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Tell me twice: A multi-study analysis of the functional connectivity between the cerebrum and cerebellum after repeated trait information ☆

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This multi-study analysis (6 fMRI studies; 142 participants) explores the functional activation and connectivity of the cerebellum with the cerebrum during repeated behavioral information uptake informing about personality traits of different persons. The results suggest that trait repetition recruits activity in areas belonging to the mentalizing and executive control networks in the cerebrum, and the executive control areas in the cerebellum. Cerebral activation was observed in the executive control network including the posterior medial frontal cortex (pmFC), the bilateral prefrontal cortex (PFC) and bilateral inferior parietal cortex (IPC), in the mentalizing network including the bilateral middle temporal cortex (MTC) extending to the right superior temporal cortex (STC), as well as in the visual network including the left cuneus (Cun) and the left inferior occipital cortex. Moreover, cerebellar activation was found bilaterally in lobules VI and VII belonging to the executive control network. Importantly, significant patterns of functional connectivity were found linking these cerebellar executive areas with cerebral executive areas in the medial pmFC, the left PFC and the left IPC, and mentalizing areas in the left MTC. In addition, connectivity was found between the cerebral areas in the left hemisphere involved in the executive and mentalizing networks, as well as with their homolog areas in the right hemisphere. The discussion centers on the role of these cerebello-cerebral connections in matching internal predictions generated by the cerebellum with external information from the cerebrum, presumably involving the sequencing of behaviors.

1. Introduction

When maneuvering through the social environment, it is crucial to consider the evidence on someone's behavior for making accurate assessments and predictions about that person. Telling someone for a second time about a person's behavior is therefore an important step in a continuous process to confirm, refine or change our impressions about people's trait characteristics. The aim of the present study is to explore this updating process when trait-implying information is repeated, and in particular to investigate the contribution of the cerebellum in addition to that of the cerebrum. We not only focus on brain areas that are recruited during this process, but also on the functional connectivity between these areas.

The capacity to accurately infer the underlying mental states and traits of a person is termed "mind reading" or mentalizing. Social neuroscientific research has shown that several social judgments involving mind reading recruit a number of brain areas, collectively termed the mentalizing network (for meta-analyses, see Schurz et al., 2014; Van Overwalle, 2009). Based on a suggestion by Van Overwalle (2009) and recent research (Ma et al., 2012a, 2012b), it appears that the temporo-parietal junction (TPJ) is primarily recruited when analyzing the intention underlying behaviors, whereas the medial prefrontal cortex (mPFC) is more particularly involved in trait inferences (Ma et al., 2011; Mitchell et al., 2006; Mitchell et al., 2004; Mitchell et al., 2005; Schiller et al., 2009). The mentalizing network also encompasses posterior medial areas such as the precuneus and posterior cingulate cortex (PCC; e.g., Mitchell et al., 2005), involved in the reconstruction of autobiographic memories, as well as temporal areas such as the

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middle temporal cortex (MTC; e.g., Bhanji and Beer, 2013; Mende-Siedlecki et al., 2013a, 2013b) presumably supporting the understanding of semantic knowledge, social scenarios and stories (Andrews-Hanna et al., 2014). The mentalizing network is a large subsystem of the default network that is recruited when participants are at rest under the scanner (Andrews-Hanna et al., 2010; Gusnard and Raichle, 2001; Raichle et al., 2001; Spreng et al., 2013) and which primes an intentional stance to mentalize about and understand other people (Spunt et al., 2015).

Research on repeated presentation of trait-relevant behavioral information for updating person impressions revealed that this recruits not only the mentalizing network, but also the executive control network (Bhanji and Beer, 2013; Cloutier et al., 2011a, 2011b; Ma et al., 2012a, 2012b; Mende-Siedlecki et al., 2013; Mende-Siedlecki et al., 2013; Schiller et al., 2009). The executive control network engages in action-outcome predictions, and its signals serve as early warnings for the likelihood of errors (Alexander and Brown, 2011; Brown, 2013; Nee et al., 2011; Shenhav et al., 2013). Therefore, potential or actual inconsistencies with earlier trait impressions after trait repetition may activate this network. Key areas in this network, such as the posterior medial frontal cortex (pmFC; including the dorsal part of the anterior cingulate cortex or dACC) monitors conflicts (Botvinick et al., 2004; Botvinick et al., 1999; Kerns et al., 2004) and errors (Carter, 1998; Kiehl et al., 2000; Van Veen et al., 2004), while the bilateral prefrontal cortices (PFC; including the inferior frontal cortex, IFC) that subserve working memory contribute to resolving these conflicts and attaining one's goals. The inferior parietal cortex (IPC) may also aid in controlling appropriate task execution as it subserves maintenance in working memory (Champod and Petrides, 2010; McNab et al., 2008; Van Hecke et al., 2010; Vergauwe et al., 2015).

Till recently, social neuroscientific research has focused predominantly on the role of the cerebrum and core areas that support social mentalizing (for reviews see Schurz et al., 2014; Van Overwalle, 2009). However, there is a growing interest in the contribution of the cerebellum. In a large-scale meta-analysis on social mentalizing and the cerebellum that included over 350 functional magnetic resonance imaging (fMRI) studies, Van Overwalle et al. (2014) found robust activation of the cerebellum, primarily in the posterior bilateral lobules VI and Crus 1. Cerebellar activity was found in about one third of most mentalizing 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 trait judgments as opposed to visual descriptions of the same behaviors (e.g., respectively judging "why" versus "how" a person is reading a book; Baetens et al., 2015). In support of this view, recent connectivity analyses during social judgments applying meta-analytic connectivity (34 fMRI studies, 578 participants; Van Overwalle et al., 2015b) as well as functional connectivity of individual participants pooled across multiple studies (5 fMRI studies, 92 participants; Van Overwalle and Mariën, 2016) found evidence for robust functional cerebro-cerebellar links involving the mentalizing/default network (Buckner et al., 2011).

Undoubtedly, updating trait impressions is also a complex process that not only recruits mentalizing, but also executive control processes in order to deal with changes of the current activated trait based on new information or with an enrichment of the current trait with new behavioral examples. Given this complexity, trait impressions may also recruit the cerebellum. To explore the role of the mentalizing and executive networks during trait information updating at the level of the cerebellum, and the potential connectivity with the cerebrum, the present analysis collectively analyses the data of 6 fMRI studies (146 participants) from our lab. These studies were selected because they involved repeated trait formation that confirmed an initial behavioral description and showed enhanced activity in the mentalizing network in both the cerebrum and cerebellum during these trait repetitions. Thus, only the cumulative effect of repetition, and not of inconsistency, was investigated (Heleven and Van Overwalle, 2016a, 2016b, 2016c; Ma et al., 2014b, 2014b; Van Overwalle et al., 2016). Moreover, to investigate trait repetition decoupled from person updating processes, in each study we selected a condition involving consistent trait-implying behaviors performed by different persons. Consequently, no processes related to the person (e.g., readjustment of a trait-link with a specific person) can confound the trait updating process itself. Note that a defining characteristic of abstract concepts such as traits is that they refer to many concrete behaviors in different contexts (Barsalou and Wiemer-Hastings, 2005). Presenting multiple behavioral examples of a trait (e.g., giving a compliment, giving a hug) without necessarily referring to a specific person, may in and of itself enrich and refine the trait's meaning without an adjustment of the core abstract trait concept.

Our hypothesis with respect to brain activation is that repetition of trait-implying information will generate activation in mentalizing areas to identify the implied trait as well as in the executive control areas to integrate multiple pieces of information. However, because the updating information in the present analysis does not change the overall goal of the behaviors and their implied traits, we expect relatively little activity in the TPJ and mPFC responsible for goal and trait inferences respectively (Ma et al., 2012a, 2012b; Van Overwalle, 2009). Indeed, the selected studies demonstrated that repeating trait-relevant information typically leads to suppression of activation in the mPFC; such suppression is diagnostic of the neural population encoding the trait(Heleven and Van Overwalle, 2016a; Ma et al., 2014b, 2014b; Van Overwalle et al., 2016).

To explore functional connectivity, psycho-physiological interaction (PPI) analyses (Friston et al., 1997; O'Reilly et al., 2012) were conducted on all selected studies. Briefly put, a PPI analysis explores to what extent the activity in one brain area after repetition of trait-relevant information further increases activity in some other areas. It is important to note that this analysis does not identify the mere existence of neural crosstalk between two brain areas, but rather how much this crosstalk is increased after trait information is repeated. Our prediction is that trait repetition increases the connectivity between mentalizing and executive areas of the cerebrum and the cerebellum. It remains to be elucidated which mentalizing and executive areas are most involved in the neural communication with the cerebellum, and whether these functional connections are realized only within the same network, or show crosstalk between networks.

2. Method

2.1. Selected studies

The current connectivity analysis was conducted on six fMRI studies from our lab (Heleven and Van Overwalle, 2016a, 2016b, 2016c; Ma et al., 2014b, 2014b; Van Overwalle et al., 2016). As noted earlier, these studies were selected because they showed activity in the mentalizing network in both the cerebrum and cerebellum, and involved initial trait formation on the basis of a first (prime) behavioral description followed by trait updating on the basis of a second (target) behavioral description. Importantly, we selected in all studies a condition in which the repeated information implied the same (consistent) trait, among other conditions that involved inconsistent or irrelevant information. Moreover, different persons were involved in the prime and target behaviors. The selected studies also used the same experimental

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