

Social Cognition and the Cerebellum: A Meta-Analytic Connectivity Analysis

Frank Van Overwalle,^{1*} Tine D'aes,¹ and Peter Mariën^{2,3}

¹*Faculty of Psychology and Educational Sciences, Vrije Universiteit Brussel, Pleinlaan 2, Brussels 1050, Belgium*

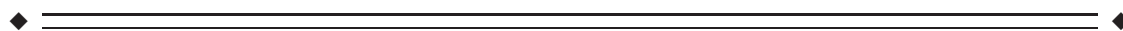
²*Faculty of Arts, Department of Clinical and Experimental Neurolinguistics, CLIN, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium*

³*Department of Neurology and Memory Clinic, ZNA Middelheim Hospital, Lindendreef 1, Antwerp, B-2020, Belgium*



Abstract: This meta-analytic connectivity modeling (MACM) study explores the functional connectivity of the cerebellum with the cerebrum in social cognitive processes. In a recent meta-analysis, Van Overwalle, Baetens, Mariën, and Vandekerckhove (2014) documented that the cerebellum is implicated in social processes of “body” reading (mirroring; e.g., understanding other persons’ intentions from observing their movements) and “mind” reading (mentalizing, e.g., inferring other persons’ beliefs, intentions or personality traits, reconstructing persons’ past, future, or hypothetical events). In a recent functional connectivity study, Buckner et al. (2011) offered a novel parcellation of cerebellar topography that substantially overlaps with the cerebellar meta-analytic findings of Van Overwalle et al. (2014). This overlap suggests that the involvement of the cerebellum in social reasoning depends on its functional connectivity with the cerebrum. To test this hypothesis, we explored the meta-analytic co-activations as indices of functional connectivity between the cerebellum and the cerebrum during social cognition. The MACM results confirm substantial and distinct connectivity with respect to the functions of (a) action understanding (“body” reading) and (b) mentalizing (“mind” reading). The consistent and strong connectivity findings of this analysis suggest that cerebellar activity during social judgments reflects distinct mirroring and mentalizing functionality, and that these cerebellar functions are connected with corresponding functional networks in the cerebrum. *Hum Brain Mapp* 36:5137–5154, 2015. © 2015 Wiley Periodicals, Inc.

Key words: social cognition; cerebellum; functional neuroimaging; meta-analysis; functional connectivity



INTRODUCTION

In 2014, Van Overwalle et al. conducted a large-scale meta-analysis on social cognition and the cerebellum that included over 350 functional magnetic resonance imaging (MRI) studies. Social cognition is an important human ability that allows understanding the social origin and 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). Van Overwalle et al. (2014) found robust clusters of activation in the cerebellum that were recruited during these social-cognitive processes. These

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*Correspondence to: Frank Van Overwalle, Department of Psychology, Vrije Universiteit Brussel, Pleinlaan 2, B - 1050 Brussels, Belgium. E-mail: Frank.VanOverwalle@vub.ac.be

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clusters seemed to overlap with non-social functions reported in earlier meta-analyses on the role of the cerebellum in motor functions, emotions, executive control and language [E et al., 2014; Stoodley and Schmahmann, 2009]. Van Overwalle and colleagues (2014, p. 563) therefore suggested that “the cerebellum does not play a domain-specific role in social cognition, but most probably provides domain-general executive and semantic support.”

But is this correct? The same authors recently put forward an alternative interpretation of the cerebellum that focuses on function-specific social cognitive processes [Van Overwalle, Baetens, Mariën, and Vandekerckhove, 2015]. This novel perspective was based on a connectivity study by Buckner et al. (2011; Buckner, 2013), who explored the organization of circuits between the cerebrum and cerebellum using resting-state functional connectivity MRI for a total sample of 1000 participants, resulting in a complete topography of the cerebellum in relationship with major networks of the cerebrum (Yeo et al., 2011). The study revealed similar network structures in the cerebellum as in the cerebrum, spanning approximately the same relative volumes (see Fig. 1 for their location and organization). Of interest among the networks in the cerebrum identified by Yeo et al. (2011) were a *default* network that includes many mentalizing areas recruited during “mind” reading (see meta-analyses by Schurz et al., 2014; Van Overwalle, 2009), as well as two somatomotor networks that reflect *primary somatomotor* and *somatomotor integration* functions which show substantial overlap with mirror areas recruited during “body” reading [see meta-analysis by Molenberghs et al., 2012; Van Overwalle and Baetens, 2009]. To our knowledge, Buckner et al. (2011) is the only publication to date that provides an empirical parcellation of the cerebellum at such a large scale, and that allows a rough interpretation of the cerebellar networks based on the connectivity with networks of the cerebrum previously described in the literature [see also Habas et al., 2009; O’Reilly et al., 2010]. Importantly, Van Overwalle et al. (2015) detected a remarkable similarity between the results of their meta-analysis of social mentalizing in the cerebellum and the default/mentalizing network of Buckner et al. (2011), as well as between areas involved in social mirroring or behavior understanding (i.e., “body” reading) in the cerebellum and the somatomotor networks described by Buckner et al. (2011). Van Overwalle et al. argued that their results might therefore be

better explained as a reflection of the role of specific social mentalizing and mirroring functions.

However, in past research on the cerebellum, most of the networks [Buckner et al., 2011] were identified using clusters of intrinsic functional connectivity during resting state, without independent verification of their assumed functionality during the alleged tasks or processes. Likewise, the novel analysis by Van Overwalle et al. (2015) was based on a close similarity with Buckner’s cerebellar networks, without independent verification of the functional connectivity underlying the parcellation by Buckner et al. (2011). Thus, the reinterpretation by Van Overwalle et al. (2015) in terms of these functional networks is post-hoc, solely based on spatial similarity. In order to provide stronger empirical evidence for the claim by Van Overwalle et al. (2015) that the cerebellar areas involved in mentalizing and mirroring activity are connected to the corresponding functional networks in the cerebrum, the aim of the present study is to conduct meta-analytic connectivity modeling (MACM), which takes co-activations across studies in a meta-analysis as indices of functional connectivity.

Some words on the terminology of the networks (Fig. 1). First, we renamed one of the major networks of Yeo et al. (2011) the *mentalizing* network, although it was originally labeled the *default* (red) network. This default network reflects activity during undirected thought and daydreaming at rest. Its function is not entirely clear, although several meta-analyses have consistently demonstrated that functional activity in this network strongly overlaps with the social mentalizing network in the cerebrum [Mars et al., 2012; Schilbach et al., 2012; Spreng et al., 2009]. Given the consistent and substantial correspondence between the functional activity during rest and mentalizing, Barrett and Satpute (2013) suggested the term “default/mentalizing” for this network and argued that its main function is conceptualization by constructing a “mental model of the past, the present moment, or the future” (p. 365). Second, although actually a subset of the *somatosensory integration* network (green) defined by Buckner et al. (2011), we use the term *mirror* network to indicate those areas that correspond most closely to action understanding by the observation of human motion (also labeled *mirroring*, see next paragraph). Note also that Buckner et al.’s (2011) parcellation results (Fig. 1) are based on the strongest connectivity in each voxel, and hence do not reflect the uncertainty with respect to the assigned network. Thus, areas close to the demarcation between networks may involve populations of neurons of mixed connectivity to different networks.

Abbreviations

ALE	activation likelihood estimation;
MACM	meta-analytic connectivity modelling;
mPFC	medial prefrontal cortex;
MRI	magnetic resonance imaging;
pSTS	posterior superior temporal sulcus;
ROI	regions of interest;
TPJ	temporo-parietal junction

Four Themes in Social Cognition

The meta-analysis by Van Overwalle et al. (2014) disclosed four themes or subdomains that coherently recruited the cerebellum, and were related to very similar

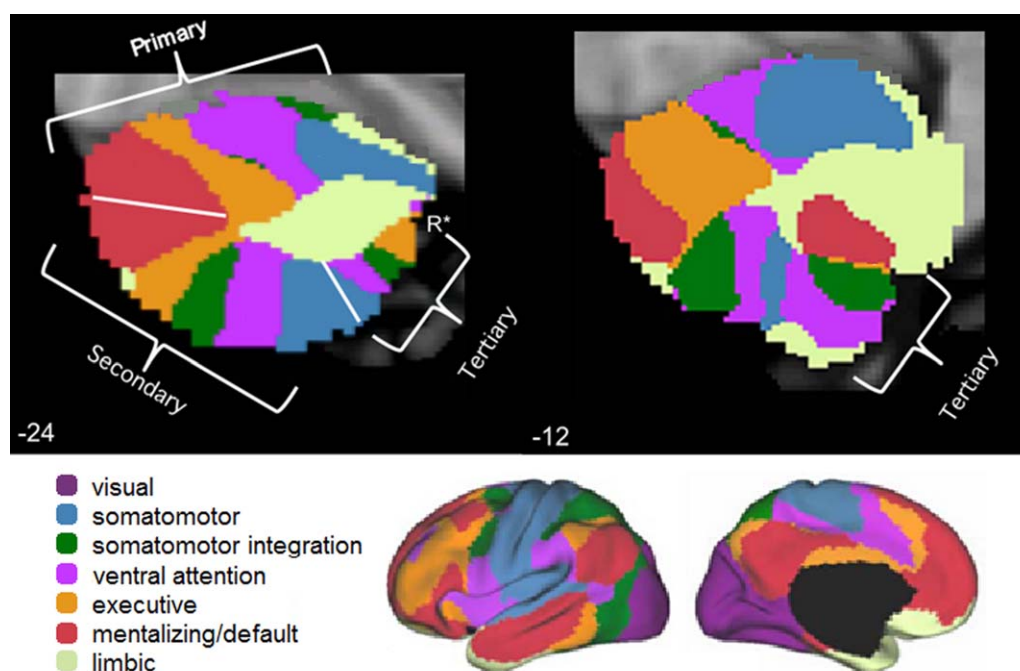


Figure 1.

Parcellation of the cerebellum showing three distinct representations, labeled the primary, secondary, and tertiary representations. Each is a mirror-image ordering of the adjacent map. Networks are color-coded with their function as proposed by Bruckner et al. (2011, p. 2332). The networks refer to the 7-network parcellation of the cerebrum shown in the bottom of the figure. The white lines demarcate estimated boundaries between the maps and do not have significance in

relation to sulcal boundaries. R* refers to the red network, which can be seen in the $x = -12$ section. Adapted with permission from Figure 16 of Buckner R, Krienen F, Castellanos A, Diaz JC, Yeo BT, *J Neurophysiol*, 2011, 106:2322–2345, © Americal Physiological Society and from Figure 11 of Yeo BTT, Krienen FM, Sepulcre J, Sabuncu MR, Lashkari D, Hollinshead M, Buckner RL, *J Neurophysiol*, 2011, 106, 1125–1165, © Americal Physiological Society.

tasks and stimulus types. These four themes involved studies on (1) mirroring (i.e., related to the mirror network in the cortex) which refers to the understanding of visual or other perceptual input from human movements, (2) mentalizing (without human movements) focusing on specific events, (3) general traits, and (4) abstractions. The first three themes were used in two earlier meta-analyses on social neuroscience by Van Overwalle (2009) and Van Overwalle and Baetens (2009), while the latter theme was inspired by recent research on abstraction in social mentalizing [cf. Trope and Liberman, 2010]. These four themes were identified based on the similarities and overlap between stimulus input, task requirements, and empirical clusters revealed by an activation likelihood estimation (ALE) analysis. To briefly summarize the findings (see Table I for examples):

- **Mirroring** involves the observation of human motion (e.g., by hands and fingers, face, and legs) with or without a focus on the intention of the agent, which typically recruits the mirror network in the cortex

[Van Overwalle and Baetens, 2009]. Cerebellar activity was found in about 28% of the mirror studies.

- **Event Mentalizing** encompasses mentalizing about the actor's momentary intentions and beliefs, given a behavioral (event) description that does not involve perceptual input from human motion [Van Overwalle and Baetens, 2009]. Approximately 22% of the studies in the meta-analysis revealed cerebellar activity.
- **Person Mentalizing** involves inferring enduring characteristics of a person or the self, such as traits and preferences [Van Overwalle, 2009]. Again, cerebellar activity was limited to 25% of the studies.
- **Abstract Mentalizing** includes studies that contrast high against low abstraction in social cognition [Trope and Liberman, 2010]. For instance, contrasting person judgments against visual descriptions of the same behaviors (e.g., respectively judging “why” or “how” a person is reading a book), or by contrasting the more distant and abstract past or future, or even contrasting hypothetical events with the momentary

TABLE I. Themes and task categories, and cerebellar activity in the connectivity meta-analysis

Theme	Categories (2000–2012) ^a	Exemplary stimuli	Exemplary instruction	Exemplary target condition	Exemplary control condition	N ^b	% ^c
Mirroring (visible motions of body parts)							
	1. Body part motion	body part motion	passive viewing	motion/manipulating object	no motion	81	26%
	2. Reflecting on intention	body part motion	passive viewing	intentional/incorrect motion	unintended/correct motion	33	31%
	Total N of contrasts/Mean %					114	29%
Event mentalizing (no visible motions of body parts)							
	3. Goal-directed shape motion	animations with shapes	viewing	goal-directed reactivity	random motion	17	31%
	4. Goal-directed action	action/event stories	choose story ending	intentional action	physical event	17	31%
	5. ToM belief	action/object stories	several questions	(false/true) belief	physical event	38	8%
	6. Morality	action stories	appropriateness action	moral	nonmoral	20	10%
	7. Social Games	games	playing the game	human opponent	computer opponent	13	33%
	Total N of contrasts/Mean %					105	23%
Person mentalizing (no visible motions of body parts)							
	8. Traits of distant others	trait words	describe person	person judgment	non trait judgment	37	35%
	9. Traits of close others	trait words	describe person	close other judgment	non trait judgment	13	38%
	10. Self-reference	trait words	describe self	self descriptive	non self descriptive	79	22%
	Total N of contrasts/Mean %					129	32%
Abstraction in mentalizing							
	12. General Abstraction	person pictures	describe person	trait category	non trait category (visual)	4	100%
	13. Social Categories	action stories	action judgment	social category	trait category	3	67%
	14. Hypothetical	action stories	remember/imagine	hypothetical (counterfactual)	semantic memory	3	67%
	15. Past and Future	actions/events	remember/imagine	autobiographic past + future	semantic memory	56	75%
	Total N of contrasts/Mean %					66	77%
	Grand total N of contrasts/Grand mean %					414	40%

Taken from Van Overwalle et al. (2014), except for the auxiliary task conditions 11, 16 & 17, which were omitted.

^aSearch period of inclusion.

^bNumber of studies included in the search.

^c% Of studies reporting cerebellar activation. Some studies participated in several contrasts across task categories.

present. Abstraction recruited very strong and robust cerebellar activity in 67%–100% of the studies.

Present Meta-Analytic Connectivity Analysis

In order to identify the functional connectivity (i.e., co-activations) between the cerebellar activation identified in the meta-analysis by Van Overwalle et al. (2014), and other brain networks in the cerebrum, our general plan of analysis consisted of the following steps:

- As a first step, we selected all the studies (> 350) on social cognition from the meta-analysis by Van Overwalle et al. (2014) that showed cerebellar activity. This resulted in 133 studies. None of these studies involved any motor activity by the participants (e.g., tasks using imitation and judgment of self-agency) so that only the effect of pure perception or observation was examined. We used the same overarching division in four themes from this meta-analysis, as described above. Each theme strikes an optimal balance between a sufficient number of studies on the one hand, and a relatively small number of task categories and functions that are quite homogeneous and consistent with each other. This methodology makes it possible to detect reliable connectivity between the cerebellum and cerebrum.
- As a second step, and in addition to the cerebellar coordinates extracted from the previous meta-analysis [Van Overwalle et al., 2014], we coded the coordinates of significant clusters in the cerebrum that were reported in the selected studies. FVO extracted the coordinates, while TD checked them, and FVO double checked and corrected them.
- As a final step, we identified regions of interest (ROI) in the cerebellum based on the meta-analytic results of Van Overwalle et al. (2014). Next, we selected the studies that contained at least one ROI, and then conducted an activation likelihood estimation (ALE) analysis on the coordinates in the cerebrum in order to identify the clusters of consistent co-activations with cerebellar activity in that ROI. We then determined whether these clusters were part of a mentalizing or mirror/somatosensory networks in the cerebrum, or of the other major networks identified in the parcellation study by Yeo et al. (2011).

Given the close correspondence between the mentalizing and mirroring networks in the cerebellum and the cerebrum [Buckner et al., 2011], and the close correspondence with the mentalizing and mirroring tasks identified in the meta-analysis of the cerebellum by Van Overwalle et al. (2014), we hypothesize that the cerebellum is intrinsically involved in function-specific mentalizing and mirroring processes of social cognition. Consequently, we predict that the areas of the cerebellum involved in these proc-

esses are functionally connected (i.e., co-activated) with the same mentalizing and mirroring/somatomotor networks in the cerebrum.

METHOD

Selection of Studies and Coordinates

The fMRI studies reviewed in the current study were taken from the earlier meta-analysis on cerebellar activity during social cognitive tasks or judgments by Van Overwalle et al. (2014). Originally, these studies were identified by a search in PubMed using the term “fMRI” along with at least one of the following terms in the title or abstract: “person”, “social”, “self” or “autobiographic[al]” from 2000 to the end of 2012. Additional studies were added from several meta-analyses on various aspects of social cognition, including mirror studies and mentalizing studies on goal-directed action, beliefs and theory of mind, morality, traits of others and the self, and several forms of abstraction (i.e., higher construal) including episodic autobiographic studies on the past and future [Bzdok et al., 2012; Carrington and Bailey, 2009; Denny et al., 2012; Lombardo et al., 2011; Mar, 2011; Martinelli et al., 2012; Moltenberghs et al., 2012; Qin et al., 2012; Schilbach et al., 2012; Shkurko, 2013; Spreng et al., 2008; Svoboda et al., 2006; van der Meer et al., 2010].

All studies or conditions that involved the participant’s own actions, such as imitation of the behavior of others or one’s sense of agency during movement, were excluded, because motor activity in itself might activate the cerebellum. As reported in Van Overwalle et al. (2014), studies were only included if they investigated unmedicated healthy adults or adolescents (i.e., between ages 10 and 19 according to the definition of the World Health Organization), used fMRI scanning, involved non-emotional stimuli or tasks, and reported the coordinates of activations in the space of the MNI template [Collins et al., 1994] or the atlas of Talairach and Tournoux (1988). Clinical studies were included if they reported the results of healthy control participants separately. When activations were reported in MNI space, they were transformed into Talairach and Tournoux coordinates by means of a non-linear Brett transformation [<http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach>; Brett et al., 2001] so that all the coordinates had a common stereotaxic framework. As noted earlier, all studies were sorted in the same task categories and four overarching themes from the earlier meta-analyses by Van Overwalle (2009) and Van Overwalle and Baetens (2009).

Connectivity Meta-Analysis Using ALE

For each cerebellar cluster reported by Van Overwalle et al. (2014), we identified a ROI based on the (sub)peak coordinates of the cluster by drawing a sphere with a

TABLE II. Meta-analytic clusters of Van Overwalle et al. (2014) in function of the networks identified by Buckner et al. (2011) with the peak coordinates serving as ROI seeds for the connectivity analysis

Network	Theme	Cerebellar Label		Volume	x	y	z
Mentalizing network							
	Mirroring						
		Right Posterior - Uvula	Crus I	192	30	-78	-24
	Event Mentalizing						
		Left Posterior - Uvula	Crus I	4128	-24	-86	-24
		Left Posterior - Tuber			-30	-80	-28
		Left Posterior - Pyramis			-14	-80	-30
		Right Posterior - Pyramis	Crus I	624	20	-80	-28
	Person Mentalizing						
		Right Posterior - Tuber	Crus I	2544	24	-82	-28
	Abstract Mentalizing						
		Right Posterior - Uvula	Crus I	8112	16	-84	-26
		Right Posterior - Uvula	& VI		28	-80	-26
		Right Posterior - Tuber			40	-72	-28
		Right Posterior - Tonsil			36	-60	-42
		Right Posterior - Tonsil	IX	4064	8	-48	-38
		Left Posterior - Tonsil			-4	-42	-44
		Left Posterior - Tonsil			-8	-48	-38
		Left Posterior - Tuber	Crus I	816	-22	-84	-28
		Left Posterior - Tuber			-36	-86	-30
		Left Posterior - Uvula			-28	-82	-24
		Left Posterior - Uvula			-34	-74	-24
Somatomotor networks							
	Mirroring (somatomotor integration network)						
		Right Posterior - Uvula	VIIIB	800	10	-78	-32
		Left Posterior - Uvula	VIIIB	360	-12	-78	-32
		Left Posterior - Inf. Semi-Lunar	VIIIB	232	-22	-70	-38
	Person Mentalizing (somatomotor network)						
		Right Anterior - Lingual (self ^a)	IV	1016	8	-46	-18
		Right Anterior - Culmen (self ^a)	VI	576	26	-40	-16
Other Networks							
	Mirroring (visual network)						
		Right Anterior - Culmen	VI	504	38	-54	-22
	Person Mentalizing (executive network)						
		Left Posterior - Pyramis	VI	136	-10	-70	-26

Anatomical labels given according to the atlas of ALE and Schmahmann et al. (2000). Volume in mm³ for each cluster; All coordinates according to the Talairach & Tournoux (1988) atlas.

^aCluster preferentially involved in self-references.

5 mm radius around it. This relatively small radius was chosen given the smaller size of the cerebellum [and its mentalizing and somatomotor networks; cf. Buckner et al., 2011], so that all ROIs were largely within the boundaries of these cerebellar networks. In their reinterpretation of cerebellar activity, Van Overwalle et al. (2015) identified each cluster as belonging to one of the cerebellar networks from Buckner et al. (2011), most often a mentalizing or a somatomotor (integration) network. Subsequently, the ROIs were categorized along each network and along each of the four task themes (Table II). The focus here was on the analysis of the mentalizing (red) and somatomotor (blue and green) networks.

The cerebellar ROIs served as “seeds” for the connectivity analysis. That is, for each cerebellar network and task

theme, we identified the studies that reported activation in at least one of the ROIs. Connectivity was then analyzed by identifying the coactivation in the cerebrum. Thus, for all studies that revealed activation in a cerebellar ROI, the reported peak coordinates in the cerebrum were analyzed using the Activation Likelihood Estimation (ALE) procedure as implemented by GingerALE 2.1 [Eickhoff et al., 2009; Laird et al., 2005]. ALE attempts to reveal clusters of consistent activation across selected studies. More specifically, based on the collection of peak coordinates from each study, ALE estimates the probability that at least one of the peaks lies within a voxel. This computation is repeated for each voxel in the cerebrum and results in an ALE map. A statistical threshold for the ALE map is computed using a nonparametric permutation test. This test

identifies real activation if the null hypothesis that the activation foci are spread uniformly throughout the brain (i.e., random clustering) is rejected. We thresholded the non-parametric permutation test for each voxel at a false discovery rate corrected threshold of $p < 0.05$ and an additional cluster extend threshold of 500 mm^3 [Laird et al., 2005].

Next, to isolate the distinct connectivity pattern related to each network, we contrasted the resulting connectivity analysis of each network with one another. To that end, we ran several ALE subtraction analyses. ALE subtraction analyses are processed in a similar manner as simple ALE analyses, although z score images are used to compute the contrast results.

RESULTS

To analyze the connectivity of the cerebellum with the cerebrum, we ran an ALE analysis on the coactivations in the cerebrum of studies that reported cerebral activity. We conducted this analysis for the cerebral mentalizing network (Table III) and the two somatomotor networks (Table IV) because these were of theoretical interest and involved a sufficient number of studies. All analyses were run for each task theme separately (mirroring, event, person, and abstract mentalizing) as well as combined. Note that MACM has limited selectivity because studies that are selected for, for instance, somatomotor activity in the cerebellum may also contain task elements that trigger mentalizing activity in the cerebrum. Therefore, to isolate the distinct connectivity pattern related to each network, we also conducted contrast analyses on the connectivity results, comparing mentalizing connectivity with somatomotor connectivity and vice-versa (Table V).

Our expectation was that if the reinterpretation of cerebellar activity by Van Overwalle et al. (2014) based on the connectivity analysis by Buckner et al. (2011) is correct, we should find a strong and function-specific connectivity between the cerebellum and the cerebrum for mentalizing as well as for somatomotor activity. We discuss the results for each network below.

Mentalizing Connectivity

Table III shows the connectivity (i.e., coactivation) results for mentalizing. The mentalizing ROIs in the cerebellum show strong connectivity with the mentalizing network in the cerebrum, including the dorsal and ventral parts of the medial prefrontal cortex (mPFC), the temporo-parietal junction (TPJ), posterior cingulate, and temporal pole. These are the largest clusters, spanning volumes of $704 - 11,912 \text{ mm}^3$. These coactivations were revealed for all three mentalizing tasks, and for none of the mirror tasks. Apart from this, we also observed substantial connectivity in parahippocampal areas ($2704 - 5936 \text{ mm}^3$) and some temporal areas ($< 1000 \text{ mm}^3$). Figure 2 depicts the

mentalizing connectivity clusters and illustrates a substantial similarity with the mentalizing network (red) of the cerebrum (Yeo et al., 2011).

Table V shows the mentalizing > somatomotor contrast analysis which reveals that, in line with our expectations, only the mentalizing areas in the (ventral and dorsal) mPFC, TPJ, and posterior cingulate (but not the temporal pole) survived the contrast analysis, together with the parahippocampal areas.

Somatomotor Connectivity

Table IV shows the connectivity (i.e., coactivation) results for the somatomotor networks. The somatomotor ROIs showed strong connectivity with the mirror/somatomotor network in the cerebrum. There was connectivity with all major areas of the mirror network, including the posterior superior temporal sulcus (pSTS), inferior frontal gyrus and parietal lobule, spanning volumes of $640 - 4248 \text{ mm}^3$. In addition, connectivity with other somatomotor areas was found, including the precentral, postcentral and middle frontal gyri ($792 - 1592 \text{ mm}^3$), and the insula (896 mm^3) which is responsible for somato-sensory integration. These coactivations were revealed not only for the mirror tasks as one might expect, but also for person trait tasks. Apart from this, there was also connectivity with mentalizing areas ($< 1680 \text{ mm}^3$), but only for person trait tasks. Figure 2 depicts the somatomotor connectivity with the somatomotor integration (green) network in the cerebrum predominantly, and also with the primary somatomotor (blue) network (Yeo et al., 2011).

Table V shows the somatomotor > mentalizing contrast. In line with our expectations, this analysis revealed that only the mirror areas in the pSTS and inferior frontal gyrus survived the contrast analysis, as well as the primary somatomotor areas in the precentral and postcentral gyrus.

DISCUSSION

This study investigated whether the mentalizing and mirroring clusters identified in a recent large-scale meta-analysis of social cognition in the cerebellum [Van Overwalle et al., 2014], are functionally connected with mentalizing and mirror/somatomotor networks in the cerebrum. To do so, we explored robust and systematic cerebellar-cerebral coactivations across studies using ALE, as signatures of functional connectivity. We found substantial and function-specific connectivity between the cerebellar clusters reported in the original meta-analysis of Van Overwalle et al. (2014) and activation in the cerebrum. In line with our hypothesis, the mentalizing clusters in the cerebellum that are recruited mainly during mentalizing tasks about an event, person or more abstract judgments (past, future, or hypothetical events; Van Overwalle et al., 2015), were strongly and distinctly connected to the mentalizing

TABLE III. Clusters and peak coordinates in the cerebellum of the ALE connectivity meta-analysis given mentalizing seeds in the cerebellum in function of task theme.

Network and anatomical label	All themes					Abstraction					Person					Event					Mirroring				
	x	y	z	Volume	Extrema	x	y	z	Volume	x	y	z	Volume	x	y	z	Volume	x	y	z	Volume				
Mentalizing Areas in Cerebrum ventral mPFC ^a	-4	32	-20	5584	0.036	-4	32	-20	2600	0	54	-10	160												
	-2	50	-12		0.030	-4	48	-12																	
	4	54	12		0.025	-4	60	4																	
	10	56	20		0.023																				
	6	54	-2		0.017	14	38	14	144																
	4	34	0	704	0.027	6	32	-2	368						4	56	12	440							
dorsal mPFC ^a	-12	36	50	1952	0.029	-18	34	40	576	-12	34	50	1224												
	-12	26	52		0.023	-22	26	42		0	-52	28	2168												
	-18	34	40		0.017	-10	40	44							4	34	2	352							
	-14	50	30	888	0.025	-14	50	32	688	-4	58	30	216												
	-4	58	30		0.017	24	30	36	152																
	8	48	44	1272	0.028	12	54	22	272																
TPJ ^a	-44	-60	28	6872	0.047	-44	-60	30	5088	-48	-68	32	2064												
	44	-62	24	3816	0.033	44	-60	26	2848	-46	-54	28													
Posterior Cingulate ^a	52	-62	26		0.029	50	-68	32																	
	52	-56	36		0.022	52	-56	38																	
	-2	-54	28	11912	0.056	-8	-52	16	7584																
	-8	-52	16		0.044	-6	-50	28																	
	10	-46	6		0.027	10	-50	30																	
Inferior Temporal Gyrus (Temporal Pole)					—																				
	-56	-8	-18	6200	0.067					-58	-6	-12	992												
Other Areas in Cerebrum Parahippocampal Gyrus ^a																									
	-22	-20	-12	5936	0.039	-24	-20	-12	6552																
	-24	-36	-8		0.027	-24	-36	-8																	
	20	-14	-14	2704	0.035	20	-14	-14	2640																
Superior Temporal Gyrus Middle Temporal Gyrus																									
	44	14	-30	904	0.025																				
	46	0	-26		0.018	58	-4	-20	344																
	-58	-40	-2	872	0.025	-58	-40	-4	544																
	58	-4	-20	720	0.023	-54	-6	-20	4504																
						46	2	-24	112																
						-56	-24	-10	104																

Connectivity in the cerebrum given cerebellar mentalizing ROIs as seeds (see Table II). Anatomical labels given according to the ALE atlas. Volume in mm^3 for each cluster; Value = ALE Extrema value; All x - y - z coordinates are according to the Talairach & Tournoux (1988) atlas or transformed from MNI to Talairach & Tournoux (1988) using the Brett transform. All ALE peaks are significant at $P < 0.05$, FDR corrected and with volume $> 500 \text{ mm}^3$ for all themes. The number of studies, foci, and participants were respectively for abstraction: 20, 325, 316; person: 4, 51, 71; event: 8, 79, 146; and mirroring: 2, 43, 45.

*Survives the contrast analysis (see Table V).

TABLE IV. Clusters and peak coordinates in the cerebrum of the ALE connectivity meta-analysis given somatomotor seeds in the cerebellum in function of task theme

Network and anatomical label	All themes						Person			Mirroring		
	x	y	z	Volume	Extrema		x	y	z	x	y	z
Mentalizing Areas in Cerebrum												
ventral mPFC	4	36	4	872	0.018		4	36	4			
Precuneus	8	-62	24	664	0.018		8	-62	24			
Temporal Pole	-54	2	-24	1680	0.020							
	-56	-10	-14		0.021		-56	-10	-16			
	-54	-6	-22		0.019		-54	-6	-22			
Mirror Areas in Cerebrum												
pSTS ^a	48	-54	10	4248	0.020		48	-3	0			
	52	-56	14		0.021		52	-56	16	50	-56	6
												2672
Inferior Frontal Gyrus ^a	-44	8	30	640	0.017					-46	8	28
	44	12	24	976	0.013					44	12	24
Inferior Parietal Lobule	-34	-40	52		0.022		-50	-42	30	-34	-40	52
Superior Parietal Lobule	28	-48	56	720	0.015					28	-48	56
										-30	-50	42
Other Somatomotor Areas in Cerebrum												
Precentral Gyrus ^a	42	8	32	976	0.015					42	8	32
Middle Frontal Gyrus	50	20	20		0.013		-26	31	36	50	20	20
	-28	-4	52	792	0.017					-28	-6	52
Postcentral Gyrus ^a	-34	-30	52	1592	0.015		-32	-30	54			
							-32	-20	54			
Insula	48	-2	0	896	0.020							
Other Areas in Cerebrum												
Fusiform Gyrus	42	-60	-8	4248	0.026					46	-62	-8
	-44	-50	-14	1040	0.022		-20	-83	-13	-44	-66	-8
Parahippocampal Gyrus	12	-36	-2	1056	0.014		12	-36	-2			
Lingual Gyrus	14	-48	2		0.020		14	-48	2			
Middle Occipital Gyrus	-46	-68	6	712	0.018					-46	-68	6
Cuneus										-10	-98	8

Connectivity in the cerebrum given cerebellar ROIs as seeds (see also Table II): Somatomotor (person) and somatomotor integration (mirroring). Anatomical labels given according to the ALE atlas. Volume in mm³ for each cluster; Value = ALE Extrema value; All x-y-z coordinates are according to the Talairach & Tournoux (1988) atlas or transformed from MNI to Talairach & Tournoux (1988) using the Brett transform. All ALE peaks are significant at $P < 0.05$, FDR corrected and with volume $> 500 \text{ mm}^3$ for all themes. The number of studies, foci and participants were respectively for person:6, 69, 118; and mirroring:5, 98, 113.

^aSurvives the contrast analysis (see Table V).

TABLE V. Clusters and peak coordinates of the ALE connectivity contrast meta-analysis

Contrasts and Anatomical labels	x	y	z	Volume	Extrema
Mentalizing > Somatomotor seeds in cerebellum					
Mentalizing areas in Cerebrum					
ventral mPFC	-1	55	10	472	3.353
	-4	58	14		3.090
	6	52	12		2.948
dorsal mPFC	-8	51	29	808	3.719
	-6	56	26		3.540
	-4	57	30		3.353
	-10	42	42	104	3.353
TPJ	-52	-62	35	1592	3.540
	-40	-58	30		2.911
	-48	-74	34		2.652
Posterior cingulate	0	-52	28	1728	3.719
	-1	-52	29		3.540
	4	-47	30		3.353
	-10	-56	28		3.156
Other Areas in cerebrum					
Parahippocampal gyrus	-21	-14	-20	2264	3.540
	-25	-17	-19		3.353
	-21	-18	-15		3.239
	-28	-22	-17		3.156
Somatomotor > mentalizing seeds in cerebellum					
Mirror Areas in cerebrum					
pSTS	54	-59	8	720	3.239
	55	-59	4		2.794
	47	-54	2		2.848
	50	-55	1		2.748
Inferior frontal gyrus	-37	30	6	120	2.948
	-38	34	6		2.911
Other Somatomotor areas in cerebrum					
Precentral gyrus	-30	-30	52	464	3.540
Postcentral gyrus	-32	-34	52		3.353
	-34	-29	54		3.156

Anatomical labels given according to the ALE atlas.

Volume in mm³ for each cluster; Value = ALE Extrema value.

All x-y-z coordinates are according to the Talairach & Tournoux (1988) atlas or transformed from MNI to Talairach & Tournoux (1988) using the Brett transform. All ALE peaks are significant at $P < 0.05$, FDR corrected and with volume > 100 mm³.

network (red) in the cerebrum, including major areas of the mPFC, TPJ and posterior cingulate (Fig. 2). Likewise, the clusters in the cerebellum involving mainly mirroring and person trait tasks [Van Overwalle et al., 2015] were substantially and distinctly connected to the somatomotor areas in the cerebrum, including the typical mirror network (green) that encompasses the pSTS and inferior frontal gyrus, as well as the primary somatomotor (blue) network that includes the precentral and postcentral gyri (Fig. 3). Although mentalizing activity and connectivity prevailed for all three mentalizing processes involving event, person and abstract tasks (across cerebellum and cerebrum), there was a small exception when judging a person's traits (mainly the self; see Van Overwalle et al., 2014), which also revealed activity and connectivity of somatomotor networks. This finding confirms the original interpretation of Van Overwalle et al. (2014) that bodily

experiences and awareness play a role in evaluating the self.

The present connectivity findings confirm the recent interpretation of the meta-analytic results on distinct networks in the cerebellum by Van Overwalle et al. (2015), and thus shed new light on the function of the cerebellum in social cognition. In the original meta-analysis by Van Overwalle et al. (2014), cerebellar activity was interpreted in relation to non-social functions as described in other meta-analyses of the cerebellum that investigated evolutionary "older" motor and emotional functions as well as "younger" executive and language functions [E et al., 2014; Stoodley and Schmahmann, 2009]. It was concluded that the cerebellum plays a general role in supporting social cognition across different functional tasks. The present analysis suggests a markedly different conclusion. Rather than a general function, the distinct connectivity

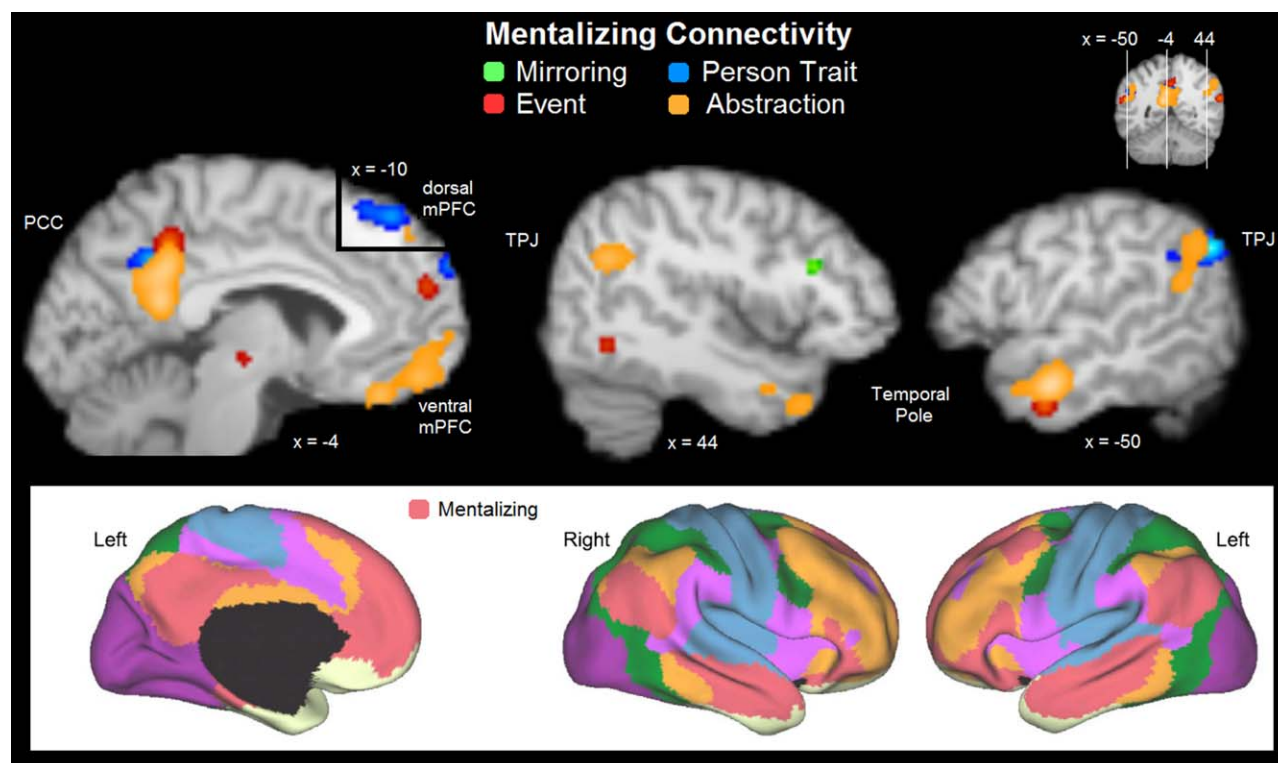


Figure 2.

Functional connectivity in social mentalizing from the cerebellum to the cerebrum. All ALE clusters are significant at $P < 0.05$, FDR corrected, and with volume $> 100 \text{ mm}^3$. The bottom of the figure shows the 7-network parcellation of the cerebrum (Yeo

et al., 2011). Adapted with permission from Figure 11 of Yeo BTT, Krienen FM, Sepulcre J, Sabuncu MR, Lashkari D, Hollinshead M, Buckner RL, *J Neurophysiol*, 2011, 106, 1125–1165, © American Physiological Society

patterns indicate that social cognition in the cerebellum triggers activity in function-specific cerebellar networks that are connected to function-specific networks in the cerebrum serving an identical function.

Moreover, the functional connectivity patterns identified in these analyses, provide further meta-analytic support for the parcellation of the cerebellum conducted by Buckner et al. (2011; see also Buckner, 2013) founded on the functional connectivity with networks in the cerebral cortex (Yeo et al., 2011). While the connectivity results of this group of researchers were based on activity during idle rest in the scanner, the present study revealed the same connectivity patterns for some of the major networks while participants were actively engaged during various social judgment tasks. The present results are also consistent with earlier anatomical findings reporting topographically ordered reciprocal cerebellar-cerebral loops via the pons (Schmahmann, 1996). Animal studies indicated that the majority of these connections are characterized by circuits that reflect predominantly contralateral closed loops [Kelly and Strick, 2003] although more open-ended, ipsilateral loops have also been reported [Suzuki et al., 2012]. Human research exploring structural connectivity using diffusion

imaging reported similar cerebellar-cerebral circuits [Salimi et al., 2010; Sokolov et al., 2014].

An important limitation of the present approach is that functional connectivity was measured through shared activity across studies. Specifically, the analysis identified which brain areas reveal coactivation (i.e., peak coordinates reported together) and how systematic these coactivations are across studies. The unit of analysis was a complete study, not a participant. Hence, the present data do not demonstrate that real functional connectivity exists within individual brains of the participants. Another limitation of this study is that the direction of the connectivity was not assessed, because there was no access to the exact timing of the shared activity.

At a theoretical level, it remains unclear what specific purposes and processes the cerebellum serves in social cognition. Several authors [Andreasen and Pierson, 2008; Bower, 1997; Schmahmann, 1998] suggested that the cerebellum regulates mental operations in much the same way as it regulates movements. According to Schmahmann (1998), its general function is to facilitate “actions harmonious with the goal, appropriate to context, and judged accurately and reliably according to the strategies mapped

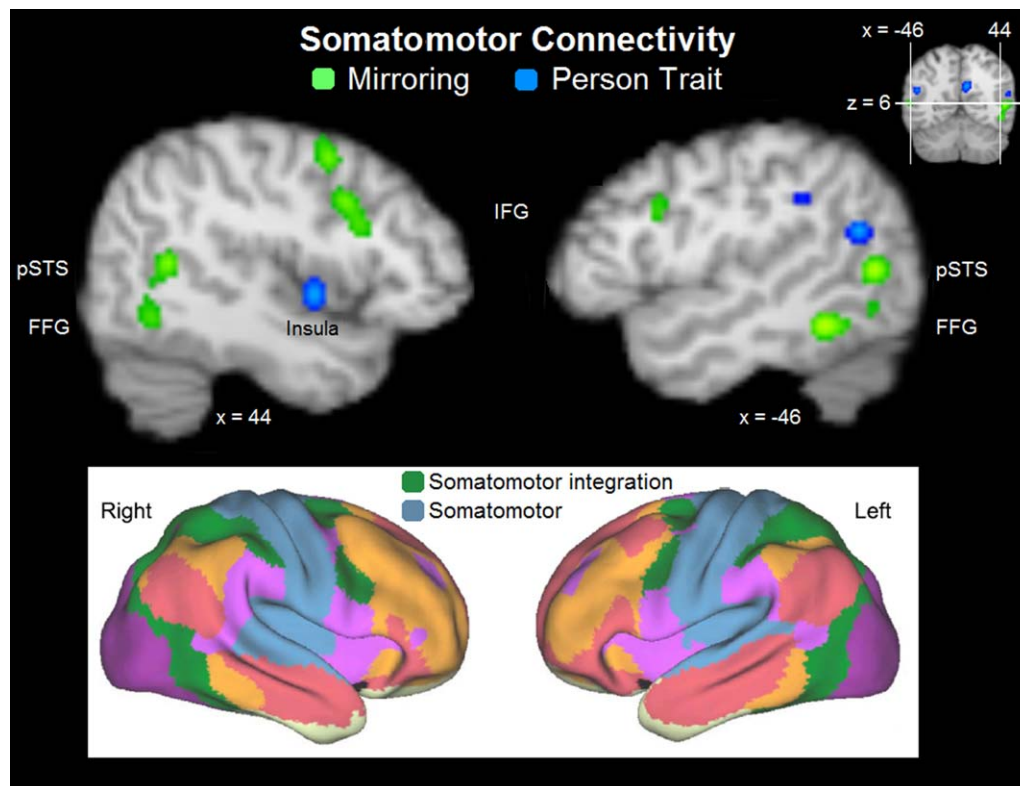


Figure 3.

Functional connectivity in somatomotor/mirroring processes from the cerebellum to the cerebrum. All ALE clusters are significant at $P < 0.05$, FDR corrected, and with volume $> 100 \text{ mm}^3$. The bottom of the figure shows the 7-network parcellation of the cere-

brum (Yeo et al., 2011). Adapted with permission from Figure 11 of Yeo BTT, Krienen FM, Sepulcre J, Sabuncu MR, Lashkari D, Hol-linshead M, Buckner RL, *J Neurophysiol*, 2011, 106, 1125–1165, © Americal Physiological Society.

out prior to and during the behavior. In this view, the cerebellum detects, prevents, and corrects mismatches between intended outcome and perceived outcome of the organism's interaction with the environment" (p. 367). And more specific to social cognition, he also noted that disturbed cerebellar functionality leads to "unpredictability to social and social interaction" (p. 368). Thus, the cerebellum might be a general modulator to prevent and correct errors of actual movement as well as unobserved thought, and it is doing so for distinct functional processes, including social cognitive functions.

The critical role of the cerebellum is perhaps better understood from the perspective of its essential function in constructing internal models of mental processes involving sequencing and planning of action, in order to automate and fine-tune not only voluntary motor processes, but also cognitive processes where event sequences play a role [Ito, 2008; Pisotta and Molinari, 2014]. This sequencing role is most evident and prominent in mental reconstructions of autobiographic past, future or hypothetical events.

Thus, to understand observed events and their underlying goal, or to infer traits from a person's observed behavior, it is imperative that sequences of actions can be imagined or interpreted into a meaningful whole. The cerebellum may play a functional role in this sequencing process during social cognition. One view [Ito, 2008; Pisotta and Molinari, 2014] suggests that such internal models are a copy from the social event implications generated in mentalizing areas in the cerebrum and allows humans to anticipate better action sequences during social interaction in an automatic and intuitive way and to fine-tune these anticipations. Thus, signals from the cerebellum might continuously check whether an anticipated event sequence based on (abstract) social information fits with current behavior. For example, if we meet a neighbor whom we attribute a friendly trait to based on past observations, we learn to reciprocate with appropriate behaviors (e.g., we approach her with friendly remarks). This behavioral anticipation might be copied into and reconstructed by an internal model in the cerebellum holding predictable patterns of

behavior and learned social responses. This allows us to act automatically and socially adept each time we see our neighbor, and to be quickly on alert when mismatches in these predictions occur.

This reasoning suggests that the role of the cerebellum might be relatively automated during the processing of typical events (revealing minimal neural activity), but less so in reconstructing novel past or future events, or in more complex events (revealing more activity). This is in line with the finding that the level of cerebellar recruitment differs between social tasks. The meta-analysis by Van Overwalle et al. (2014) revealed higher involvement of the cerebellum (77% of the studies) in more abstract and complex social-cognitive inferences (e.g., projecting oneself into future or hypothetical events, or recalling autobiographical past events), while cerebellar activity was more limited for ordinary social judgments (e.g., mirroring, event, and person mentalizing; 23%–32% of the studies). Interestingly, the present results showed stronger mentalizing connectivity also with parahippocampal gyri under abstract, often autobiographic task conditions. Likewise, recent findings from our lab indicate that the cerebellum is strongly recruited when trait-implicating behavioral descriptions are repeated, that is, when novel behaviors need to be integrated with prior behavioral information [Heleven and Van Overwalle, 2015; Ma et al., 2014a,b]. Hence, it is quite likely that in order to reconstruct or integrate appropriate sequences from past events or to construct *de novo* future or hypothetical events, extra cerebellar capacity has to be recruited.

Thus, although distinctly connected with function-specific input and networks, the cerebellum might play a more common basic role in acquiring and predicting motor and cognitive sequences which underlie not only the understanding of planned and observed actions, but also the construction of internal mental models about current events, traits (abstracted out of events), and past, counterfactual or future autobiographic events. This function would be taxed more heavily when imagining novel or complex event sequences. These ideas concerning the role of the cerebellum are admittedly still at an early stage. One obvious avenue for future research is to test the idea that sequencing is an important aspect of the cerebellar function in social cognition.

CONCLUSION

The present connectivity analysis provides support for an alternative interpretation of the meta-analysis of Van Overwalle et al. (2014). Instead of being involved in general non-social functions as originally suggested in the 2014 article, the cerebellum seems to play a crucial role in social cognition by function-specific mentalizing and somatomotor processes. This conclusion is based on the distinct coactivation between these respective networks in the cerebellum and the cerebrum. Future research is

needed to explore the functional connectivity at the level of individual participants, and to resolve theoretical questions with respect to the basic processes underlying cerebellar activity in social cognition. It is suggested that event sequences might be the common underlying functionality.

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