), or the more distant and abstract past or future, or even hypothetical events as opposed to the momentary present.

In a later paper, these meta-analysis results were interpreted in terms of domain-specific social processes (Van Overwalle et al., 2015a). It was argued that the cerebellar clusters involved in social cognition during mind and body reading show a strong overlap with the default and somatomotor networks respectively, as identified by Buckner et al. (2011; see also Buckner, 2013). Buckner et al. (2011) investigated the large-scale organization of circuits between the cerebrum and cerebellum using resting-state functional connectivity neuroimaging for a total sample of 1000 participants, resulting in a complete topography of the cerebellum in relation to major networks of the cerebrum (Yeo et al., 2011). This topography revealed similar network structures in the cerebellum as in the cerebrum, spanning approximately the same relative volumes. In particular, Van Overwalle et al. (2015a) found a large overlap between the clusters identified in their meta-analysis of (a) social mentalizing ("mind" reading; Schurz et al., 2014; Van Overwalle, 2009) and the mentalizing/default network of Buckner et al. (2011), as well as between (b) social behavior understanding (i.e., "body" reading; interpreting the intentionality of humans by movements of their hands, face, legs etc.; Molenberghs et al., 2012; Van Overwalle and Baetens, 2009) and the somatomotor networks of Buckner et al. (2011). A recent meta-analytic connectivity analysis involving 34 studies ($n = 578$) strongly supported the unique functional cerebro-cerebellar

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☆ This research was funded by a Strategic Research Program (SPR15) awarded by the Vrije Universiteit Brussel, Belgium.

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http://dx.doi.org/10.1016/j.neuroimage.2015.09.001
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links of these two distinct mentalizing/default and somatomotor networks (Van Overwalle et al., 2015b). It is important to note that these meta-analytic connectivity results provided independent support for these two networks under social task conditions that greatly differ from Buckner et al.'s (2011) resting state condition. Taken together, this research demonstrates the role of domain-specific specialization in the cerebellum into distinct networks for “mind” reading (a social mentalizing functionality; Schurz et al., 2014; Van Overwalle, 2009) and “body” reading (a mirror/somatomotor functionality; Molenberghs et al., 2012; Van Overwalle and Baetens, 2009) which implies different inputs, computations, and outputs of these networks.

However, the earlier meta-analytic connectivity analysis by Van Overwalle et al. (2015b) has some major limitations. A first limitation is that the unit of analysis is a complete study, not a participant. Specifically, this type of analysis uncovers which areas have shared activity in each study (i.e., which peak coordinates are reported together) and how systematic findings are across studies. However, it does not test whether shared activity also holds within the single brain of the participants. A second limitation is that the specificity and direction of the connectivity cannot be assessed, because there is no access to the original data and the exact timing of the shared activity. Thus, for instance, it does not allow to identify in detail the functional connections between mentalizing areas in the cerebrum and in the cerebellum.

To amend these limitations, the present analysis focuses on the mentalizing network, and collectively analyzes the data of 5 published studies ($n = 92$) from our lab. These studies were selected because they showed activity in the mentalizing network in both the cerebrum and cerebellum, and involved higher-level complex social inferences involving a person's traits, a person's past, and group stereotypes (Baetens et al., 2014; Ma et al., 2012a, 2012b; Van der Cruyssen et al., 2015; Van Hoeck et al., 2013). The selected studies also used the same experimental and scanning procedures and software program (SPM). Functional connectivity using psycho-physiological interaction (PPI) analysis (O'Reilly et al., 2012) on each participant within these studies was conducted, followed by a group-wise analysis across all participants and studies. One study also included a non-social condition in which characteristics of objects (instead of a person traits) were analyzed (Baetens et al., 2014), and these connectivity results are also briefly reported for comparison.

How is the cerebro-cerebellar connectivity organized at a deeper anatomical level of neural tracts and connections? Earlier animal studies indicated that the majority of these connections are characterized by contralateral closed-loop circuits (Kelly and Strick, 2003). That is, an area of the cerebrum typically projects to a contralateral area of the cerebellum, and receives input from that same cerebellar area. Both areas thus form a closed connectivity loop. However, recent research has qualified this interpretation and has shown that cerebro-cerebellar connectivity may be more open-ended, whereby the cerebellum receives inputs from multiple functional cerebral areas, including orbitofrontal areas from contra- and ipsilateral hemispheres (Suzuki et al., 2012). Human research exploring structural connectivity using diffusion imaging confirmed that cerebral fiber tracts connect predominantly to contralateral cerebellar areas, although they also show important ipsilateral connections (Salmi et al., 2010; Sokolov et al., 2014). A large-scale functional connectivity study revealed that 20%–30% of the connections from the cerebral cortex terminate on ipsilateral areas in the cerebellum (Krienen and Buckner, 2009).

Ito (2008) presented an influential theory on the functionality of the cerebellum, stressing its role in making internal predictions on sequences in motor and cognitive/mental processes (see also discussion section). Ito (2008) predicted that “to provide an internal model for mental activity, the cerebellar hemispheres should have connections with the prefrontal and temporo-parietal cortices”. Likewise, the meta-analytic connectivity analysis of Van Overwalle et al. (2015b) suggests a strong connectivity between mentalizing areas of the cerebrum and the cerebellum. Consequently, our hypothesis is that there is functional connectivity between mentalizing areas of the cerebrum and mentalizing areas of the cerebellum. It remains to be elucidated which mentalizing areas are most involved in the neural communication with the cerebellum, and whether these functional connections involve the same areas (closed-loops) or different areas (open-ended loops). At the level of the cerebrum, the analysis was focused on the medial prefrontal cortex (mPFC), medial parietal cortex (precuneus/posterior cingulate) and the bilateral temporo-parietal junction (TPJ), which are core mentalizing areas (Schurz et al., 2014; Van Overwalle and Baetens, 2009; Van Overwalle, 2009). Al the level of the cerebellum, the analysis focused on the mentalizing/default network (Buckner et al., 2011) located in the anterior and posterior parts of both cerebellar hemispheres.

Method

Selected studies

The current connectivity analysis was conducted on five published fMRI studies from our lab (Baetens et al., 2014; Ma et al., 2012a,b; Van der Cruyssen et al., 2015; Van Hoeck et al., 2013). All studies involved human actions, either depicted visually (e.g., showing a person reading a book) or described verbally by short sentences (e.g., “gives his mother a slap”) or by verbal cues triggering personal memories of the participants. All studies revealed an increased activation in core mentalizing areas including the mPFC, precuneus and bilateral TPJ, as well as in the cerebellum, during the critical condition in comparison with a control condition.

Participants

Participants in all of the studies were healthy and right-handed (formally assessed) with no neurological or psychiatric antecedents. Participants' total number, gender and age is given in Table 1. The studies were approved by the Medical Ethics Committees of the University Hospital of Ghent (where the study was conducted) and the Vrije Universiteit Brussel (of the principal investigator FVO). A written informed consent was obtained from each participant.

Design, stimulus material and procedure

The essentials of the design (primary contrast between the critical experimental versus control/contrast conditions), as well as the material and procedure of each study are summarized below (for details see Baetens et al., 2014; Ma et al., 2012a,b; Van der Cruyssen et al., 2015; Van Hoeck et al., 2013). The main results of each study are listed in Table 2.

- Study 1 (Ma et al., 2012a): Inconsistent (>consistent) trait inferences on the basis of brief trait-implying behavioral sentences ($n = 15$ intentional and $n = 15$ spontaneous trait inferences). The participants read 16 sets of 3 or 4 behavioral sentences that implied a social trait of a person (e.g., "Jun gives a smile" implying friendly). In the experimental condition, the last sentence was inconsistent with the prior sentences, while in the contrast condition the last sentence was consistent.
- Study 2 (Ma et al., 2012b): Trait (>no trait) inferences on the basis of brief trait-implying behavioral sentences ($n = 13$). In the experimental condition, the participants read 20 behavioral sentences that implied a social trait of a person (similar as in Study 1); while in the contrast condition they read 20 no-trait sentences describing intransitive behaviors which did not involve any interaction with other objects or persons (e.g., “Tolvan moves her right hand”).
- Study 3 (Baetens et al., 2014): Trait inferences (>visual descriptions) on the basis of photos depicting human behavior ($n = 18$). In the experimental condition, participants saw 30 pictures of a person

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