

# Connectivity between the cerebrum and cerebellum during social and non-social sequencing using dynamic causal modelling



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## ABSTRACT

This analysis explores the effective connectivity of the cerebellum with the cerebral cortex during the generation of correct sequences of social and non-social events, using dynamic causal modelling (DCM). Our hypothesis is that during human evolution, the cerebellum's function evolved from a mere coordinator of fluent sequences of motions and actions, to an interpreter of action sequences without overt movements that are important for social understanding. This requires efficient neural communication between the cerebellum and cerebral cortex. In a functional magnetic resonance imaging (fMRI) study, participants generated the correct chronological order of (non-)social events, including stories involving mechanical and social scripts, and true or false beliefs. Across all stories, a DCM analysis of these data revealed, as predicted, bidirectional (closed-loop) connections linking the bilateral posterior cerebellum with the bilateral temporo-parietal junction (TPJ) associated with behavior understanding, and this connectivity pattern was almost entirely significant. There was also a unidirectional connection from the right posterior cerebellum to the precuneus, but no direct connections with the dorsomedial prefrontal cortex (dmPFC). Moreover, all connections emanating from the bilateral posterior cerebellum were negative, indicative of some kind of error signal. Within the cerebral cortex, there were unidirectional connections from the bilateral TPJ to the dmPFC, as well as bidirectional connections between the precuneus and dmPFC, and between the bilateral TPJ. These results confirm that the effective connectivity between the posterior cerebellum and mentalizing areas in the cerebral cortex play a critical role in the understanding and construction of the correct order of social and non-social action sequences.

## 1. Introduction

Recent research revealed that the cerebellum plays a critical role in social understanding. In a large-scale meta-analysis of functional magnetic resonance imaging (fMRI) studies, Van Overwalle et al. (2014) found robust activation of the cerebellum during social judgments, including inferences about other persons' mental states based on their actions ("mentalizing" or "mind reading"). The cerebellum is also implicated in a large range of neuropsychiatric and neurodevelopmental disorders related to social functioning such as autistic spectrum disorders (ASD), attentional deficit and hyperkinetic disorder (ADHD), depression, and schizophrenia (Bauman and Kemper, 2005; D'Mello et al., 2015; Penn, 2006; Wang et al., 2014).

But what is the exact role of the cerebellum in social understanding?

Given its classical role in motor production, a number of authors have argued that the primary function of the cerebellum is to support learning and recollection of sequences that underpin skill and acquisition of fluent motion, which develops slowly with practice and is inaccessible to consciousness (Braitenberg et al., 1997; Leggio and Molinari, 2015; Pisotta and Molinari, 2014). To do this, the cerebellum constructs internal models of motor processes involving automatic sequencing and planning of movement, and the anticipated external perceptions and somatosensory sensations in a given context. During action execution the cerebellum functions as a 'forward controller', by using these internal models to generate predictions which are compared with feedback from external and proprioceptive sources, so that the behaviors can be adjusted on-line during their execution instead of only after failure of execution, which provides a great survival advantage (Pickering and Clark, 2014). Of

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critical interest, during human evolution, a more advanced function developed which allowed the cerebellum to construct internal models of purely mental processes in which event sequences play a role, without overt movements and somatosensory feedback. Thus, the cerebellum generates internal models of all temporally or spatially structured events that can be used to make predictions about any type of event, including social event sequences which are the focus of this study. Evidence suggests that, generally, more recently developed higher-level processes including social cognition involve the posterior cerebellum, while ancient motor processes involve the anterior cerebellum (Buckner et al., 2011; Van Overwalle et al., 2014).

Unfortunately, clinical studies with cerebellar patients that addressed dysfunctions of social cognition often did not focus on the sequencing of actions, and reported mixed findings in comparison with healthy controls. To illustrate, Sokolovsky et al. (2010) reported impairments in some but not all cerebellar patients, while Roca et al. (2013) found no significant differences in mentalizing (Faux Pas test; Baron-Cohen et al., 1999). Hoche et al. (2016) found worse performance on the Reading the Mind in the Eyes test (Baron-Cohen et al., 2001).

Studies investigating social action sequencing found stronger and more robust impairments of cerebellar patients than healthy matched controls. In a first study, Leggio et al. (2008) found that cerebellar patients performed worse on cartoon-like drawings and verbal sentences which had to be reproduced in a chronologically correct sequence. Using a very similar task with action photos (Cattaneo et al., 2012), reported that cerebellar patients performed significantly worse, especially on photos of biological action and less so on mechanical movements. These two studies clearly point to the potential diagnostic value of action sequencing. However, they did not involve inferences on others' beliefs, so that the implications on social mentalizing are unclear.

To explore action sequence generation during mentalizing, Van Overwalle and colleagues (Van Overwalle et al., 2019) used a *Picture Sequencing* task with cartoon-like drawings developed by Langdon and Coltheart (1999; see Fig. 1). This task involves stories in which another person holds a *false belief*. False beliefs are a crucial test of the capacity to mentalize, because they require the understanding that another person may hold mental beliefs that are contradicted by reality and our own beliefs. For instance, another person may hold a false belief on an object's current location as a result of the object's displacement during the person's earlier absence, and thus may look for the object in the wrong location (Baron-Cohen et al., 1985; Wimmer and Perner, 1983). Consequently, participants have to infer the agent's false belief in order to understand the agent's behavior. The results of this study showed strong impairments of cerebellar patients compared to healthy controls on false belief story sequences which involved novel (i.e., non-routine) action sequences, and normal performance on social and non-social routine

actions (i.e., social scripts and mechanical sequences; Van Overwalle, De Coninck et al., 2018).

Based on these results, Heleven et al. (2019) extended the *Picture Sequencing* task with a *true belief* condition, which involved very similar social story elements as the false belief condition, but without false mental content. Moreover, they also developed a *Verbal Sequencing* task, containing the same four conditions of mechanical events, social scripts, true and false beliefs. When healthy participants executed these two tasks under the fMRI scanner, all experimental conditions in which sequential orders were generated, recruited several areas of the cerebellum compared to a non-sequential control condition measuring reading comprehension. More importantly, the true and false belief conditions activated the bilateral posterior cerebellum more strongly than the (non) social routine conditions (social scripts and mechanical stories). These results demonstrate that ordering correct action sequences, especially for novel actions involving true and false beliefs, depends on the activation of the posterior cerebellum (i.e., Crus 1 and 2) in comparison with overlearned social and non-social sequences.

Further support for the role of the posterior cerebellum in action sequencing during social mentalizing can be amassed if we can demonstrate that this cerebellar lobule is activated in neural synchrony with mentalizing cortical areas, especially during (true and false) belief action sequences. Such synchrony has been revealed in earlier research. Based on resting-state connectivity, Buckner et al. (2011) identified a distinct mentalizing network in the posterior cerebellum that was directly connected to the mentalizing network in the cerebrum (Molenberghs et al., 2016; Schurz et al., 2014; Van Overwalle, 2009). Of more importance, during social mentalizing, the posterior cerebellum is strongly connected to the mentalizing cerebral cortex as demonstrated by a recent *meta-analytic connectivity* analysis on social cognition (Van Overwalle, D'aes, & Mariën, 2015) and a *dynamic causal modelling* (DCM) analysis of effective connectivity across 5 fMRI studies involving inferences on other person's traits and one's past (Van Overwalle, Van de Steen and Mariën, 2019).

Dynamic causal modelling (DCM; Friston et al., 2003; Stephan et al., 2010) is used in the present analysis, and is of particular interest because it overcomes limitations of alternative approaches such as psycho-physiological interaction (PPI; Friston et al., 1997). First, a DCM approach estimates and tests the two directions of connectivity separately (from one area to the other and vice versa) so that it is possible to make a causal interpretation of neural processing loops. Second, DCM allows to specify "fixed" or "endogenous" connectivity unmodulated by the experimental manipulation, as well as "modulatory" connectivity regulated by the experimental conditions. Third, DCM allows to estimate and test all connections at once in a single model, so that "indirect" connections via other areas (which may create "false" connectivity) are better controlled for. Evidently, this is only the case when all relevant

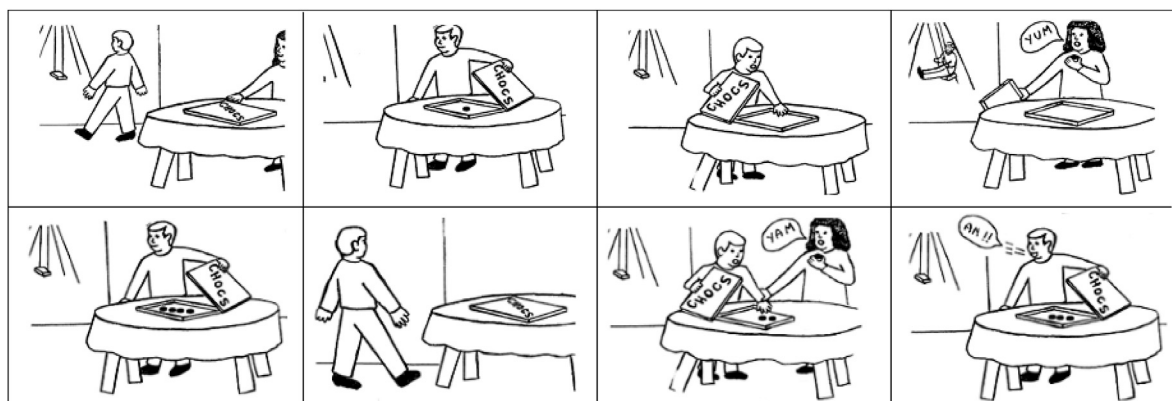


Fig. 1. An example of a false belief (top) and true belief (bottom) sequence in the *Picture Sequencing* task (respectively from Langdon and Coltheart, 1999, and Heleven et al., 2019; the correct order is 2–1–4–3). Participants had to select, in the correct order, the first picture, then the second picture, and so on. After each selection, the pictures moved in the order indicated by the participant.

task-activated areas are included in the model.

Given these powerful analytical features, DCM analysis provides a more biologically plausible test of connectivity, and condition-related changes in connectivity. So far, anatomical studies indicate that the majority of cerebro-cerebellar connections are characterized by closed-loop circuits, where an area of the cerebrum projects to an area of the cerebellum, and receives input from that same cerebellar area. This is strong evidence for internal forward cerebellar models that communicate with the cerebrum. Anatomical studies on animals found mainly contralateral closed-loop circuits (Kelly and Strick, 2003), while some studies revealed the existence of additional ipsilateral loops in rats (Suzuki et al., 2012) and humans (Cui et al., 2000; Salmi et al., 2010; Sokolov et al., 2014). In support of this anatomical evidence, a human resting-state connectivity analysis by Krienen and Buckner (2009) revealed that the connections from the cerebral cortex terminate on contralateral areas of the cerebellum in 70–80%, and on ipsilateral areas in 20–30%. In line with this evidence, the DCM analysis on five mentalizing studies mentioned earlier (Van Overwalle, Van de Steen and Mariën, 2019) found closed-loops between the right posterior cerebellum and the bilateral TPJ, and only a unidirectional link from the right posterior cerebellum to the precuneus.

The aim of the present study is to investigate the effective connectivity between mentalizing areas of the cerebrum and the cerebellum, by applying a biologically plausible DCM analysis on the fMRI study on (non)social pictorial sequencing by Heleven et al. (2019). By doing this, we can shed more light on the specific processes that take place in the posterior cerebellum, in particular, processes involving chronological sequencing of social and non-social actions. This would support the general hypothesis that the cerebellum is involved in sequencing in concert with the cerebrum, also in the domain of social mentalizing.

In particular, we expect to replicate and extend many findings of the earlier multi-study DCM analysis by Van Overwalle, Van de Steen and Mariën (2019). We expect to replicate the contralateral and ipsilateral closed-loops between the right posterior cerebellum and cerebrum, and extend it to the left posterior cerebellum because this area was also activated in the fMRI study by Heleven et al. (2019). We also expect to replicate the closed-loops with cerebral mentalizing areas of the bilateral temporo-parietal junction (TPJ), and the lack of closed-loops with the precuneus or dorsomedial prefrontal cortex (dmPFC). Moreover, we expect to replicate the finding that connections originating from the cerebellum reflect a (negative) error signal that is used by the cerebral cortex to adjust its activation in the opposite direction. Finally, the DCM analysis will allow us to see whether and which connections between the cerebrum and cerebellum are modulated during mentalizing beliefs as opposed to (non)social routine events as suggested by the study of Heleven et al. (2019).

## 2. Method

### 2.1. Participants

As described in Heleven et al. (2019), there were 49 participants (24 men) conducting the Picture Sequencing task. All participants were right handed, native Dutch speaking with no neurological or psychiatric antecedents, and had normal or corrected-to-normal vision. Informed consent was obtained in a manner approved by the Medical Ethics Committee at the Hospital of University of Ghent, where the studies was conducted. Participants were paid 20 euro in exchange for their participation.

### 2.2. Stimulus material and procedure

Participants saw 16 scenarios that represented 4 mechanical, 4 social script, and 4 false belief events from the original task developed by Langdon and Coltheart (1999; for an example see Fig. 1), and 4 true belief events developed by Heleven et al. (2019). As a control condition, there

was a non-sequential reading comprehension task. All stimuli are available upon request.

The experiment under the scanner started with the control trials, followed by the experimental trials in a random order. Before the start of the control and experimental conditions, instructions were shown on the screen, then practice trials, and finally the actual trials. Each trial started with a fixation cross (1 s), followed by the presentation of 4 pictures in a correct chronological order (control trials) or random order (experimental trials). At the end of each trial, for the control condition, participants read a factual question and gave a self-paced response. For the experimental trials, participants had to line up the pictures in the correct order at a self-paced tempo. This was done by first selecting the first picture on the screen, then the second picture, and so on, while the pictures moved on the screen along the order indicated.

### 2.3. fMRI processing and statistical analysis

Images were collected with a 3 T S Magnetom Prisma fit scanner system (Siemens Medical Systems, Erlangen, Germany) using a 64-channel radiofrequency head coil. 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) running under Windows XP. Participants were placed head first and supine in the scanner bore and were instructed not to move their heads to avoid motion artifacts. Foam cushions were placed within the head coil to minimize head movements. First, a high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence [TR = 2250 ms, TE = 4.18 ms, TI = 900 ms, acquisition matrix = 256 × 256 × 176, sagittal FOV = 256 mm, flip angle = 9°, voxel size = 1 × 1 × 1 mm]. Second, a fieldmap was calculated to correct for inhomogeneities in the magnetic field (Cusack and Papadakis, 2002). Next, whole brain functional images were collected in a single run using a T2\*-weighted gradient echo sequence, sensitive to BOLD contrast (TR = 2000 ms, TE = 29 ms, image matrix = 64 × 64, FOV = 224 mm, flip angle = 90°, slice thickness = 4.0 mm, distance factor = 10%, voxel size = 3.5 × 3.5 × 4.0 mm, 35 axial slices, acceleration factor GRAPPA = 2).

To process the fMRI data, SPM12 was used (Wellcome Department of Cognitive Neurology, London, UK). To remove sources of noise and artifact, data were preprocessed. Inhomogeneities in the magnetic field were corrected using the fieldmap (Cusack and Papadakis, 2002). Functional data were corrected for differences in acquisition time between slices for each whole-brain volume, realigned to correct for head movement, and co-registered with each participant's anatomical data. Then, the functional data were transformed into a standard anatomical space (2 mm isotropic voxels) based on the ICBM152 brain template of the Montreal Neurological Institute (MNI). Normalized data were then spatially smoothed (6 mm full-width at half-maximum, FWHM) using a Gaussian Kernel. Finally, using the Artifact Detection Tool software package (ART; <http://web.mit.edu/swg/art/art.pdf>; [http://www.nitrc.org/projects/artifact\\_detect](http://www.nitrc.org/projects/artifact_detect)), the preprocessed data were examined for excessive motion artifacts and for correlations between motion and experimental design, and between global mean signal and experimental design. Outliers were identified in the temporal differences series by assessing between-scan differences (Z-threshold: 3.0 mm, scan to scan movement threshold: 0.5 mm; rotation threshold: 0.02 radians). These outliers were omitted from the analysis by including a single regressor for each outlier. Six directions of motion parameters from the realignment step as well as outlier time points (defined by ART) were included as nuisance regressors. A default high-pass filter was used of 128s and serial correlations were accounted for by the default auto-regressive AR(1) model.

To conduct the statistical analyses of the fMRI data, the general linear model approach of SPM12 was used (Wellcome Department of Cognitive Neurology, London, UK). At the first (single participant) level, the event-related design was modeled for each condition time-locked at the

presentation of the first picture, and convolved with a canonical hemodynamic response function with time and dispersion derivatives. Event duration was set to 4 s for all conditions. Given that the beginning period of each trial was most essential, all correct and incorrect trials were included. At the second (group) level, a whole-brain random effects analysis was performed using a within-participants one-way analysis of variance, contrasting each experimental condition with the non-sequential control condition, as well as contrasting all experimental conditions with each other. In addition, a conjunction of the contrasts of all experimental conditions against the control condition was performed.

#### 2.4. Selection of regions of interest

We took the same region of interest (ROI) *a priori* coordinates and procedure used in the earlier DCM study (Van Overwalle et al., 2018). Specifically, the cortical mentalizing ROIs were centered around the mean MNI coordinates reported in the meta-analyses by Van Overwalle, 2009 and Van Overwalle and Baetens (2009) and included the dmPFC (with MNI center: 0 50 35), bilateral TPJ ( $\pm 50$ -55 25) and pre-cuneus/posterior cingulate (Pcun: 0-60 40). The cerebellar ROI was identified by Van Overwalle and Mariën (2016) and involved lobule VIIA - Crus 2 in the right posterior cerebellum (rpCB: 25-75 -40).

In order to explore whether there were additional cerebral areas that were robustly activated under all experimental sequencing conditions, and to rely on a broader database that would be somewhat more independent, we searched for exploratory ROIs not only in the original data of the Picture Sequencing task, but also in a similar Story Sequencing task reported in the same article (Heleven et al., 2019), and conducted a between-participant analysis on all data. Specifically, we conducted the same second level whole-brain statistical analysis as in the original fMRI study (Heleven et al., 2019) using the conjunction of the contrasts of all experimental conditions against the control condition. This analysis revealed, apart from the mentalizing clusters covered by the *a priori* ROIs above, additional clusters in the cerebellum, the bilateral hippocampus and the bilateral insula. (The DCM results on the Story task are not reported because the DCM estimation failed to converge for 7 participants, leaving only 17 valid participants, even after doubling the default maximum number of iterations).

To identify additional cerebellar ROIs, clusters were considered significant at a Family Wise Error (FWE) corrected peak threshold  $p < .05$ , with a minimum cluster extent of 10 voxels. This analysis revealed cerebellar clusters with MNI peak coordinates -42 -72 -40, 24-54 -50, and 22-50 -22 (which were very close to the original coordinates of the Picture Sequence study: 40 -78 -40, 22-58 -48, and 24-52 -24). These peak coordinates were rounded to the next 5 mm to serve as center for additional exploratory cerebellar ROIs: a left posterior cerebellar ROI (lpCB: 40 -70 -40) which was located somewhat more peripherally than the rpCB and served as left counterpart, and two more anterior cerebellar ROIs including the right lobule VIII (rCBVIII: 25-55 -50) and right lobule IV-V (rCBIV-V: 20-50 -20). This addition results in eight ROIs in total.

Using the same procedure, we also specified for secondary DCM analyses, two subcortical ROIs in the bilateral hippocampus ( $\pm 25$ -40 5) and two cortical ROIs in the bilateral insula ( $\pm 50$  5 5).

Individually-tailored cerebral ROIs were created by extracting the time-series using the eigenvariate within a sphere with a radius of 8 mm around the nearest local maximum within 15 mm of the corresponding ROI centers listed above, after setting a whole-brain threshold of the contrast at  $p < .05$  (uncorrected). All voxels contributing to the ROI were conducted on an F-contrast involving all contrasts of the experimental conditions against the control condition, and adjusted using an F-contrast involving all experimental effects. Individually-tailored cerebellar and subcortical ROIs were created in a similar manner, except that the radius was confined to 5 mm around the nearest local maximum within 10 mm of the corresponding ROI center, given the smaller size of the cerebellum and subcortical areas. If the ROI did not contain a peak surviving the  $p < .05$  uncorrected threshold, the same procedure was repeated with

$p < .10$  and  $p < 1.00$  (uncorrected) so that time series of all ROIs were included for all participants (see Table 1 for details). In the latter case of  $p < 1.00$ , ROIs were centered around the group-based centers listed above (see also Zhou et al., 2007). This procedure was used because pairwise exclusion is not possible in a DCM analysis as all time-series from all ROIs are required. Setting a more tolerant threshold in some individual cases implies an optimal compromise between maximizing the effect of interest at the individual level while having all participants in the DCM analysis so that the results are not biased by excluding some participants (Zhou et al., 2007).

#### 2.5. Dynamic causal modelling

We used exactly the same procedure as in the earlier DCM analysis (Van Overwalle et al., 2018). Specifically, we followed the procedures described in Friston et al. (2016) and Friston et al. (2015), and detailed in <https://en.wikibooks.org/wiki/User:Peterz/sandbox>:

First, a full DCM was specified and estimated for each participant using SPM12 (cf., SPM procedure: *spm\_dcm\_fit*). A full model allows all connectivity parameters in all directions to be freely estimated. We specified a bilinear deterministic DCM without centering around the mean (Friston et al., 2003), which included (a) all forward and backward *fixed connections* between the ROIs, (b) all the *modulatory connections* or parameters that reflect condition changes due to each experimental condition and (c) *direct input* parameters that reflect the input driving the activity in the ROIs in all experimental and control conditions. Stated differently, the driving input in matrix C consists of one vector with all the onsets of all experimental and control conditions combined as one input, and the modularity connections in Matrix B are specified only for the experimental conditions, so that both matrix inputs are non-redundant to each other (Hillebrandt et al., 2015).

Second, we constructed a Parametric Empirical Bayes (PEB) model for the whole group of participants over all parameters (cf., SPM procedure: *spm\_dcm\_peb*). This makes it possible to estimate the effective connectivity averaged across all participants (cf., group average), taking into account the within-participants variability on the connectivity parameters, unlike a classical test (e.g. *t*-test) which ignores the estimated uncertainty (variance) about the connection strengths.

Third, we automatically pruned away any connectivity parameter from the group-level PEB which did not contribute to the model evidence using Bayesian model reduction (cf. SPM procedure: *spm\_dcm\_peb\_bmc*). This approach has the advantage that any reduced model at the group level can be estimated efficiently without having to re-estimate the reduced models at the lower level (single-participant levels) and is therefore recommended (Friston et al., 2015). Specifically, a greedy search iteratively prunes connection parameters from the full model until model-evidence starts to decrease, so that the most relevant nested models from the full PEB model are tested (a greedy search is recommended because the model space of all possible nested models is too large to be fully evaluated). Bayesian model averaging of the parameters of the best 256 pruned models is applied and used for group-inferences (Zhou et al., 2018, p. 707, 2.7.4), and so determines the winning model empirically. We considered connectivity parameters as significant when their posterior probability  $p > .95$  (based on model comparisons with and without each parameter). This Bayesian approach both for first-level connectivity analysis (DCM) as well as group-level inference (PEB) on connectivity parameters eschews the multiple comparisons problem (Friston et al., 2003, p. 1276, 1.3).

### 3. Results

Tables 2 and 3 show the fixed and modulatory estimates respectively of the connectivity between cerebellar and cerebral mentalizing ROIs of the reduced model (after pruning). The estimates in the off-diagonal cells correspond to rate constants and are expressed in units of 1/s (Hz), or the amount by which activation in the source ROI changes the activation in



**Table 1**

Total number of participants (n) and number of participants with ROIs at reduced thresholds.

	rpCE		lpCE		rCEVIII		rCEIV-V		Pcun		ITPJ		rTPJ		dmPFC	
n	<.10	<1	<.10	<1	<.10	<1	<.10	<1	<.10	<1	<.10	<1	<.10	<1	<.10	<1
49	1	1	4	2	2	2	-	-	-	-	-	-	-	-	-	-

**Table 2**

Averaged fixed connections in units of 1/s (Hz).

to \ from	rpCB	lpCB	rCBVIII	rCBIV-V	Pcun	ITPJ	rTPJ	dmPFC
rpCB	-0.63*	0.00	0.12*	-0.06*	0.00	0.07*	0.08*	-0.01
lpCB	0	-0.73*	0.10*	0	0.07*	0.04*	0.05*	-0.01
rCBVIII	0.03	0	-0.64*	0.03	0.01	0	0.04*	-0.05*
rCBIV-V	-0.04*	0	0.09*	-0.66*	-0.03	0	0.10*	-0.01
Pcun	-0.06*	0	0.17*	0.16*	-0.67*	0.11*	0.10*	-0.10*
ITPJ	-0.07*	-0.03	0	0	0	-0.79*	0.10*	0.01
rTPJ	-0.09*	-0.09*	0	0	-0.05*	0.15*	-0.85*	0
dmPFC	0	0	0	-0.06*	0.10*	0.12*	-0.05*	-0.78*

Note: Cell entries refer to connections with \* denoting posterior probability  $p > .95$ . l = left, r = right, p = posterior, CB = cerebellum, Pcun = precuneus, TPJ = temporo-parietal junction, dmPFC = dorsomedial prefrontal cortex.

**Table 3**

Averaged modulatory connections in units of 1/s (Hz).

to \ from	rpCB	lpCB	rCBVIII	rCBIV-V	Pcun	ITPJ	rTPJ	dmPFC
Modulatory connectivity of Mechanical Scripts								
rpCB	-0.01	0.00	0.01	-0.01	0.02	-0.03	0.00	-0.01
lpCB	0.00	-0.01	0.00	0.00	-0.01	-0.01	-0.04	0.02
rCBVIII	0.00	0.02	-0.01	0.01	-0.01	0.01	-0.03	0.04
rCBIV-V	0.03	0.01	0.00	-0.01	0.02	-0.03	-0.05	0.02
Pcun	0.01	0.01	0.02	-0.02	-0.59*	0.00	-0.30*	0.39*
ITPJ	0.03	-0.03	0.00	0.22	0.00	-0.29	0.00	-0.01
rTPJ	0.04	0.01	0.00	0.00	0.06	-0.02	-0.03	-0.01
dmPFC	0.02	-0.02	-0.01	0.01	-0.28*	-0.02	0.02	-0.01
Modulatory connectivity of Social Scripts								
rpCB	-0.01	0.02	0.02	0.01	0.02	-0.02	-0.02	0.02
lpCB	-0.02	-0.02	0.01	0.00	0.01	-0.01	-0.02	0.04
rCBVIII	-0.02	0.01	-0.01	0.00	-0.01	0.00	-0.04	0.05
rCBIV-V	0.02	0.04	0.00	-0.01	0.02	-0.02	-0.02	0.01
Pcun	0.00	0.01	0.02	-0.01	-0.47*	-0.02	-0.30*	0.06
ITPJ	0.02	0.02	0.03	0.01	0.00	-0.58*	-0.04	0.00
rTPJ	0.03	0.00	0.44*	-0.02	0.06	-0.01	-0.03	0.01
dmPFC	0.01	0.00	0.00	0.02	-0.28*	0.02	0.00	-0.03
Modulatory connectivity of False beliefs								
rpCB	-0.02	0.00	0.00	0.00	0.01	-0.01	-0.02	0.02
lpCB	0.00	-0.02	0.02	-0.03	0.00	0.00	-0.03	0.01
rCBVIII	0.00	0.01	-0.02	0.02	-0.01	0.00	-0.03	0.03
rCBIV-V	0.02	0.01	0.00	-0.02	0.01	-0.01	-0.02	0.01
Pcun	-0.02	-0.01	0.03	-0.01	-0.45*	-0.01	-0.02	0.31*
ITPJ	0.02	-0.01	0.03	0.03	-0.01	-0.51*	-0.02	0.02
rTPJ	0.02	0.01	0.02	0.00	0.04	-0.01	-0.02	0.02
dmPFC	-0.01	0.03	0.00	0.01	-0.31*	-0.02	0.00	-0.03
Modulatory connectivity of True Beliefs								
rpCB	-0.52*	0.01	0.01	0.01	0.01	-0.04	-0.04	0.00
lpCB	-0.01	-0.01	0.02	0.00	0.00	-0.02	-0.06	0.00
rCBVIII	-0.01	0.03	-0.01	0.01	-0.03	-0.01	-0.04	0.03
rCBIV-V	0.01	-0.01	0.00	0.00	0.02	-0.02	-0.04	0.00
Pcun	0.00	0.03	0.02	-0.02	-0.49*	-0.03	-0.17	0.04
ITPJ	0.02	0.01	0.02	0.41*	0.00	-0.46*	-0.01	0.00
rTPJ	0.03	0.04	0.20	0.03	0.06	-0.03	-0.03	-0.03
dmPFC	0.02	0.01	-0.01	0.02	-0.31*	-0.02	0.02	-0.03

Note: Cell entries refer to connections with \* denoting posterior probability  $p > .95$ . l = left, r = right, p = posterior, CB = cerebellum, Pcun = precuneus, TPJ = temporo-parietal junction, dmPFC = dorsomedial prefrontal cortex.

the target ROI per unit of second. The estimates in the diagonal cells, which are of less interest, express inhibition by self-connections in the format of a log scale. Negative values of the log scale indicate a scaling factor between 0 and 1, or weak self-inhibition, while positive values indicate a Hertz above 1, or strong self-inhibition. During Bayesian inversion, the scaling factor is multiplied with a fixed negative self-connection of 0.5 Hz so that in effect the self-connections are always

inhibitory in nature.

We predicted contralateral and ipsilateral bidirectional connections (i.e., closed-loops) between the posterior cerebellar ROIs with key mentalizing cerebral areas, most likely the bilateral TPJ. Moreover, we predicted that connections originating from the cerebellum would reflect some sort of negative error signal.

Consistent with these predictions, we found significant closed-loops

between the bilateral posterior cerebellum with the bilateral TPJ, except for a unidirectional connection from the left TPJ to the left posterior cerebellum which was part of the reduced model, but did not reach significance (Table 2 & Fig. 2). In addition, there was a unidirectional connection from the cerebellum to the precuneus, but no reverse link. There were no cerebral connections with the dmPFC. Also consistent with our prediction is that the cerebellum sends out a negative error signal, while all connections going toward the cerebellum were positive. We also explored the possibility of closed-loops with the two exploratory, more anterior cerebellar ROIs (rCBIV-V and rCBVIII), and found significant links with the precuneus, TPJ and dmPFC, but all of these were unidirectional: Significant connections were revealed from the right TPJ and dmPFC to one or both exploratory cerebellar ROIs, and reverse connections from one or both exploratory cerebellar ROIs to the precuneus and dmPFC. Finally, there was no modulation of the cerebral connections with the posterior cerebellar ROIs, and there were only two modulations with the exploratory cerebellar ROIs (Table 3).

The connections within the cerebral cortex were largely as one might expect (Table 2 & Fig. 2). There were bidirectional connections between the left and right TPJ, and unidirectional connections from the precuneus and bilateral TPJ to the dmPFC, but almost no reverse connections from the dmPFC except to the precuneus. There were also bidirectional connections from the bilateral TPJ to the precuneus, except from the precuneus to the left TPJ. Finally, modulation of connectivity between the mentalizing ROIs was very rare and involved downregulating as well as upregulating a limited number of connections (Table 3).

In addition, none of the driving inputs to the ROIs reached significance.

We also explored the potential role of the hippocampus and insula in

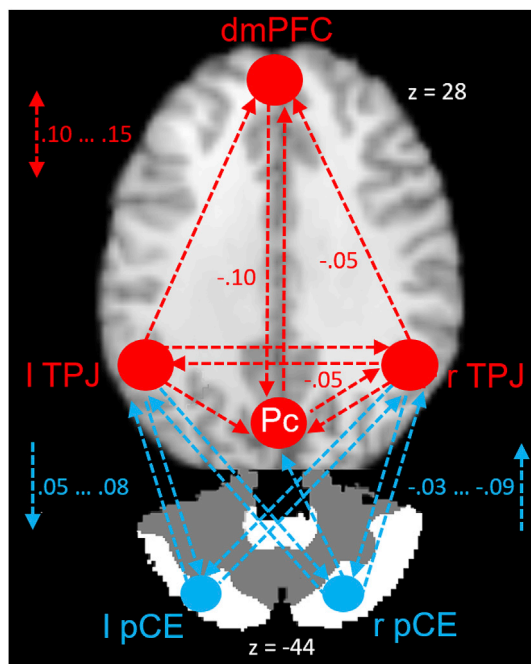


Fig. 2. Direct connections between key left and right (l/r) areas including the posterior cerebellum (pCE), precuneus (Pc), temporo-parietal junction (TPJ) and dorsomedial prefrontal cortex (dmPFC) retained in the reduced model. All connections have posterior  $p > .95$ , except for the link from left TPJ to left pCE with  $p = .62$ . The connectivity estimates correspond to rate constants and are expressed in units of  $1/s$  (Hz). To avoid cluttering the figure, the estimates are summarized on the left and right side of the figure (with a red double arrow indicating all directions), and only estimates outside these ranges are indicated at specific connections. The white area in the cerebellum refers to the mentalizing network identified by Buckner et al. (2011).

cortico-cerebellar connectivity, because these ROIs were also strongly activated in the original study (Heleven et al., 2019). This was done by exploring two alternative models in which either the bilateral hippocampus ROIs, or the bilateral insula ROIs replaced the two anterior cerebellar ROIs of less interest (as the number of ROIs in DCM is technically limited to 8 by default). The results, did not reveal any connections between the posterior cerebellar ROIs and the bilateral insula. However, there was one significant connection (among all cortical ROIs) from the right TPJ to the right hippocampus (0.04), and from the right (and left) hippocampus to the right posterior cerebellum ( $-0.12$  &  $0.08$  respectively), but no reverse links from or between the hippocampal ROIs. Note that this indirect connection emits at the end a negative signal to the cerebellum ( $0.04 \times -0.12$ ), which contradicts the positive direct connection from the TPJ to the right posterior cerebellum (0.08; Table 2).

#### 4. Discussion

This study investigated whether cerebellar areas involved in the generation of action sequences, are activated in synchrony with social mentalizing areas located in the cerebral cortex by using DCM. We used recent fMRI data on social action sequencing (Heleven et al., 2019) which revealed robust cerebellar ROIs, and we expected to confirm and extend the evidence for closed-loop circuits as demonstrated by a recent DCM connectivity analysis (Van Overwalle et al., 2018). This evidence would further support the hypothesis that internal forward models in the cerebellum communicate with cerebral cortical areas and are responsible for the formation and predictions involving action sequencing.

As explained in the introduction, DCM has many strong features. First and perhaps most importantly, DCM allows to specify the directionality of the connections so that we can verify the existence of closed-loops. Second, it also allows to distinguish between (a) connections that are fixed and independent from experimental manipulation, and (b) the modulation of the experimental conditions on these connections. Third, DCM identifies only direct connections by controlling for indirect effects via other connections specified in the model. In this respect, DCM allows a much more accurate insight on the flow of neural propagation of activity between cerebrum and cerebellum.

After pruning away connections that were not contributing to the model evidence, the analysis offered a group-level model of effective connectivity, or dynamic causal model, that provided the best fit with the data (see Table 2 and Fig. 2). This model identified closed-loops between the bilateral posterior cerebellar lobes and the bilateral TPJ, a key area of the mentalizing network (except for one connection from the left posterior cerebellum to the left TPJ which was part of the final model so that it should not be ignored, but its strength by itself was not significant). There were no closed-loops with other mentalizing areas in the cortex, such as the precuneus and the mPFC. Moreover, all connections originating from the posterior cerebellum were negative while the reverse connections to the posterior cerebellum were positive, which raises the speculation that the cerebellum emits a kind of error signal that is different from the signal it receives from the cerebrum. Considering the lack of differentiation between social and non-social events in connectivity, this observation does not involve uniquely social sequencing, but all types of sequences in general. However, the present data do not allow to say whether the negative connections from the posterior cerebellum extend to the whole cerebellum. Together, the data confirm and extend the earlier evidence of closed-loop circuits between the cerebellum and cerebrum during social reasoning from an earlier DCM analysis, which also revealed positive connections from the TPJ to the cerebellum, and negative connections in the reverse direction (Van Overwalle et al., 2018).

The closed-loops between the bilateral posterior cerebellum and the bilateral TPJ support the role of the TPJ in understanding actions and events provided in the study by Heleven et al. (2019). This connectivity pattern indicates that social processes in the mentalizing TPJ trigger further activity in mentalizing areas of the bilateral posterior cerebellum,

and vice-versa. This provides support for domain-specific connectivity circuit between mentalizing areas of the cerebrum and cerebellum.

The connections are also consistent with recent anatomical research showing predominantly closed-loops from the cerebellum terminating on contralateral cerebral areas in animals (Kelly and Strick, 2003; Suzuki et al., 2012) and humans, although a minority of functional connections in humans terminate also on ipsilateral cerebral areas (Krienen and Buckner, 2009; Salmi et al., 2010; Sokolov et al., 2014). The present finding of ipsilateral connections to the human cerebral cortex with quite significant functional influence, requires further research. Of interest is that research with humans reported ipsilateral connections mainly in posterior mentalizing cerebellar areas, including Crus 1, during the perception of human movements (Sokolov et al., 2014) or human musical sounds (Salmi et al., 2010). Future research might explore whether the presence of significant ipsilateral TPJ connectivity with the bilateral posterior cerebellum is accidental or systematic, and what these ipsilateral links might imply for the functionality of the cerebellum in social cognition.

We tested for relay stations in the connectivity between the cerebellum and cortex, and found no connectivity at all with the insula, but some evidence for an indirect ipsilateral TPJ → hippocampus → cerebellum link on the right hemisphere, but no reverse indirect link. Moreover, the total signal of this indirect right TPJ link was negative, contradicting the positive direct signal from the right TPJ. Together, these findings provide only weak evidence for intermediate relay stations, which seems to contradict the general notion that closed-loops connect the cerebellum to the cortex through multi-synaptic pathways (Kelley and Strick, 2003). Several methodological factors in the original study (Heleven et al., 2019) might have contributed to this, including a control condition which was insufficient to reach significant contrast activation in classic motor-related relay stations such as the basal ganglia. Note, however, that this area did not show activation either in the earlier DCM analysis on mentalizing (Van Overwalle, Van de Steen and Mariën, 2019). Structural neuroimaging data such as diffusion tensor imaging or tracing studies are needed to make stronger claims on anatomical tracts along which social mentalizing information might propagate.

Within the cerebrum, the model identified closed-loop connectivity between the bilateral TPJ, and between the dmPFC and precuneus, but only unidirectional connections from the bilateral TPJ to the dmPFC. These findings suggest that there is mainly input from the precuneus and TPJ to the mPFC, responsible for higher order mentalizing (Baetens et al., 2013; Baetens et al., 2017). This is in line with data showing faster neural activity in the TPJ than in the mPFC as revealed by EEG findings (Van der Cruyssen, Van Duynslaeger, Cortoos and Van Overwalle, 2009; Van Duynslaeger, Sterken, Van Overwalle and Verstraeten, 2008; Van Duynslaeger, Van Overwalle and Verstraeten, 2007) and fMRI studies (Ma et al., 2012). Note that a lack of direct connections between the posterior cerebellum and the dmPFC, an important area in the mentalizing network, should not obscure the finding that this area reveals indirect bidirectional connections with the posterior cerebellum via the TPJ and the precuneus.

The identification of close-loop circuits between the cerebellum and cerebrum, with negative error signals from the cerebellum, is in line with the cerebellar theory of Ito (2008) and further strengthens the role of the cerebellum in social cognition. This is consistent with the hypothesis that the evolutionary older cerebellar function of building forward models for motor control, recently evolved and extended toward purely mental control during cognitive operations and social reasoning in which event sequences play an important role (Ito, 2008; Pisotta and Molinari, 2014). By building internal cerebellar models of social events, humans can anticipate action sequences during social interaction and joint action in an automatic and intuitive way. This role of internal sequence prediction is perhaps most prominent in mental reconstructions, devoid of direct observations, in preparation of such interactions. When these internal anticipations fail on the basis of novel evidence, it is assumed that the cerebellum makes corrective adjustments while the action is unfolding,

and fine-tunes existing anticipations to create an improved internal model (Ito, 2008; Pisotta and Molinari, 2014). Taken together, our connectivity data provide strong evidence for a circuit in which sequences of social actions, extracted in the cerebrum are further propagated to an internal model in the cerebellum, which acts as a forward controller that sends error signals to improve predictions on the implicated social behavioral sequences to facilitate fluent and automatic social interaction.

One aspect of this analysis was rather unexpected. The results identified mainly fixed connections between the cerebrum and cerebellum with very little modulation by the experimental conditions, thus revealing little differentiation between social and non-social events, much like the earlier DCM analysis on social mentalizing (Van Overwalle et al., 2018). The lack of modulation seems to speak against the view that the current cerebro-cerebellar connections are specifically related to belief understanding during social mentalizing in contrast to the other (non)social routine conditions. This result might seem surprising at first sight, because it seems to suggest that even purely mechanical sequences recruit synchronized activation of mentalizing areas in the cerebellum and cerebral cortex. However, the finding of substantial fixed connectivity may be interpreted differently. It may suggest that varying high and low levels of activity in both the cerebellum and the cerebrum as observed across the different experimental conditions (Heleven et al., 2019), occur in close synchrony regardless of condition, and this provides even stronger evidence for the close connectivity between these two brain parts. If true, this interpretation suggests that the same connections should also be observed during resting state, which is supported by earlier research (cf. Buckner et al. 2011). In addition, this high level of synchrony across conditions might perhaps have been increased by the fact that most experimental conditions contain substantial social elements (i.e., persons). Moreover, by providing all experimental trials in a random order, some spontaneous mentalizing processes triggered by the belief conditions might have leaked to the other conditions as well.

## 5. Conclusion

The present dynamic modelling analysis supports the recently acknowledged relation between the cerebellar function of sequence processing and social mentalizing. It demonstrates that there are domain-specific mentalizing closed-loops between the cerebrum and the cerebellum. This analysis sheds more light on the specific processes that take place in the posterior cerebellum, in particular, the sequencing of social actions. This supports the view that the cerebellum is a forward controller that matches internal cerebellar models of event sequences against external sources and contexts in the cerebrum. It is a first step towards broadening our knowledge on cortico-cerebellar connectivity for other social sequences and processing modes during social mentalizing.

## Data and code availability statement

The data and code for the present analyses are available from the first author upon request.

## Ethics statement

As noted in the participant section, "Informed consent was obtained in a manner approved by the Medical Ethics Committee at the Hospital of University of Ghent, where the studies was conducted. Participants were paid 20 euro in exchange for their participation."

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