



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

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## ABSTRACT

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.

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## 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-implicating 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-implicating 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-implicating 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

and scanning procedures and software program (SPM). Across all studies and participants, we conducted a pooled analysis of the recruitment of brain areas, as well as of the functional connectivity using PPI.

The critical trials that are investigated here involved two sentences describing human actions (e.g., “gives his brother a hug”, “gives his mother a compliment”). The first (prime) and second (target) sentence implied the same trait (e.g., friendly), but the persons in the two sentences differed (i.e., there was never repetition of persons). The persons were described in Star Trek-like names to avoid any familiarity, except in two studies which involved names of close friends or family (Heleven and Van Overwalle, 2016a) or the self (Heleven and Van Overwalle, 2016c). All the sentences were in Dutch and consisted of four to seven words that were presented at once in the middle of the screen for a duration of 5.5 s. Each prime and target sentence was separated by a variable interstimulus interval of 2.5 to 4.5 s randomly drawn from a uniform distribution, during which participants passively viewed a fixation crosshair. After each trial, a fixation cross was shown for 500 ms and then the trait question appeared until a response was given.

Most important for the present analysis, a target > prime contrast investigates repetition enhancement or the increase of activation given repetition of consistent trait-implying information. This enhancement is explained as an increase in mental effort necessary to process traits, and indicates which brain areas are involved in this process.

## 2.2. Participants

Participants in all of the studies ( $n=146$ ) were healthy and right-handed (formally assessed by means of the Edinburgh Handedness Inventory) with no neurological or psychiatric antecedents. Participants' total number in each study 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.

## 2.3. Stimulus material and procedure

The essentials of the design, the material and procedure of each study are detailed in each study (see Heleven and Van Overwalle, 2016a, 2016b, 2016c; Ma et al., 2014b, 2014b; Van Overwalle et al., 2016). In summary, in the critical condition across all studies that we analyze here, participants read a first (prime) sentence (e.g., “gives his brother a hug”) followed by a second (target) sentence (e.g., “gives his mother a compliment”) implying the same trait

(e.g., friendly). Next, they were asked: “is [person's name] friendly/nice/generous/trustworthy/honest” (or the trait opposites “unfriendly/unkind/stingy/untrustworthy/dishonest”; fully counter-balanced) and participants responded by pressing the appropriate response key varying between 1 (*not at all*) to 4 (*very much*). For familiar persons, to avoid inconsistency with one's own long-lasting impressions, the question was slightly reworded so as to ask whether this person was “often” friendly and so on, and responses ranged between 1 (*never*) to 4 (*always*). Occasionally, a trait judgment was requested after the first prime sentence (i.e., singleton condition of no interest consisting of as many trials as the other conditions) to make sure that participants read all sentences attentively. Valence of the sentences was fully counter-balanced. All trials were presented in a random order for each participant.

Apart from these similarities, differences between studies mainly involved the other conditions in the study with different prime sentences. Specifically, in the other conditions, the target sentences also implied a trait (e.g., “gives his mother a compliment”) but were preceded by the following prime sentences (see summary in Table 2):

1. Van Overwalle et al. (2016): Sentences implying ability-related traits (e.g., “is weak in maths”) or no traits (trait-irrelevant: e.g., “looks at the snow falling”).
2. Ma et al. (2014a): Sentences implying opposite traits (e.g., “gives his mother a slap”) or no traits (trait-irrelevant).
3. Ma et al. (2014b): Sentences implying no traits (trait-irrelevant) or implying characteristics of objects (e.g., “the bread smells good”).
4. Heleven and Van Overwalle (2016a): Trait-implying sentences involving the same familiar person (i.e., family or close friend) or implying no trait (trait-irrelevant).
5. Heleven and Van Overwalle (2016b): Same as 4, but involving unfamiliar persons.
6. Heleven and Van Overwalle (2016c): Same as 4, but involving familiar persons or the self (“I”).

## 2.4. Imaging procedure

The imaging procedure was identical for all studies. Images were collected with a 3 Tesla Magnetom Trio MRI scanner system (Siemens medical Systems, Erlangen, Germany), using a head coil with 8 (Ma et al., 2014b, 2014b; Van Overwalle et al., 2016) or 32 (Heleven and Van Overwalle, 2016a, 2016b, 2016c) channels. One might generally expect a higher stimulus-to-noise ratio given a coil with more channels. However, Kaza et al. (2011) reported that without pre-scan normalization (as is the case here), a 32-channel head coil might reveal less activation in subcortical areas and the cerebellum,

**Table 1**  
Number of participants involved in the PPI analysis for each ROI seed.

Study	Total	pmFC	l IFC	l preC	l MTC	l IPC	l Cun	l IOC	r Ins	r STC	r MTC	r MTC2	r IPC	l Cer6	l Cer7	r Cer6	r Cer7	Thal
Van Overwalle et al. (2016)	17	16	16	17	16	15	16	14	13	15	13	15	16	8	8	9	11	12
Ma et al. (2014a)	17	17	17	17	17	17	17	15	17	15	14	16	17	11	13	12	13	15
Ma et al. (2014b)	17	17	16	16	14	14	14	11	16	13	15	14	16	8	8	9	10	12
Heleven and Van Overwalle (2016a)	42	37	40	38	33	39	36	36	36	31	33	32	34	22	22	24	20	25
Heleven and Van Overwalle (2016b)	28	25	25	25	27	26	27	22	27	26	26	25	28	20	20	19	19	22
Heleven and Van Overwalle (2016c)	25	23	23	22	22	20	23	22	20	18	21	16	18	12	12	16	15	17
Total across all studies	146	135	137	135	129	131	133	120	129	118	122	118	129	81	83	89	88	103
% across all studies		92%	94%	92%	88%	90%	91%	82%	88%	81%	84%	81%	88%	55%	57%	61%	60%	71%

Note: The studies are listed in the chronological order in which they were conducted and initially analyzed. ROIs are defined in the next tables.

**Table 2**

Illustration of the persons in the studies and of the sentences in the critical (i.e., repeated) and other conditions (i.e., Alternative and No Trait prime sentences).

Study	Persons	Alternative prime sentence	No trait prime sentence	Critical prime sentence	Critical target sentence
Van Overwalle et al. (2016) Ma et al. (2014a)	Star-Trek like Star-Trek like	<i>Ability</i> : is weak in maths <i>Opposite</i> : gives his sister a slap <i>Object</i> : the bread smells good	<i>All Studies</i> : looks at the snow falling	<i>All Studies</i> : gives his brother a hug	<i>All Studies</i> : gives mother a compliment
Ma et al. (2014b)	Star-Trek like	–			
Heleven and Van Overwalle (2016a)	Family & friends	–			
Heleven and Van Overwalle (2016b)	Star-Trek like	–			
Heleven and Van Overwalle (2016c)	"I", family & friends	–			

although *t*-values (which determine the threshold of a cluster) were not significantly affected. Stimuli were projected onto a screen at the end of the magnet bore that participants viewed by way of a mirror mounted on the head coil. Stimulus presentation was controlled by E-Prime 2.0 ([www.pstnet.com/eprime](http://www.pstnet.com/eprime); Psychology Software Tools) under Windows. Foam cushions were placed within the head coil to minimize head movements. A high-resolution T1-weighted structural scan (MP-RAGE) was collected followed by one functional run (30 axial slices; 4 mm thick; 1 mm skip). Functional scanning used a gradient-echo echoplanar pulse sequence (TR=2 s; TE=33 ms; 3.5 × 3.5 × 4.0 mm in-plane resolution).

## 2.5. Image processing and statistical analysis

The fMRI data were preprocessed and analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK), except for two early studies that used SPM5 (Ma et al., 2014a; Van Overwalle et al., 2016). Given that the preprocessing steps were not altered between these two successive versions of SPM (except for movement artifacts, see below), we started our new analyses from the existing preprocessing and first-level (individual) analyses. If anything differed between versions, we should only expect an improvement of signal-to-noise ratio in the studies conducted and analyzed later. The data were collected in a single functional run, and preprocessed to remove sources of noise and artifacts. Functional data were corrected for differences in acquisition time between slices for each whole-brain volume, realigned within and across runs to correct for head movement, and coregistered with each participant's anatomical data. Functional data were then transformed into a standard anatomical space (2 mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurological Institute). Normalized data were then spatially smoothed (6 mm full-width-at-half-maximum [FWHM]) using a Gaussian kernel.

The preprocessed data in SPM8 were additionally examined for excessive motion artifacts and for correlations between motion or global mean signal and any of the conditions using the Artifact Detection Tool software package (ART; [www.nitrc.org/projects/artifact\\_detect](http://www.nitrc.org/projects/artifact_detect)). Outliers were identified in the temporal difference series by assessing between-scan differences (Z-threshold: 3.0, scan to scan movement threshold: 0.5 mm; rotation threshold: 0.02 radians). These outliers were omitted in the analysis by including a single regressor for each outlier. Participants included in the studies had less than 10% outliers and showed no correlations between motion and experimental design or global signal and experimental design (see Table 1).

The timing for the analysis of all conditions was set at the start of the behavioral sentences. Statistical analyses were performed using the general linear model of which the event-related design

was modeled with one regressor for each condition, using a canonical hemodynamic response function and 6 movement artifact regressors, and when using ART, additional outlier vectors. A default high-pass filter of 128 seconds was used and serial correlations were accounted for by the default autoregressive AR (1) model. All anatomical labels were derived from the SPM Anatomical Toolbox (although "gyrus" was replaced by the more general "cortex").

## 2.6. Target > prime contrast

For the present analysis, we first computed target > prime contrasts for the consistent trait condition. This analysis was conducted at the second (group) level with SPM8, using the parameter estimates for each participant from the original studies, and with a group level threshold for the peaks of  $p < .0001$  FWE-corrected and voxels > 100. This analysis reveals the areas of significant activation during trait repetition, which were subsequently used to create *post hoc* regions of interest (ROI) that served as seeds for the connectivity analysis. To control for potential procedural differences between studies (cf. Table 2) and between scan procedures, the same analysis was repeated with two additional covariates/regressors in the design, reflecting (a) each individual study and (b) each coil (8 or 32 coil).

## 2.7. Connectivity analysis

To explore functional connectivity, novel PPI analyses were conducted on all studies using SPM8. A PPI analysis tests the hypothesis that activity in one brain area can be explained by an interaction between the presence of a cognitive process and activity in another part of the brain. A first, psychological regressor (or cognitive process) in the PPI analysis is a contrast revealing a social judgment of interest (e.g., target > prime sentence). A second, physiological regressor is the activity in each ROI selected as seed region. A third regressor represents the interaction between the first and second regressors, that is, how much the psychological process increases activation in the seed ROI. A PPI analysis focuses on the connectivity with this interaction regressor, and so identifies how the activity in the ROI seed region results in increased activity at other locations of the brain given the cognitive process (Friston et al., 1997). Many of the parameters used in this analysis are similar to those used in an earlier functional connectivity analysis pooled across multiple studies (Van Overwalle and Mariën, 2016).

To run the PPI analysis, we used similar parameters for the cerebrum and cerebellum, except that given the relatively smaller volume of the cerebellum, we took for the ROI definition a radius of 8 and 5 mm in the cerebrum and cerebellum



**Table 3**Trait repetition contrasts involving second trait-implying sentence (target) > first trait-implying sentence (prime) across all studies ( $n=146$ ).

Cluster and anatomical label		ROI	x	y	z	t	Voxels	Covariates
1	l Posterior Medial Frontal Cortex	pmFC	−2	12	52	14.37	10,200	0
	l Inferior Frontal Cortex	l IFC	−48	16	26	13.44		0
	l Precentral Cortex	l preC	−40	8	34	13.36		41
2	l Cuneus	l Cun	−16	−88	0	12.72	4618	0
	l Inferior Occipital Cortex	l IOC	−32	−76	−6	11.16		0
	l Middle Temporal Cortex	l MTC	−56	−40	4	12.23		0
3	l Inferior Parietal Cortex	l IPC	−30	−56	48	13.40	11,538	0
	r Inferior Parietal Cortex	r IPC	36	−52	50	12.56		0
	r Insula	r Ins	36	24	0	11.84		108
4	r Middle Temporal Cortex	r MTC	50	−36	2	9.58	645	0
	r Middle Temporal Cortex	r MTC2	62	−42	−2	7.11		17
	r Superior Temporal Cortex	r STC	48	−28	−4	9.21		0
5	r Cerebellum Lobule VI	r Cer6	8	−72	−30	10.11	288	0
	l Cerebellum Lobule VI	l Cer6	−8	−72	−24	9.12		0
	l Cerebellum Lobule VIIa Crus I	l Cer7	−12	−72	−32	7.96		0
6	r Cerebellum Lobule VIIa Crus I	r Cer7	34	−60	−30	9.23	142	0
7	r Thalamus	Thal	12	−16	8	7.46	85	0
8	l Hippocampus	−	−16	−36	14	6.89	19	None
9	l Cerebellum Lobule VI	−	−28	−60	−30	7.62	40	None

Note: Clusters thresholded at FWE-corrected  $p < .0001$ . x, y, z = Montreal Neurological Institute (MNI) coordinates of the peak values; l=left; r=right, ROI=Region of Interest created by a sphere around the peak voxel as center for the subsequent connectivity analysis with labels derived from SPM's Anatomical Toolbox,  $t=t$ -values of the peak activation, covariates=distance in mm of the peak coordinates from the same analysis with study and coil as additional covariates/regressors in the design, none=not above threshold in that analysis.

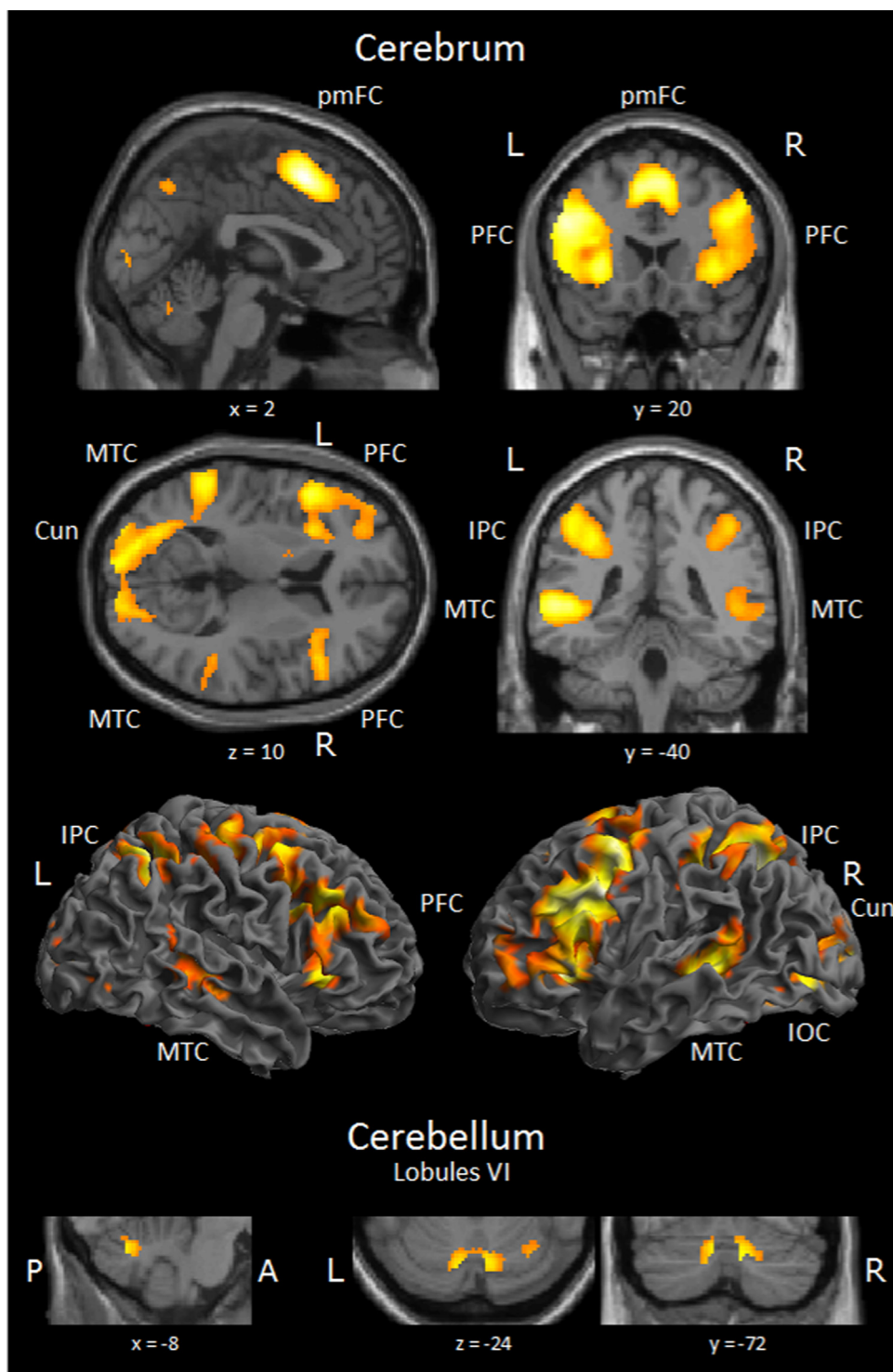
respectively, and twice this radius for detecting both connectivity and activation (see details below). We first computed the statistical target > prime contrasts (for the condition in which the persons differed as described earlier) at the first (participant) level. Second, we created group-based ROIs by taking a sphere (with a radius of 8 mm for the cerebrum and 5 mm for the cerebellum) around the centers of significant clusters in the prior group-based analysis (see also Table 3), after setting a whole-brain threshold of the contrast at  $p < 0.05$  (uncorrected) with a minimum voxel extent of 5. This liberal threshold ensured that most participants were included in the analysis. Third, for each participant, the nearest local maximum in the group-based ROI was identified. Around that shifted center, an individually-tailored sphere with the same radius was created, which then served as seed region. If no seed ROI was found above the threshold, or if the shifted center was too far away from the original center ( $> 16$  mm for the cerebrum or 10 mm for the cerebellum) the participant was excluded from the subsequent PPI analysis of this particular seed region (see number of participants in each seed region in Table 1). Finally, a PPI analysis was conducted on all pooled (non-excluded) participants of all studies with a whole-brain threshold of  $p < 0.05$  (uncorrected, with minimum voxel extent 5). To analyze the resulting connectivity, brain activity correlated with the PPI interaction was explored using the same ROIs as before, but now taking a wider radius (16 mm for cerebral areas and 10 mm for cerebellar areas) so that no activation would go unnoticed. The smaller radius for the cerebellum ensured that the resulting (group-level) activation in cerebellar ROIs could only reflect major cerebellar activity. In the results section, activation at ROIs is discussed that survived  $p < .05$  after FWE correction.

### 3. Results

Table 3 and Fig. 1 show the activation in the cerebrum and cerebellum for the target > prime trait-implying sentence contrast ( $p < .0001$  FWE-corrected with  $> 100$  voxels). To control for potential procedural and scan differences between studies, the same analysis was repeated with “study” and “coil” as additional covariates/regressors in the design. As can be seen, the results of both analyses are highly similar, with the exception of a limited number of peaks that shifted their original position or fell below threshold (cf. last column of Table 3).

As predicted, activation in the cerebrum is found in the executive network including the pmFC, bilateral IFC extending to the left precentral cortex (preC), and the bilateral IPC extending to the right insula (Ins); as well as in the mentalizing network including the bilateral MTC and the right superior temporal cortex (STC). These activations in the executive and mentalizing networks were predicted from previous research, although the core mentalizing areas involving the TPJ and mPFC were not significantly recruited as we had anticipated. The activation localized in the precentral cortex and the insula, however, proved to be less reliable as the peaks showed a substantial shift ( $> 40$  and  $> 100$  mm respectively) in the analysis with covariates. These areas should therefore be treated with great caution. We also observed unexpected activation in the left cuneus (Cun) and the left inferior occipital cortex (IOC) of the visual network. As predicted, activation in the cerebellum was found in the executive network comprising lobules VI and VII bilaterally. No cerebellar areas from the mentalizing network were activated.

Finally, we also observed activation in subcortical cerebellar areas of the right thalamus (Thal) and left hippocampus (Hipp). That latter area and the left cerebellum lobule VI were the smallest ( $\leq 40$  voxels), and also fell below threshold in the analysis with



**Fig. 1.** Brain activation after trait repetition (target > prime contrast of trait-implicating sentences) in the cerebrum and the cerebellum ( $p < .0001$  FWE-corrected, > 100 voxels). pmFC=posterior medial Frontal Cortex, PFC=Prefrontal Cortex, IPC=Inferior Parietal Cortex, MTC=Middle Temporal Cortex, Cun=Cuneus, IOC=Inferior Occipital Cortex. L=left hemisphere, R=right hemisphere, P=Posterior, A=Anterior.

covariates. We therefore ignored these clusters in all subsequent analyses in order to focus on the most important and reliable findings.

We extracted from Table 3 ROIs centered around all the reported peaks (with a radius of 5 or 8 mm; see methods), which then served as seeds for the PPI analysis. The resulting activation in the target > prime contrast from the PPI analysis was measured in the same ROIs with a larger radius (of 10 or 16 mm) to detect all relevant activation. The connectivity results are presented in

Tables 4–6 ( $p < .05$  FWE-corrected), and visually summarized in Fig. 2. For a clear and coherent visual presentation, the ROIs from the same clusters (from Table 3) are shown together in Fig. 2, except when they were situated in a different hemisphere or at a medial location. In addition, the cerebellar ROIs were combined per hemisphere. To show that these cerebellar ROIs are located in the executive network, we visualized the network's contours using the 7-network parcellation by Buckner et al. (2011). Connectivity is shown in Fig. 2 when more than 2 out of 3 connections from a

**Table 4**

Functional connectivity from left cerebral seeds (clusters 1–2).

Cluster &	Seeds (8 mm):											
ROI (16 mm)	Cluster 1 (executive)											
	pmFC (–2 12 52)				l IFC (–48 16 26)				l preC (–40 8 34) *			
	x	y	z	p <sub>FWE</sub>	x	y	z	p <sub>FWE</sub>	x	y	z	p <sub>FWE</sub>
1 - pmFC	–6	4	60	.000	–6	4	60	.000	–6	4	60	.000
1 - l IFC					–38	10	22	.011	–40	12	22	.003
1 - l preC					–38	10	22	.011	–40	12	22	.003
2 - l MTC	–50	–38	6	.002	–56	–28	0	.000	–58	–30	0	.000
2 - l Cun	–12	–86	–2	.000	–16	–90	–4	.000	–16	–88	–2	.000
2 - l IOC	–32	–84	–6	.000	–22	–88	–4	.000	–34	–88	2	.000
3 - l IPC												
3 - r IPC												
4 - r MTC												
4 - r MTC2												
4 - r STC									54	–14	–8	.025
Cluster &	Seeds (8 mm):											
ROI (16 mm)	Cluster 2 (mentalizing)											
	l MTC (–56 –40 4)				l Cun (–16 –88 0)				l IOC (–32 –76 –6)			
	x	y	z	p <sub>FWE</sub>	x	y	z	p <sub>FWE</sub>	x	y	z	p <sub>FWE</sub>
1 - pmFC												
1 - l IFC									–42	12	24	.001
1 - l preC									–42	12	24	.001
2 - l MTC					–46	–38	2	.033				
2 - l Cun	–12	–88	–2	.000	–12	–88	–4	.000	–12	–88	–2	.000
2 - l IOC	–24	–88	–4	.000	–28	–88	–6	.000	–24	–88	–4	.000
3 - l IPC												
3 - r IPC												
4 - r MTC												
4 - r MTC2												
4 - r STC												

Note: Psycho-physiological analyses (PPI) thresholded at a FWE corrected  $p < .05$ . x, y, z=Montreal Neurological Institute (MNI) coordinates of the peak values; l = left; r = right; pmFC = posterior medial Frontal Cortex, IFC= Inferior Frontal Cortex, preC=precentral cortex, MTC=Middle Temporal Cortex, IPC=Inferior Parietal Cortex, Cun = Cuneus, IOC=Inferior Occipital Cortex, STC=Superior Temporal Cortex. Seeds were Regions of Interest (ROI) spheres with radius 8 mm. There were no significant PPI clusters in the insula and cerebellum. Between parentheses are tentative functions of the clusters according to Yeo et al. (2011). \* =less reliable seed.

cluster were significant (all  $p < .05$  FWE corrected), ignoring the two less reliable areas (preC and Ins).

Tables 4–5 and Fig. 2 show the connectivity from cerebral seeds. As expected, there is reliable connectivity between all ROIs of the executive network in the cerebrum. These executive ROIs also connect with the left MTC in the cerebrum, and the left IPC also with the right MTC. Many of these also connect to the visual ROIs (not shown in Fig. 2). Contrary to our hypothesis, none of the cerebral seed regions project to the cerebellum.

Table 6 (left panel) and Fig. 2 show the connectivity from cerebellar seeds. Consistent with our hypothesis, all cerebellar seeds (which all belong to the executive network) connect to cerebral ROIs involving the executive and mentalizing network, and predominantly so on the left and medial cerebral hemisphere. There are also connections to the visual network (not shown in Fig. 2).

None of the cerebral or cerebellar seeds connect to the subcortical thalamus. Nonetheless, Table 6 (right panel) reveals that this subcortical area connects to many cerebral ROIs involving the executive, mentalizing and visual network, in much the same way as the cerebellar seeds.

#### 4. Discussion

This analysis pooled together data from 6 fMRI studies to investigate whether trait adjustments after repetition of consistent

trait-implicating behavioral information recruits mentalizing and executive control areas, not only in the cerebrum but also in the cerebellum. In addition, the connectivity between the brain regions involved in mentalizing and executive control was investigated. A crucial role of the cerebellum in social reasoning was recently pointed out in a large-scale meta-analyses (Van Overwalle et al., 2014, 2015a). Moreover, recent connectivity analyses at rest (Buckner et al., 2011) and during social judgment tasks (Van Overwalle et al., 2015b; Van Overwalle and Mariën, 2016) revealed that mentalizing areas located in the cerebellum are functionally connected with mentalizing areas in the cerebrum. However, these studies did not explore how trait judgments are updated after repeating consistent information among otherwise inconsistent or irrelevant information, decoupled from a specific person. To investigate trait updating itself without additional processes related to the resolution of inconsistent information or the updating of a person's impression, we reanalyzed several studies from our lab that involved a condition in which consistent trait-implicating behaviors were performed by different persons. The analysis revealed robust activation of the cerebellum even when there was no fundamental change in the implied trait nor coupling with a specific person. Note that another interesting comparison between trait-relevant and trait-irrelevant information failed to consistently recruit the cerebellum. Obviously, such a contrast does not reflect learning about trait concepts, which appears to be an important function of the cerebellum.

**Table 5**  
Functional connectivity from left and right cerebral seeds (clusters 3–4).

Cluster & ROI (16mm)	Seeds (8 mm):											
	Cluster 3 (executive)						Cluster 4 (mentalizing)					
	l IPC (-30 -56 48)			r IPC (36 -52 50)			r Ins (36 24 0)*			r MTC (50 -36 2)		
	x	y	z	x	y	z	x	y	z	x	y	z
1 - pmFC	-6	4	60	-4	2	64	-4	2	64	-4	2	64
1 - l IFC	-42	10	26	-48	16	24	-42	12	24	-44	16	26
1 - l preC	-42	10	26	-48	16	24	-42	12	24	-44	16	26
2 - l MTC	-54	-34	2	-52	-36	2	-58	-34	2	-58	-34	2
2 - l Cun	-14	-86	-4	-14	-88	0	-14	-88	0	-12	-88	-4
2 - l IOC	-34	-86	-2	-34	-84	-4	-34	-84	-4	-32	-84	-6
3 - l IPC	-22	-54	52	-22	-56	50	-24	-56	50	-32	-84	-6
3 - r IPC	52	-26	0	52	-32	4	52	-32	4	28	-58	50
4 - r MTC	52	-30	0	52	-32	4	52	-32	4	54	-14	-8
4 - r MTC2	54	-14	-8	54	-14	-8	52	-32	4	54	-14	-8
4 - r STC												

Note: Psycho-physiological analyses (PPI) thresholded at a FWE corrected  $p < .05$ , x, y, z = Montreal Neurological Institute (MNI) coordinates of the peak values; l = left; r = right; pmFC = posterior medial Frontal Cortex, IFC = Inferior Frontal Cortex, preC = precentral cortex, MTC = Middle Temporal Cortex, IOC = Inferior Occipital Cortex, Cun = Cuneus, Ins = Insula, STC = Superior Temporal Cortex. Seeds were Regions of Interest (ROI) spheres with radius 8 mm. There were no significant PPI clusters in the insula and cerebellum. Between parentheses are tentative functions of the clusters according to Yeo et al. (2011). \* = unreliable seed.

With respect to activations, the present analysis largely confirms our hypothesis of a strong activation in the pmFC, bilateral PFC/IFC and bilateral IPC which are part of the executive control network as defined in the cerebrum by Yeo et al. (2011). Specifically, the pmFC is recruited when inconsistencies in input information might arise (Ma et al., 2012a, 2012b) and the bilateral PFC is implicated in working memory which implements the resolution of conflicting information (Botvinick et al., 2004; Shenhav et al., 2013; Yeung et al., 2004). Also part of this control network is the IFC, which is recruited when general abstract concepts are processed (Wang et al., 2010) and the IPC, which subserves maintenance in working memory (Chamod and Petrides, 2010; McNab et al., 2008; Van Hecke et al., 2010; Vergauwe et al., 2015). In the cerebellum, activation was found bilaterally in lobules VI and VII, which are part of the executive network as identified by Buckner et al. (2011). In our view, activation of these executive control areas might be interpreted as an increase in mental effort necessary to change or renew the current activated trait, or for the comparison and integration of novel information in order to enrich a trait representation. Nevertheless, it is also possible that participants exerted more effort for the repeated presentation (in the second sentence) because they expected that a question would follow (while for the first sentence a question appeared only in less than 25% of the trials, i.e., singleton condition). Given a systematic involvement of the executive control network in trait repetition but not of the attention networks, alternative interpretations such as differences in attention allocation are less likely.

Overall, little activation was obtained in the mentalizing areas. This finding was predicted on the ground that the overall goal of the behaviors and the implied traits remained identical across the first and second behavioral description, so that no meaningful updating of one's impression was required. As mentioned before, there is even strong evidence for a decrease of mPFC activation when the same trait is processed twice (Heleven and Van Overwalle, 2016a; Ma et al., 2014a, 2014b; Van Overwalle et al., 2016). Mentalizing activity was only found for the bilateral MTC. This may suggest that participants focused on the concrete aspects of behaviors that changed across repetitions, and perhaps tried to imagine vividly these behaviors in order to infer their underlying social goal and trait. These processes typically recruit the MTC (Schurz et al., 2014). However, given that the left MTC is also involved in general semantic memory (Binder et al., 2009), it is possible that this activation merely reflects effortful attempts to fully understand the distinct behaviors in the sentences.

Activation was observed in some areas that was not predicted. Specifically, there was unexpected activation in the visual areas of the cuneus and occipital lobe. We suspect that participants checked the implication of the repeated trait information by reading the second sentence again on the screen, and so recruited the occipital lobe and cuneus related to visual word processing (Cohen et al., 2008). The activation in the subcortical thalamus is also unexpected – a recent detailed meta-analysis (Schurz et al., 2014) did not show robust activation in this area during trait inferences. This activation may have a similar origin, that is, the increased visual scrutiny of repeated information may have led to heightened sensory processing in the thalamus. The activation of the insula was also unexpected, but after statistically controlling for differences between the studies, appeared to be unreliable.

With respect to connectivity, the PPI analysis demonstrates considerable connectivity between the executive and mentalizing ROIs in the cerebrum, including the subcortical thalamus. There was no direct connectivity of cerebral seeds to the cerebellum. Future research is needed to uncover the subcortical role in social information updating, although the tight connectivity of the thalamus seems consistent with a supporting sensory function during visual checking of the repeated input, as alluded above.

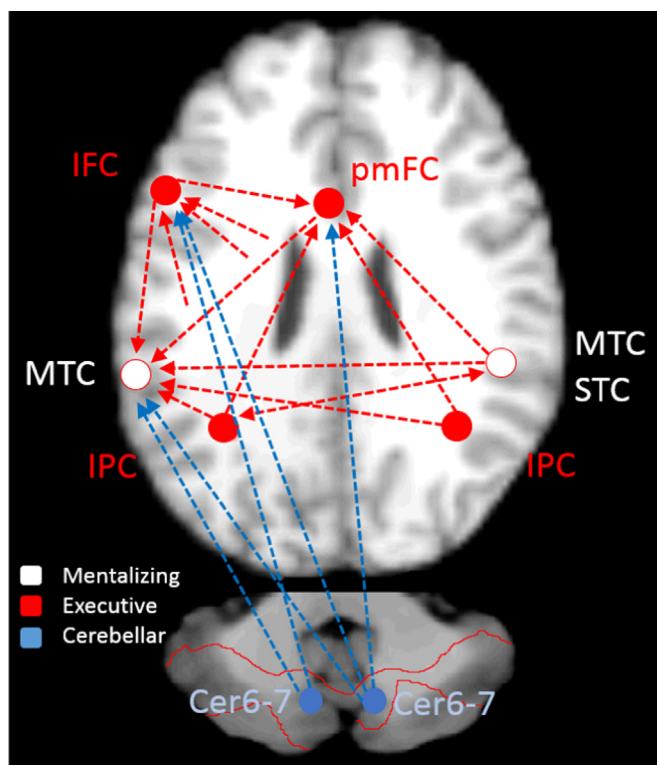


**Table 6**

Functional connectivity from bilateral cerebellar seeds (clusters 5–6) and subcortical cerebral seeds (cluster 7).

Cluster & ROI (16mm)	Cerebellar Seeds (5 mm):												Subcortical Seeds (8 mm):			
	Cluster 5 (executive)												Cluster 6 (executive)			
	l Cer6 (–8 –72 –24)				r Cer6 (8 –72 –30)				l Cer7 (–12 –72 –32)				r Cer7 (34 –60 –30)			
	x	y	z	p <sub>FWE</sub>	x	y	z	p <sub>FWE</sub>	x	y	z	p <sub>FWE</sub>	x	y	z	p <sub>FWE</sub>
1 - pmFC					–4	2	62	.034	–4	2	64	.021	–6	4	60	.011
1 - l IFC	–42	14	24	.020	–48	14	24	.039	–46	14	24	.000	–40	10	24	.042
1 - l preC	–46	0	46	.043	–48	14	24	.044	–46	14	24	.000	–40	10	24	.042
2 - l MTC	–54	–40	6	.000	–52	–40	4	.001	–56	–36	4	.000	–48	–40	4	.031
2 - l Cun	–14	–90	–4	.000	–14	–90	–4	.000	–14	–90	–4	.000	–12	–88	–2	.000
2 - l IOC	–34	–84	–4	.000	–34	–86	–2	.000	–34	–84	–4	.000	–32	–84	–4	.000
3 - l IPC																
3 - r IPC																
4 - r MTC																
4 - r MTC2																
4 - r STC	52	–18	–6	.019											54	–16
															–12	.036

Note: Psycho-physiological analyses (PPI) voxel-wise thresholded at a FWE corrected  $p < .05$ . x, y, z=Montreal Neurological Institute (MNI) coordinates of the peak values; l=left; r=right; Thal=Thalamus, pmFC=posterior medial Frontal Cortex, IFC=Inferior Frontal Cortex, preC=precentral cortex, MTC=Middle Temporal Cortex, IPC=Inferior Parietal Cortex, Cun=Cuneus, IOC=Inferior Occipital Cortex, Ins=Insula, STC=Superior Temporal Cortex, Cer6=Cerebellum Lobule VI, Cer7=Cerebellum Lobule VII. Seeds were Regions of Interest (ROI) spheres with radius 5 or 8 mm. Between parentheses are tentative functions of the clusters according to Buckner et al. (2011).



**Fig. 2.** Functional connectivity after trait repetition between the cerebellar and the cerebral clusters shown on horizontal slices. The location of each cluster is determined by the first mentioned ROI. The red and white color coding of the clusters and the cerebellar areas is from the 7-network of Buckner et al. (2011) and Yeo et al. (2011). Some clusters are subdivided along their lateral versus medial hemisphere, and the cerebellar ROIs (Cer6 and 7) are regrouped in the left versus right hemisphere (within red contours delineating the executive network). Arrows show PPI effects originating from ROI seeds on the other target ROIs and are shown when more than 2 out of 3 of these effects from a cluster were significant (all  $p < .05$  FWE corrected). For better visualization, the clusters and arrows involving the Pre-cuneus, Inferior Occipital Cortex and subcortical clusters are not shown, and the arrows involving the left IFC are only drawn in part. pmFC=posterior medial Frontal Cortex, IFC=Inferior Frontal Cortex, MTC=Middle Temporal Cortex, STC=Superior Temporal Cortex, IPC=Inferior Parietal Cortex, Cer6-7=Cerebellum Lobule VI-VII. The left–right hemisphere is in accordance with a left–right view.

In contrast, many bilateral cerebellar seeds belonging to the executive control network connected to many executive and some mentalizing ROIs (i.e., MTC) in the cerebrum, predominantly on the medial and left side. Thus, the cerebellar-cerebral connections involved no closed-loops, in which an area of the cerebrum typically emits output to and receives input from the same area of the cerebellum. Rather they formed open-ended loops, involving mainly connections within the executive network, with limited cross-talk with mentalizing areas. However, note that although a PPI analysis “suggests that activity in one area may be driven by activity in the [seed area] ... the direction of causality is unknown” (O’Reilly et al., 2012, p. 605), and this is because “there is no implication that the seed region is the driver rather than the driven area, or whether the connection is direct, rather than mediated by other areas” (p. 605). Thus, it is possible that some connectivity between cerebellum and cerebrum is always open, that is, does not depend on the specific contrast (i.e., second > first sentence) in the current PPI analysis and thus remains undetected. Moreover, it is also possible that some connections are indirect, organized via other brain areas, that were not included in our analyses. Apart from this, it is interesting to note that the majority of the activations and connections involve cerebral areas on the left hemisphere. Probably this is due to the verbal nature of the stimulus material.

The contralateral connectivity from the right cerebellar seeds in lobules VI and VII to the left cerebral clusters is consistent with earlier anatomical evidence showing a preference for contralateral connectivity (Kelly and Strick, 2003). In contrast, the ipsilateral connectivity of the left cerebellar seeds in lobules VI and VII is consistent with recent anatomical research showing a sizeable amount of ipsilateral cerebellar-cerebrum loops in animals (Suzuki et al., 2012) and humans (Krienen and Buckner, 2009; Salmi et al., 2010; Sokolov et al., 2014). Although these ipsilateral links are intriguing phenomena as they point to more open-ended cerebellar-cerebrum circuits, they might as well result from indirect connections via other brain areas.

What is the role of the cerebellum in trait repetition and updating? Previous research showed that the cerebellum is not involved in the neural representation of trait or person knowledge, because it did not show suppression when repeating consistent

information (Heleven and Van Overwalle, 2016a, 2016b, 2016c; Ma et al., 2014a, 2014b; Van Overwalle et al., 2016). In contrast, it does play a robust role in repetition enhancement of traits as observed in the present analysis, and of persons in overlapping areas as reported by Heleven and Van Overwalle (2016a). Based on the presumed role of the cerebellum in building internal models of motor sequences that allow fine-tuning and automatization of action and interaction (see more below), and together with the present connectivity findings (Fig. 2), we suggest the following speculative interpretation. When trait-implicating behavioral information requires a potential update of one's activated trait, the executive control network including the pmFC and bilateral PFC and IPC is recruited, together with the bilateral MTC of the mentalizing network. These areas inform the cerebellum about potential upcoming inconsistencies between the activated trait and new behavior, although it is currently unclear via which connections. Research by Van Overwalle and Mariën (2016) suggests that this information might come from mentalizing areas such as the dorsal mPFC, that project onto the right posterior cerebellar lobule that is part of the mentalizing network (i.e., the inferior semi-lunar lobule with MNI coordinates 25 -75 -40). Potential inconsistencies are explored in the cerebellum and if mismatches are detected, adjustments in social judgments or behaviors are propagated back to the cerebrum. The present analysis suggests that this matching process is either performed by or propagated to the executive cerebellar lobules VI and VII, and then propagated further back to the cerebral executive areas including the pmFC, PFC and IPC.

Whatever the precise interpretation of the functional mechanisms underlying the observed connections might be, the present connectivity pattern indicates that potential behavior-trait inconsistencies during trait updating not only trigger activity in executive brain areas of the cerebrum, but also in executive areas of the cerebellum, and that these areas are robustly connected. The present analysis also provides support for a distinct executive control network in the cerebellum (Buckner et al., 2011; see also Buckner, 2013). While the identification of this network by this group of researchers was based on functional connectivity during idle rest in the scanner, the present study confirms the cerebellar-cerebral connectivity for the executive network while participants were actively engaged during trait judgments.

What might be the function of the cerebellum in the service of social updating processes? The general consensus seems to be that the cerebellum supports sequence learning and memories that underpin skill acquisition, develop slowly with practice and are inaccessible to consciousness (Ferrucci et al., 2013). To do this, an original function of the cerebellum is to construct internal models of motor processes involving sequencing and planning of action, in order to automate and fine-tune voluntary motor processes. During evolution, presumably a more advanced function developed which allowed the cerebellum to construct internal models of purely mental processes during cognitive and social reasoning in which event sequences play a role (Ito, 2008; Pisotta and Molinari, 2014). This internal model is a copy of the social event implications generated in the mentalizing areas of the cerebrum (e.g., mPFC or TPJ), and which allows humans to better anticipate action sequences during social interaction in an automatic and intuitive way and to fine-tune these anticipations. This role of internal sequencing predictions is perhaps most prominent when making inferences on traits based on a person's behavior. The present analysis demonstrates that during this process of checks and updates, the executive areas in the cerebrum and cerebellum are strongly involved and interconnected. For instance, if a person likes you, this anticipation is copied into an internal model of relevant behaviors in the cerebellum, which allows you to interact automatically and socially adept in the person's presence (Ito,

2008; Pisotta and Molinari, 2014). Now, if another person appears to react less friendly, such a mismatch with the previously inferred trait leads to an error signal that recruits the executive network and corrects the ongoing social interaction as well as the relevant internal model in the cerebellum. Note that in the present studies, a mismatch was plausible (given the other inconsistent or irrelevant conditions), but actually never occurred in the condition analyzed here. The involvement of the executive network in this case can be explained as due to a renewal or refinement of the inferred trait.

This study has several limitations. First, there is some heterogeneity between studies. The three studies that came chronologically first (51 participants) used a head coil with 8 channels, while the other three (95 participants) used 32 channels. The last four studies used a later version of SPM for the preprocessing of the data. They also included more participants. This may have increased the signal to noise ratio in the latter studies so that they weighted more heavily on the results. However, note that a recent study (Kaza et al., 2011) reported that a 32-channel head coil might reveal less activation in subcortical regions and the cerebellum, although *t*-values for thresholding did not alter significantly. Thus, the inclusion of activated areas seems to be minimally affected. Moreover, an analysis with additional regressors controlling for potential differences between studies and head coil, showed that most activations remained robust despite these differences. Second, a PPI analysis has a number of shortcomings. As noted earlier, PPI provides information on the direction of the connectivity from seed to target, but causality cannot be inferred (Friston et al., 1997). The reason is that lack of PPI connectivity (e.g., in the other direction) does not necessarily imply a complete lack of neural propagation, but rather that the experimental versus control contrast might not differentiate between the target areas, or that connectivity is realized indirectly via other connections. Other functional techniques such as dynamic causal modeling might provide more evidence on these aspects, because they might point out which connections are dependent on conditions or contrasts between them, and which are not. Structural neuroimaging data such as diffusion tensor imaging or tracing studies are needed to make stronger claims about anatomical tracts along which neural information might propagate. However, at the current state of art of diffusion tensor imaging, the extraction of tracts between cerebellum and cerebrum is limited (Jbabdi et al., 2015). Third, it is possible that the present pattern of connectivity is unique for the task and specific conditions used in the studies. For instance, it is possible that the left lateralization of the connectivity circuits or the apparent lack of connections from cerebrum to cerebellum might be dependent on some unknown common task characteristics in our studies, such as the verbal modality of the input. On the other hand, finding strong patterns of connectivity across studies should increase our confidence in the robustness of the current results.

## 5. Conclusion

The present connectivity analysis supports the critical role of the cerebellum in trait updating after repeated information. It demonstrates that there is domain-specific executive connectivity between the cerebrum and the cerebellum, in addition to mentalizing connectivity observed in earlier studies (Van Overwalle et al., 2015b; Van Overwalle and Mariën, 2016). Future research is however needed to explore questions related to the basic processes underlying the propagation of information between the cerebrum and cerebellum. It is suggested that matching event sequences of internal cerebellar models versus cerebral inferences based on external sources and context might be a crucial underlying factor.

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