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Social Cerebellum in Goal-directed Navigation

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Running Head: Social cerebellum in navigation

Highlights

- The posterior cerebellar Crus is involved in sequence-based social navigation, along with the parahippocampal gyrus and social cortical areas.
- Crus II is recruited during memorizing social and non-social sequential trajectories
- Crus I is specifically recruited to memorize social trajectories.
- Cerebellar Crus I and II, and lobules VI are recruited when reproducing social and non-social sequencing trajectories.

Abstract

The posterior cerebellum is responsible for the understanding and learning of sequences of actions by others, which are a prerequisite for social understanding. This study investigates this cerebellar function while navigating towards a goal in a social context. Participants undertook a novel social navigation task requiring them to memorize and subsequently reproduce a protagonist's trajectory through a grid towards a desirable goal. As a non-social control condition, a ball underwent the same trajectory by passively rolling through the grid toward the same endpoint. To establish that memorizing and reproducing a trajectory is a critical cerebellar function, two non-sequencing control conditions were created, which involved the observation only of the trajectory by the protagonist or ball. Our results showed that the posterior cerebellar Crus II was involved in memorizing both social and non-social trajectories, along with the parahippocampal gyrus and other cortical areas involved in social cognition. As hypothesized, cerebellar Crus I was more active when memorizing social as opposed to non-social trajectories. Moreover, cerebellar Crus I and II, and lobule VI, were activated when reproducing both social and non-social trajectories. These findings highlight the involvement of the posterior cerebellar Crus in supporting human goal-directed social navigation.

Keywords: Social navigating, Social sequence learning, Mentalizing, Posterior cerebellum, Goal-directed behavior

Introduction

Imagine a tourist visiting an unfamiliar city for the first time, walking around hesitantly and trying to find her way to settle in. Not only can we follow or reproduce her spatial trajectory, but by observing the places she visits, we can also sense what personal goals and preferences she is pursuing, and so make social judgments about her (e.g., does she like arts?).

Navigating through space and locations, and the role of the brain in this process, is investigated in the well-known topic of *spatial navigation*. A far less studied, but emerging topic, is observing how other people, rather than the self, navigate within a socially-rich environment context, and most importantly, which social inferences this elicits among observers. We term this process *social navigation* (for other views; see Tavares et al., 2015). Social navigation rests on core processes in *social cognition*, or the ability to understand the actions and mental states of others. Indeed, when people navigate through spaces filled with people or objects relevant for them (e.g., cities), their trajectory/route informs us about which goals they pursue, which preferences they have, or what kind of person they are (Tompson et al., 2020; Van Overwalle, 2009; Van Overwalle & Baetens, 2009). For example, if we learn that our tourist visited national parks rather than museums, we can safely infer that she was interested in nature rather than arts.

A major aim of this study is to investigate the role of the cerebellum in this process, because, as we will argue later, recent evidence indicates that a key function of the cerebellum is to identify and store sequences of actions, which is required in navigation when pursuing step-by-step trajectories. Before doing so, we first introduce evidence on the neural underpinnings of social cognition.

Social Cognition

Social cognition focuses on how people process, store, and apply information about other people. It relies on two main systems: the *mirror* system, also known as the *action observation* system (i.e., watching movements performed by others), by which we can decipher and predict non-verbal body language during movements that points to others' goals and emotions, and the *mentalizing* system, by which we can deduce the mental states of other people, such as their goals, beliefs, preferences, traits and so on (Van Overwalle & Baetens, 2009).

The mirror system identifies the goal of perceived biological movements by matching it to the neural representations of our own movements and associated goals. That is, when we observe a movement, this automatically triggers a similar neural representation of our own movement and the goal associated with it, which is used to infer the goal of another person (Gallese et al., 2004; Keysers & Gazzola, 2007; Keysers & Perrett, 2004). The mirror system depends on low-level behavioral input that identifies other person's goals rapidly and intuitively (Calvo-Merino et al., 2005; Calvo-Merino et al., 2006; Cross et al., 2006). Meta-analyses of neuroimaging studies (Molenberghs et al., 2012; Van Overwalle & Baetens, 2009) documented that the mirror / action observation network relies on the posterior superior temporal sulcus (pSTS), an auxiliary area that identifies biological movement, and key areas including the anterior intraparietal sulcus (aIPS) that identifies movement execution in a specific context (e.g., hand grip for drinking versus taking away a cup), and the premotor cortex (PMC) that represents the associated goal (e.g., drinking versus cleaning; Table 1).

In contrast, the mentalizing system extracts the goals, beliefs, and personality traits and other mental states of others, based on observed or communicated behaviors, as if we read the other's mind (e.g., Amodio & Frith, 2006; Gallagher & Frith, 2003; Saxe & Kanwisher, 2003). Mentalizing involves a relatively high-level cognitive process that comprises an essential function of the default mode network (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner,

2010). It relies on several subprocesses supported by specific brain areas documented in several meta-analyses of neuroimaging studies (Molenberghs et al., 2016; Schilbach et al., 2012; Schurz et al., 2014; Van Overwalle, 2009): the temporo-parietal junction (TPJ) is recruited when reorienting one's perspective to others, the medial prefrontal cortex (mPFC) is activated when inferring the traits of others, and the precuneus (PCun) is recruited when imagining the scenes behind other's actions (Table 1).

Social Cerebellum

While the cerebellum has long been exclusively associated with motor functions, in recent years, a broad range of functions of the cerebellum, such as perception, language, working memory, and cognitive control, has been identified (Diedrichsen et al., 2019). Importantly, the critical role of the posterior cerebellum in social cognition has been increasingly recognized (Van Overwalle, Manto, et al., 2019, 2020). In the present study, we focus on one of the basic functions of the cerebellum, that is, to support learning and memories of "temporally or spatially structured sequences" in motor and non-motor processes, which allow to predict, fine-tune and automatize behavior (i.e., *sequence detection hypothesis* by Leggio & Molinari, 2015). Consequently, the cerebellum not only identifies serial events as a sequence, it also detects violations in predicted sequences, and so supports error-correction of ongoing behaviors (Popa & Ebner, 2019). Given this sequential function of the cerebellum, its role in identifying and predicting spatial sequences in navigation, might be more important than assumed so far. In particular, the cerebellum might participate in the construction of motion information and prediction, which is a prerequisite for the construction of spatial representations in the hippocampus, a key area in goal-directed navigation (Lefort et al., 2015; Rochefort et al., 2013; Rondi-Reig et al., 2014). A meta-analysis by Stoodley & Schmahmann (2009) documented that the cerebellum is also involved in spatial processing.

What is the role of the posterior cerebellum in social cognition? In line with the sequence detection hypothesis (Leggio & Molinari, 2015), there is now increasing social neuroscientific evidence that the posterior cerebellar Crus I and II is recruited when observing or reproducing dynamic sequences of human actions which allow to make social mentalizing inferences (Van Overwalle, De Coninck, et al., 2019; Van Overwalle, Manto, et al., 2019, 2020). Recent research confirmed the role of the cerebellum in identifying temporal sequences of a broad range of social behaviors that require higher-level social mentalizing, such as other's beliefs and traits, in neuroimaging studies (Heleven et al., 2019; Pu et al., 2020), as well as in studies with patients suffering from cerebellar impairments (Van Overwalle, De Coninck, et al., 2019). A meta-analysis identified a domain-specific social functionality in Crus II, with about 74% of the studies showing activation in this area reflecting a process of mentalizing (Overwalle et al., 2020). Of interest, it was found that some "sequential" areas in Crus II identified in earlier research on social action sequences (Heleven et al., 2019; Pu et al., 2020) revealed more sensitivity to human action than other areas in Crus II. There is also evidence that the posterior cerebellar Crus is activated in synchrony with cortical areas of social mentalizing, so that error-correcting signals can be exchanged (Van Overwalle, Van de Steen, et al., 2019, 2020).

Prior research mainly focused on the role of the social cerebellum in identifying and/or memorizing sequences in social actions presented in sentences that implicated similar traits (Pu et al., 2020), in cartoons that implicated other's beliefs (Heleven et al., 2019), or in serial actions involving other's belief orientations (Pu, Ma & Van Overwalle in: Van Overwalle, Manto, et al., 2020). We are aware of only one functional magnetic-resonance imaging (fMRI) study that explored navigation in a socially-rich spatial environment (Kumaran & Maguire, 2005). In that study, participants determined the optimal social route between friends using social connections via other friends to deliver a package, as opposed to the optimal spatial route between friends' homes. It was found that hippocampal activation was preferentially driven by

spatial relational processing, and that activation of the posterior cerebellar Crus II was preferentially driven by social navigation. However, apart from that early fMRI study, the role of the posterior cerebellum in social navigation has been scarcely uncovered.

Spatial Navigation

In the present study, we present trajectories of protagonists moving through space from a bird's (i.e., allocentric) point of view (Iglói et al., 2015; Maguire et al., 1998). Several meta-analyses of neuroimaging studies on spatial navigation identified the hippocampus and adjacent middle temporal areas (e.g., parahippocampal gyrus) as the primordial subcortical site contributing to spatial navigation (Kong et al., 2017; Kühn & Gallinat, 2014; Qiu et al., 2019). In addition, many cortical areas were systematically reported in these meta-analyses (see Table 1), including the supplementary motor area (SMA) involved in identifying visual landmarks as cues for navigation (Qiu et al., 2019), the precentral gyrus (PreC) and angular gyrus (ANG) supporting goal-directed action observation, and the precuneus (PCUN) involved in encoding visual landmarks as part of the external environment and scene.

Of note, several brain areas supporting social cognition, overlap with spatial cognition (Table 1; see also Proulx et al., 2016). First, key areas of action observation in social cognition (i.e., aIPS and PMC) are closely located to areas in the posterior-dorsal module of the navigation network (PreC and ANG; Kong et al., 2017), suggesting a shared process of observation of biological movement by others during social cognition (Molenberghs et al., 2012; Van Overwalle & Baetens, 2009), and by the self during spatial navigation. Second, the precuneus is activated in both social cognition and spatial navigation, suggesting that it provides a background to social actions for social mentalizing, much like a scene in a theatre (Costigan et al., 2019), and a background to identify visual landmarks for spatial navigation (Qui et al., 2019). For the sake of theoretical simplicity, we will refer to overlapping areas from a social perspective that focuses on this shared process.

Present research: cerebellum and social navigation

The present study investigates the role of the cerebellum in social navigation, using a novel task where a protagonist is observed while moving step-after-step through a spatial grid in order to reach a desired goal. The task emphasizes the sequential nature of navigation, and hence the potential role of the posterior cerebellum. The paradigm is adopted from previous behavioral research on sequence observational learning among clinical populations with impaired social abilities (e.g., autistic children, Foti et al., 2014, 2015), and adjusted by adding a selection between several goals to enhance the focus on the protagonist's intentions. Also, inferring the intentions of goal-directed action and control of movement overlaps with known critical functions of the cerebellum, such as prediction (Sokolov et al., 2017) and executive control (Van Overwalle, Manto, et al., 2020).

In particular, participants were required to observe, memorize and subsequently reproduce a trajectory taken by a protagonist towards one of many desirable goals, such as cake, money and so on. To test whether neural activation is due to the social nature of the task, we created a non-social control condition, where a ball underwent the same movements toward the same endpoint, but this was described as mechanical rolling on an uneven terrain to the endpoint, where the ball came to a halt. In addition, to test whether memorizing and reproducing sequences is the main function of the cerebellum, we also created two parallel Non-sequencing conditions which only involved observation, without memorization or reproduction.

Based on the sequencing hypothesis (Leggio & Molinari, 2015) and the role of the posterior cerebellar Crus in social cognition (Ma, Heleven, Van Overwalle, 2020), our main hypothesis was that the posterior cerebellar Crus is preferentially involved when memorizing as opposed to passively observing social trajectories; and less so or not at all for non-social trajectories. We further hypothesized that cortical areas of the action observation and mentalizing networks are activated together with the cerebellar Crus, given the evidence,

reviewed earlier, that many of these areas are recruited during social mentalizing and spatial navigation. We made the same hypothesis for the hippocampus, as this is a key area in spatial navigation (Table 1). In addition, we also explored potential differences between memorizing and reproducing the trajectories, because recruitment of the cerebellum (and related cortical areas) may be likely during sequence learning in line with the sequence-detecting role of the cerebellum (Leggio & Molinari, 2015), as well as during reproduction in line with the error-correcting role of the cerebellum (Popa & Ebner, 2019). We also explored the role of the hippocampus, which is also responsible for memory encoding and retrieval in a variety of domains, such as spatial navigation (Epstein, 2008; Kong et al., 2017).

[Insert Table 1 about here]

Method

Participants

Participants were 23 right-handed, native Dutch-speaking individuals (male = 7) with age varying from 20 to 32 years (M = 23.96, SD = 3.44). They all reported no abnormal neurological history and had a normal or corrected-to-normal vision. All participants were right-handed, as assessed by the Dutch version of the Edinburgh Inventory (Oldfield, 1971). Informed consent was obtained in a manner approved by the Vrije Universiteit Brussel and the Medical Ethics Committee at the Hospital of the University of Ghent, where the study was conducted. Participants were paid 20 euro for their participation and additional reimbursement for public transportation costs.

Task and Stimulus materials

The experiment was composed of four conditions, involving a within-participant design with two factors: Domain (Social versus Non-social) and Task (Sequencing versus Non-sequencing).

The main condition was the Social Sequencing condition (Figure 1A). On each trial, participants saw an 8 by 10 grid (see Figure 1A) in which a protagonist (one out of 6 smurfs, well-known Belgian cartoon figures) was moving through the grid, populated with some desirable objects and obstacles. There were no actual (biological) movements, but quick shifts of the head of the smurf from one cell in the grid to an adjacent cell. Participants received the following instructions: “Smurfs love cake, flowers, money or other items. Each smurf loves one object and is always looking for it. First, look carefully at the correct steps in the trajectory that a smurf takes. Afterwards, repeat these steps”. The six desirable objects were shown before the experiment started. In order to explain why the movements of the smurfs were sometimes erratic and not directed straightforward towards to goal, they were further told: “You will see

different trajectories in which, in addition to these objects, some obstacles (stones, tree stump or grass) obstruct the view and the passage of the smurfs. The smurfs can only see a few steps ahead and must therefore get close to the objects to see them clearly."

To pilot test and select the material, 143 different participants rated to what extent the trajectory of the agent and the positions of the obstacles was reasonable on a 5-point scale (1 = not reasonable, 5 = very reasonable). We created 24 trajectories, of which 12 trajectories were easy (10 steps, 2 turns), and 12 were hard (14 steps, 4 turns) so that this would generate sufficient variation in performance (see also Pu et al., 2020). Half of the participants rated the easy version (age: $M \pm SD$ = 19 ± 0.86, range 17-21, female = 55) and the other half rated the hard version (age: $M \pm SD$ = 19 ± 1.34, range 17-24, female = 51). For the experiment, we selected 10 easy and 10 hard trajectories with the highest mean on the reasonability ratings. The mean rating for the selected 20 trajectories were all beyond 2.5 on the 5-point scale (Easy: $M \pm SD$ = 3.48 ± 0.26; Hard: $M \pm SD$ = 2.90 ± 0.17). We then generated three additional equivalent sets of trajectories by mirroring the selected trajectories upside-down, left-right, or both. This resulted in 80 trials in total.

To identify the role of the social nature of the task, we created a Non-social Sequencing condition (Figure 1A). In that condition, the 6 smurfs and 6 goal objects from the Social Sequencing condition were replaced by 6 balls and 6 circles respectively. On each trial, participants saw a ball, randomly selected out of the set of 6 balls. They were given the following instructions: "A number of balls have fallen on an uneven terrain. Each ball continues to roll through this terrain until it comes to rest in a circle. First, look carefully at the correct trajectory the ball follows as it rolls. Afterwards redo these movements." Note that the color of the balls and circles were composed of the colors of the distinct smurfs and goals objects respectively.

To identify the role of actively learning and reproducing sequenced-based trajectories in social navigation, we also created two Non-sequencing conditions in which the participants were instructed to passively watch the movement of the smurfs (Social Non-sequencing condition) or balls (Non-social Non-sequencing condition), without memorizing or reproducing the trajectory. The instructions were identical as in the sequencing conditions, but ended differently "…First, look carefully at the correct steps in the trajectory that a smurf takes / the correct movements that the ball follows as it rolls. Then indicate where the smurf / ball stopped." All other aspects of the task and material were identical to the experimental conditions, including the smurfs and balls.

Procedure

Before the participants entered the scanner, to get familiar with the task and the direction buttons using the keyboard, they practiced 20 easy version trajectories (which were not part of the experimental stimulus material). Feedback on their average accuracy in reproducing the trajectories was given after every five trials. They could enter the scanner when they had achieved 90% accuracy or higher. When participants were in the scanner, they also practiced five trials to get familiar with performing the task and the response box inside the scanner. Then, the task began (see Figure 1B).

Each condition involved 20 trials. The participants first finished the two Sequencing conditions where Social and Non-social trials were presented in a randomized order, and then took the two Non-sequencing conditions in a similar randomized order. We provided these two types of conditions separately, because the instructions and procedure were quite distinct. The Sequencing conditions were provided first, because they involved the critical manipulation, while the Non-sequencing conditions were provided last, because they required no memorization so that performance would be less influenced by prior learning.

Each trial started with an Observation Phase, which began with a blank screen, the duration of which was jittered randomly from 0 to 1000 ms. After a warning signal "Look carefully" presented for 3000 ms on the screen, the smurf / ball began to move at a fixed pace of 400 ms per step towards a goal / endpoint. Each trajectory started at any possible cell in the grid, except for the bordering and four center cells of the 8 x 10 grid. The grid took 71% of the width and 80% of the height of the screen.

Afterwards, the Reproduction Phase started, in which participants had to reproduce the same trajectory movements in the grid using button presses at their own pace (1 = up, 2 = down, 3 = left, 4 = right). If they made a mistake at one step, the smurf / ball did not change position, and an error warning appeared at the screen for 1000 ms, after which they could continue their movements. After reproducing the trajectory, to ensure that participants would mentalize on the goals of the smurf / focus on the endpoint of the ball, they were asked: "At which object does the smurf/ball end?" with 5 seconds to answer. During the Non-sequencing conditions, the participants completed only the Observation Phase, and immediately after answered the endpoint question.

Immediately after leaving the scanner, participants were probed for their understanding of the task. The responses showed that all participants understood the task correctly. For instance, they considered the smurfs as a "person", each pursuing specific goals, whereas they did not have that perception for the balls.

~~Questionnaire~~

~~*Autism Questionnaire.* To ensure that all participants had no ASD traits, we administered the *Autism Spectrum Quotient Test* (AQ). The AQ comprises of 50 questions that are answered using a 4-point rating scale (1 = definitely agree, 2 = slightly agree, 3 = slightly disagree, 4 = definitely disagree), assessing five different areas: social skill, attention switching, attention to~~

~~detail, communication and imagination (Baron-Cohen et al., 2001). Mean score was 20.25, with a range between 7 and 26, all scores were well below the clinical threshold of 32 for ASD symptoms. One participant failed to complete the AQ due to space limits imposed by COVID regulations in the lab, but was not discarded from the analysis.~~

[Insert Figure 1 about here]

Imaging procedure and preprocessing

Images were collected with a Siemens Magnetom Prisma fit 3T 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; Psychology Software Tools) running under Windows XP. Participants were placed headfirst 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, high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence [TR = 2250 ms, TE = 4.18 ms, TI = 900 ms, FOV = 256 mm, flip angle = 9º, voxel size = 1 × 1 × 1 mm]. Second, a field map was calculated to correct for inhomogeneities in the magnetic field (Cusack & Papadakis, 2002). Third, whole-brain functional images were collected in a single run using a T2*-weighted gradient echo sequence, sensitive to BOLD contrast (TR = 1000 ms, TE = 31.0 ms, FOV = 210 mm, flip angle = 52º, slice thickness = 2.5 mm, distance factor = 0%, voxel size = 2.5 × 2.5 × 2.5 mm, 56 axial slices, acceleration factor GRAPPA = 4).

SPM12 (Wellcome Department of Cognitive Neurology, London, UK) was used to process and analyze the fMRI data. To remove sources of noise and artifact, data were preprocessed. Inhomogeneities in the magnetic field were corrected using the field map

(Cusack & 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 standard anatomical space (2 mm isotropic voxels) based on the ICBM152 brain template (Montreal Neurological Institute). Normalized data were then spatially smoothed (6 mm full-width at half-maximum, FWHM) using a Gaussian Kernel. Finally, using the Artifact Detection Tool (ART; http://web.mit.edu/swg/art/art.pdf; 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. A default high-pass filter was used of 128s, and serial correlations were accounted for by the default auto-regressive AR(1) model. A surface-based flatmap representation of activation in the cerebellum was made using SUIT (Diedrichsen, 2006).

Statistical analysis of neuroimaging data

The general linear model of SPM12 (Wellcome Department of Cognitive Neurology, London, UK) was used to conduct the analysis of the fMRI data. At the first (single participant) level, the event-related design was modeled on the basis of the full design, involving Domain (Social versus Non-social) by Task (Sequencing versus Non-sequencing) by Difficulty (Easy versus Hard) as within-participant factors. The last factor was of no interest in the analysis (given the limited number of trials), but was included to regress out any potential effects of difficulty. We created two models for the analysis, using a one-way ANOVA analysis which is the only within-participants model in SPM allowing to correct for individual differences.

The first model involved only the Observation phase, resulting in eight separate regressors corresponding to all eight cells of the full design involving the three within-participant factors mentioned earlier: Domain (Social versus Non-social), Task (Sequencing versus Non-sequencing) and Difficulty (Easy versus Hard). The second model involved the Observation and Reproduction Phases, involving only the Sequencing conditions (because the Non-sequencing conditions have no Reproduction Phase), resulting in eight separate regressors corresponding to all four cells of the Design involving the within-participant factors Domain (Social versus Non-social) and Difficulty (Easy versus Hard) in the two Phases (Observation and Reproduction). Note that only correct steps were included in the analysis so that all analyses involve the same number of (correct) steps in the Hard and Easy conditions (see also Heleven et al., 2019). The number of errors was not introduced as an individual covariate in the analysis, since the number of errors was generally quite low. The endpoint question was not included as a separate regressor, because the goal inference was assumed to take place during the whole phase of observing the trajectory. Introducing this as a separate regressor runs the risk of multicollinearity (i.e., as a consequence of estimating the same psychological process twice in the analysis).

During the Observation Phase and during the Reproduction Phase, onsets were specified at the presentation of the first step of the trajectory (i.e., the first presence of the smurf / ball). Each trial onset was convolved with a canonical hemodynamic response function and its dispersion and temporal derivatives. Because a single trial for observing the Easy and Hard trajectories takes only 4 s and 5.6 s, respectively (i.e., 400 ms per move), we set the event duration to 0 for all conditions. During the Reproduction Phase, we did not model the responses of the participants as a separate regressor, as responses were part of reproducing the trajectories.

At the second (group) level, clusters from the whole-brain analysis were defined at threshold $p < .001$, uncorrected with a minimum cluster extent of 10 voxels, and we restricted

the analysis to clusters with a Family Wise Error (FWE) corrected threshold at cluster level with $p < .05$. For all phases and all questions, we conducted a within-participant one-way ANOVA and defined all possible *t*-contrasts between regressors of interest (see Results section).

Regions of Interest

Regions of interest (ROIs) for social mentalizing and spatial navigation were derived from prior meta-analyses on mentalizing (Van Overwalle, 2009; Van Overwalle & Baetens, 2009) and spatial navigation if they were present in at least two of three recent meta-analyses (Kong et al., 2017; Kühn & Gallinat, 2014; Qiu et al., 2019). This procedure provided a restricted number of regions of interest (ROI) with their coordinates listed in Table 1. The ROIs were specified as spheres around the coordinates from Table 1 as centers, and were used to perform a small volume correction using the same thresholds as the whole-brain analysis. We used spheres with a radius of 10 mm for cerebellar (Crus I & II) and allocortical (PHG) ROIs, while we used a radius of 15 mm for all other neocortical ROIs (mentalizing and action observation networks; see also Ma et al., 2011). This was done to accommodate volume differences in these distinct brain parts and, consequently, the areas involved. This also avoids substantial overlap between cerebellar ROIs of Crus I and II (see also Van Overwalle, Van de Steen, & Mariën, 2019; Van Overwalle, Van de Steen, van Dun, & Heleven, 2020).

Statistical analysis of behavioral data

Accuracy in the Reproduction Phase was calculated for each trial separately, by calculating the number of correct steps divided by the total steps for each trajectory. Response time (RT) to reproduce the whole trajectories was also recorded. Accuracy and RT of the Goal/Endpoint question were also recorded. All accuracy and RT data were analyzed with independent *t*-test or repeated-measures ANOVA, with Domain (Social versus Non-social) and

Task (Sequencing versus Non-sequencing) as within-participant factors. A Greenhouse-Geisser correction was used if sphericity was not assumed. Partial eta squared was calculated as a measure of effect size.

Results

Behavioral results

Reproduction of trajectory. Accuracy and reaction time (RT) were analyzed using a *t*-test with Domain (Social versus Non-social) as within-participant factors (see Table 2). No main effect on accuracy or RT was significant.

Goal/Endpoint question. Accuracy and reaction time (RT) were analyzed using a repeated measures ANOVA with Domain (Social versus Non-social) and Task (Sequencing versus Non-sequencing) as within-participant factors (see Table 2). Accuracy was generally higher in the Social than the Non-social domain [F (1, 22) = 35.53, $p < .001$, $\eta_p^2 = 0.62$, 1- $\beta = 1.00$; MD = 0.06], which was most probably because goal objects were quite distinct in the Social condition, whereas they only involved circles (i.e., representing holes) with different colors in the Non-social condition. No other main or interactive effects were significant. The RTs revealed a main effect of Task [F (1, 21) = 22.98, $p < .001$, $\eta_p^2 = 0.55$, 1- $\beta = 0.99$; MD = 2.08], indicating that the RT was generally longer in the Sequencing conditions than the Non-sequencing conditions.

[Insert Table 2 about here]

fMRI results

In order to avoid redundancy, for each contrast, we first report the results of the ROI analysis using small volume correction (Table 5), and then additional clusters of the whole-brain analysis (Tables 3 & 4). Full coordinates of the ROIs are listed in Table S1 (Supplementary Material). Note that for ease of reporting and discussing the results, we consider SMA here as part of the action observation network, given its intimate link with motor observation and preparation (Ertelt et al., 2007).

Observation phase: Memorizing sequences of trajectories

Recall that our main hypothesis was that the cerebellar Crus is preferentially involved when memorizing as opposed to passively observing social trajectories; and less so or not at all for non-social trajectories. We extended this hypothesis to related cortical areas from the mentalizing (mPFC, TPJ, precuneus) and action observation networks (PMC, aIPS, SMA), as well as to the hippocampus. To investigate this hypothesis, we constructed four pairs of contrasts comparing between Domain (Social versus Non-social) and between Task (Sequencing [memorizing] versus Non-sequencing [observing-only]) conditions (see Table 3 & Figure 2).

Social vs. Non-social Sequencing. As hypothesized, the Social Sequencing > Non-social Sequencing contrast revealed significant ROI activation of the cerebellar Crus I, the mentalizing TPJ ~~(with 15 mm radius)~~, and all ROIs of the action observation network (Figure 2A). Additional whole-brain activation was revealed in the cerebellar lobule VII, and in the right middle frontal gyrus (MFG), angular gyrus and fusiform gyrus. The opposite contrast (Non-social Sequencing > Social Sequencing) did not reveal any ROI or whole-brain activation.

Social Sequencing vs. Social Non-sequencing. As hypothesized, the Social Sequencing > Social Non-sequencing contrast revealed ROI activation in the bilateral cerebellar Crus I and II , all mentalizing areas, the PMC of the action observation network, and the PHG (Figure 2B).

Additional cerebral areas from the whole-brain analysis were revealed in the middle orbital gyrus, inferior frontal gyrus, superior frontal gyrus, temporal thalamus, including superior temporal gyrus and middle temporal gyrus, middle occipital gyrus, and bilateral cuneus. The opposite contrast (Social Non-sequencing > Social Sequencing), contrary to the hypothesis, revealed ROI activation in action observation areas PMC, aIPS and SMA. Further whole-brain activation was revealed in the right cerebellum VI, left cerebellum IV-V, VI, and VIII. In addition, we also found cerebral activations in the insula lobe, precentral gyrus, postcentral gyrus, rolandic operculum, putamen, and posterior-medial frontal cortex (Figure 2D).

Non-social Sequencing vs. Non-social Non-sequencing. The Non-social Sequencing > Non-social Non-Sequencing contrast revealed significant ROI activation of the cerebellar Crus II, the mentalizing TPJ, mPFC, and precuneus, and the PHG. As predicted, however, the whole-brain activation in the bilateral cerebellar Crus II, was smaller than for the analogous Social contrast. This was confirmed by the Social Sequencing > Social Non-sequencing contrast above, and an additional interaction, indicating increased brain activity for the Sequencing > Non-sequencing contrast in the posterior cerebellum (Crus I & II; 518 voxels, $p_{(FWE\text{-}corr)} < .001$) in the Social condition vs. the Non-social condition (see Table S2 & Figure S1 in Supplementary Material). Additional cerebral activations were shown in the superior frontal gyrus, inferior frontal gyrus, middle cingulate and paracingulate gyri, lingual gyrus, middle temporal gyrus, including superior temporal gyrus, calcarine gyrus, and left cuneus (Figure 2C). The opposite contrast (Non-social Non-sequencing > Non-social Sequencing) revealed, contrary to the hypothesis, significant ROI activation in all ROIs of the action observation network. The whole-brain analysis showed that the left cerebellum IV-V, VI, and VIII were again activated, much like the analogous social contrast. In addition, we also found cerebral activation in the posterior-medial frontal, precentral, postcentral, and middle occipital gyri (Figure 2E).

Social Non-sequencing vs. Non-social Non-sequencing. Neither ROI nor whole-brain activations were found.

[Insert Table 3 about here]

[Insert Figure 2 about here]

Reproduction phase: Reproducing sequences of trajectories

To investigate whether the cerebellum (and related cortical areas) is preferentially involved in reproducing versus memorizing the sequential steps during navigation, we focused on contrasts between the Observation and Reproduction phase (see Table 4 & Figure 3)**.**

Social Sequencing: Reproduction vs. Observation. The Social Reproduction > Observation contrast revealed ROI activation in cerebellar Crus II, and all action observation related ROIs. In addition, the whole-brain analysis showed cerebral activation in the left cerebellum lobule VI, and cerebral activation in the bilateral middle frontal gyrus, rolandic operculum, precentral gyrus and inferior parietal lobule (IPL) (Figure 3A). The opposite contrast (Observation > Reproduction) revealed ROI activation in the mentalizing (TPJ, mPFC, precuneus), PMC and the PHG. Whole-brain activations were revealed in cerebral areas of the superior frontal and medial gyrus, precentral, and postcentral gyrus, superior parietal lobule, left precuneus, middle temporal gyrus, and middle occipital gyrus (Figure 3B).

Non-social Sequencing: Reproduction vs. Observation. Similar to the previous Social contrast, the Non-social Reproduction > Observation contrast revealed ROI activation in all action observation related ROIs, and whole-brain activation in the left cerebellum IV-VI and right VIII. In addition, cerebral areas were activated in middle frontal gyrus, precentral gyrus, thalamus, and inferior parietal lobule (IPL) (Figure 3C). The opposite contrast (Observation > Reproduction), revealed ROI and whole-brain activation in Crus II, mentalizing (mPFC, TPJ, precuneus), PMC and the PHG. In addition, the whole brain analysis revealed cerebral

activation in the middle orbital, temporal and occipital gyrus, inferior frontal gyrus, superior frontal gyrus and parietal lobule, fusiform gyrus, and postcentral gyrus (Figure 3D).

Reproduction phase: ***Social vs. Non-social Sequencing:*** No activations were found when contrasting the Social and Non-social Sequencing conditions during the Reproduction phase.

[Insert Table 4 about here]

[Insert Figure 3 about here]

[Insert Table 5 about here]

Discussion

Mentalizing is pivotal for successful navigation in the social world, as it allows us to predict, interpret, and manipulate each other's behavior. We contributed to the novel research field of social navigation by exploring the role of the posterior cerebellar Crus (and related cortical areas) in sequence-based and goal-directed navigation in a social context, and so shed light on the relationship between spatial and social navigation.

Cerebellum and memorizing or observing social navigation

Our main hypothesis was that the cerebellar Crus I and II would be recruited during learning novel social trajectories that require mentalizing about the goal of the protagonist. Our results confirmed this hypothesis. We found stronger cerebellar Crus activation when learning social trajectories (Social Sequencing condition) compared to control conditions where social trajectories were observed but not learned (Social Non-sequencing condition) or where the trajectory reflected a mechanical movement (Non-social conditions). These results extend previous fMRI findings revealing cerebellar Crus activation when participants generated the correct order of cartoon-like stories, which required mentalizing about the agents' belief (Heleven et al., 2019), when participants memorized the correct order of action sequences which implied an underlying trait (Pu et al., 2020), or other socio-emotional stimuli (Arioli et al., 2021; Overwalle et al., 2020; Van Overwalle et al., 2014).

Although we found the hypothesized stronger cerebellar Crus II activations for social action sequences when memorizing as opposed to passively observing a sequence (Sequencing > Non-sequencing contrast), the same contrast for non-social mechanical movements revealed similar neural engagement in the bilateral Crus II, although the activated cluster was only half the size than in the social conditions. This was further confirmed by a significant Social > Non-social Sequencing contrast and interaction analysis. This suggests that a common underlying

sequencing process may have been engaged in the cerebellar Crus in both social and non-social conditions, with stronger Crus II activation in the social conditions, consistent with our hypothesis.

What is this common underlying sequencing process? We speculate that this is most likely memorizing the steps through the trajectory, which is similar in the sequential conditions irrespective of the social or non-social material. The fact that in both sequencing conditions, participants had to memorize the moving trajectory makes the engagement of "sequencing" and "predicting" cerebellum reasonable (Leggio & Molinari, 2015; Van Overwalle, Manto, et al., 2019). This interpretation is supported by the finding that the same social versus non-social contrast yielded no activation when memorizing was not required (i.e., in the Non-sequential conditions).

When only observation was involved without memorizing (Non-sequencing > Sequencing), whole-brain activation was revealed in the left cerebellar lobules IV-VI, and VIII for both social and non-social conditions and right cerebellar lobule VI for the social condition only. Lobules IV/V/VI and VIII are commonly interpreted as involved in motor processing, somatomotor integration, and ventral attention (Buckner et al., 2011; Van Overwalle, Manto, et al., 2020). This indicates that the activity in these motor-related lobules is relatively higher when learning social or non-social events without sequencing, perhaps as a consequence of a decrease of information processing or mental resources when memorizing the sequence is not required (e.g., paying attention only to the end goal).

In addition to activation in the cerebellum, our findings suggest an extensive network of cortical and subcortical brain regions showing specific involvement in memorizing the trajectory during social navigation (see summary in Table 5).

First, with respect to social mentalizing, as hypothesized, we found that the key cortical regions of the mentalizing network, including the TPJ, mPFC, and PCun, were often activated together with the cerebellar Crus during Social Sequencing as opposed to the Non-social and Non-sequencing control condition. The TPJ was most robustly activated, which is in line with its major function in metalizing about social agents' goals. According to Van Overwalle (2009), spatial information that suggests movement towards an expected end-point recruits an evolutionary old neural "where-to" system in the TPJ that immediately hints at the goal of an action. The results are also consistent with previous work on the effective connectivity of the cerebellar Crus with other mentalizing areas in the cortex, which revealed direct synchrony with the TPJ (Van Overwalle, Van de Steen, et al., 2019, 2020). In addition, the involvement of the posterior cerebellar Crus in social sequencing in our study confirms its role at lower levels of mentalizing involving goals, and so extends earlier research on the role of the cerebellum at higher levels of abstraction such as beliefs (Heleven et al., 2019; Van Overwalle, De Coninck, et al., 2019) and personality traits (Pu et al., 2020). Future research might investigate the dynamic connectivity between cerebellar and cortical areas in navigation, preferentially on a larger set of related tasks (see also Van Overwalle, Van de Steen, et al., 2019, 2020), so that robust connectivity patterns can be uncovered.

Second, with respect to action observation, the key PMC and aIPS areas in this network, as well as the additional SMA, showed a coherent pattern of activation. They were also activated when memorizing social action sequences as opposed to non-social object sequences (see Table 5), confirming the important role of the mirror system in detecting the goal of an observed movement in our social navigation task. This extends prior action observation research which mainly focused on stimuli such as point-light displays depicting human locomotion (Sokolov et al., 2012), grasping movements (Becchio et al., 2012), and movements of face, mouth, and eyes (Grosbras et al., 2012). However, our hypothesis with respect to

greater activation during memorizing versus passively observing (sequencing > non-sequencing contrast) of social actions was only supported for the PMC, while the aIPS and SMA showed activation in the opposite contrast. We therefore speculate that merely observing a trajectory recruits the action observation network much more strongly than memorizing it. We discuss this deviant pattern of the action observation network further below.

Finally, with respect to navigation, we found robust activation in the parahippocampal gyrus in conditions when sequential information in the trajectory had to be memorized, irrespective of social or non-social context, as hypothesized. This is consistent with the key role of the hippocampus in memory (Bird & Burgess, 2008; Voss et al., 2017).

Cerebellum and reproducing social trajectories

We further explored the differences between memorizing and reproducing a trajectory. We reasoned that both processes could potentially generate stronger cerebellar activation, in line with the sequence detection role of the cerebellum during learning (Leggio & Molinari, 2015) as well as with the error-correcting role of the cerebellum during reproduction (see also, Popa & Ebner, 2019). Surprisingly, the results revealed evidence in favor of both positions. Memorizing compared to reproducing the trajectories recruited stronger activation in mentalizing areas (most robustly the TPJ) and parahippocampal gyrus. In contrast, reproducing compared to memorizing trajectories recruited stronger activation of the action observation network. This pattern was consistent across social and non-social trajectories. There was no consistent pattern in the activation of the posterior cerebellar Crus.

First, with respect to social mentalizing, the finding that stronger activation was found in the TPJ, mPFC and precuneus during observation than reproduction, is consistent with prior research on memorizing trait-related action sequences, which revealed activation in the mentalizing network during memorizing sequences, but not during reproducing (Pu et al.,

2020). However, the same pattern of results was also found for non-social memorization. This might perhaps be explained by the random presentation of social (smurfs) and non-social (balls) trials in our task, which may have led to reduced attention to this difference, so that participants used a general strategy of taking a mentalizing stance in many trials, even for non-social material.

Second, with respect to the action observation network, we again found a different pattern as revealed by a stronger activation of all ROIs during social and non-social reproduction of the trajectory rather than during memorizing (Social and Non-social Reproduction > Observation contrast). This confirms the deviant role of the action observation network, being stronger during non-sequential observation than during memorizing of sequences as discussed above (Non-sequential > Sequential contrasts). We therefore speculate, in line with the previous explanation, that the observation of movements by others (cf. discussed above) as well as observation of self-movement while reproducing a trajectory, recruits the action observation network much stronger than simply memorizing it. Additional research is needed to demonstrate whether this is a robust result and whether our explanation is viable.

A novel finding from the whole-brain analysis, was the systematic recruitment of cerebellar lobule VI in reproducing as opposed to observing trajectories in social and non-social conditions, which was not revealed in earlier work on social mentalizing (Heleven et al., 2019; Pu et al., 2020). Note that this same lobule showed less recruitment in the non-social condition when sequences had to be memorized rather observed, indicating that it is not involved in learning sequences. Of interest is that the cerebellar lobule VI (together with IV-V and VIII) forms a motor loop with the primary motor and lateral intraparietal cortices via the thalamus (Guell et al., 2018; Ramnani, 2012; Strick et al., 2009). This suggests a potential role of the anterior lobule VI in executing not only goal-directed behavior, but perhaps other kinds

of social and non-social behavior. Further research is needed to follow up the specific role of Lobule VI in social navigation and behavior in general.

Note that the opposite contrast (Sequencing Observation > Reproduction) showed activation in the posterior cerebellum Crus II for the non-social condition, but not for the social condition. This is inconsistent with our hypothesis that predicted more posterior Crus activation during social than non-social sequencing. Although the hypothesis was confirmed for the social condition during observation and learning of the sequence (see the previous section), it leads to unexpected findings in comparison with reproducing the same sequence. Future research might reveal how robust this unexpected finding is.

Furthermore, future research could extend the current paradigm to investigate gender differences on social and spatial navigation. For example, do men perform better on navigational tasks but worse on social mentalizing? Past research has found that females are stronger empathizers and males are stronger systemizers (i.e., more attention to detail and patterns; Baron-Cohen et al., 2005). Also, men perform better on map-based tasks, yet this difference is not always validated in ecological navigation tasks (Munion et al., 2019). To investigate potential gender differences, we carried out a series of analyses on the behavioral results (the male group was too small to do this reliably for the fMRI results). However, none of the gender differences on accuracy and response times reached conventional levels of significance (all $p > .05$). Nonetheless, research on gender differences could elucidate potential factors contributing to gender differences on the task used here, and could also elucidate if and how gender shapes the neural mechanisms underlying how people navigate the social world and interpret others' behaviors.

Overall, the present research extended previous research by exploring the role of the cerebellum and related mentalizing areas in goal-directed social navigation, especially during observing and memorizing trajectories which require mentalizing. The findings are in line with

the wider literature arguing that the cerebellum provides a predictive sequential function in social cognition (Overwalle et al., 2020; Van Overwalle et al., 2014) and thus can provide complementary insights about social navigation.

Conclusion

The main contribution of the present study is that we identified a preferential role of the cerebellar Crus during goal-directed social navigation. The consensus is growing on the important predictive role of the cerebellum in social action sequences, which provides a more dynamic approach to the study of social interaction (Van Overwalle, Manto, et al., 2020). The present research extended previous research on the role of the cerebellar Crus in social cognition to navigation in a social environment, and highlights the prominent role of other brain areas, including the hippocampus and the social mentalizing network (Quadflieg & Koldewyn, 2017). The present study also revealed a systematic role of the cerebellum in other processes. For example, we found more activation in the anterior cerebellum (e.g., Lobule IV) during reproducing than observing trajectories across social and non-social conditions, which reveals its potential role in motor production, rather than learning sequences. There is still a lot to learn about the functional heterogeneity of the human cerebellum. Future studies on the social cerebellum could consider more interactive tasks, such as one agent navigating towards another agent, which may require more social synchrony between agents' action sequences.

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Data and code are available

All requested (pseudonymized or anonymous) data are available upon request to Meijia Li at meijia.li@vub.be, excluding data that allow identifying individual participants. If relevant, all manuals and code for processing the data is also available together with the data. The (pseudonymized) data are stored at a digital archive of the Vrije Universiteit Brussel, Belgium.

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CRediT authorship contribution statement

Meijia Li: Conceptualization, Methodology, Software, Formal analysis, Investigation, Visualization, Writing - original draft, Writing - review & editing. **Qianying Ma**: Writing - review & editing. **Kris Baetens**: Writing - review & editing. **Min Pu**: Writing - review & editing. **Natacha Deroost**: Writing - review & editing. **Chris Baeken**: Writing - review & editing. **Elien Heleven:** Writing - review & editing. **Frank Van Overwalle**: Conceptualization, Methodology, Software, Writing - Review & Editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors report no personal or financial conflicts of interest related to the research reported herein.

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Tables and Figure legends

Table 1. Regions of interest for social cognition and spatial navigation derived from meta-analyses

Social Cognition (Van Overwalle, 2009; Van Overwalle & Baetens, 2009, Van Overwalle et al., 2020)

	MNI coordinates			Overlap with areas in	
				Kong et al. (2017, Table 1)	Kühn et al. (2014, Table 4)
	x	y	z		
Action Sequencing					
Cerebellar Crus II	±25	-75	-40	---	---
Cerebellar Crus I	±40	-70	-40	---	---
Mentalizing					
Medial prefrontal cortex (mPFC)	0	50	20	---	---
Temporo-parietal junction (TPJ)	±50	-55	25	---	---
Precuneus (PCun)	0	-60	40	PCUN	PCUN
Goal-directed Action Observation					
Premotor cortex (PMC)	±40	5	40	PreC	PreC
Anterior intraparietal sulcus (aIPS)	±40	-40	45	ANG	---

Spatial Navigation (Kong et al., 2017, Table 1)

	MNI coordinates			Validated by	
				Kühn et al. (2014, Table 4)	Qiu et al. (2019, Table 2)
	x	y	z		
Memory (Medial-temporal Module)					
L Parahippocampal gyrus (PHG)	-25	-36	-13	✓	✓
R Parahippocampal gyrus (PHG)	26	-34	-13	✓	✓
Landmark Identification (Anterior Module)					
L Supplementary motor area (SMA)	-4	12	51	✓	✓
R Supplementary motor area (SMA)	6	12	52	---	✓
Goal-directed Action Observation (Posterior-dorsal Module)					
L Precentral gyrus (PreC)	-47	6	33	✓	---
R Angular gyrus (ANG)	34	-56	48	---	✓
Scene (Posterior-dorsal Module)					
L Precuneus (PCUN)	-6	-64	52	✓	---
R Precuneus (PCUN)	8	-61	55	✓	---

Note: For social cognition, we included all areas identified in meta-analyses on the cortex (Van Overwalle, 2009; Van Overwalle & Baetens, 2009) and the cerebellum (Van Overwalle et al., 2020), and we show the overlap with areas in spatial navigation. For spatial navigation, we included all areas from the modules identified by Kong et al. (2017), that were also identified in two other meta-analyses by Kühn et al. (2013) and Qiu et al. (2019), as denoted by ✓. Occipital/Visual areas were omitted.

Table 2. Descriptive statistics of behavioral data (Means ± Standard deviations)

	Social Sequencing	Non-social Sequencing	Social Non-sequencing	Non-social Non-sequencing
Reproduction of Trajectory				
Accuracy	97.36 ± 2.11	97.52 ± 1.4	--	--
RT (sec)	8.93 ± 2.46	8.80 ± 1.84	--	--
Goal / Endpoint Question				
Accuracy	97.83 ± 2.95	91.96 ± 7.94	99.13 ± 1.94	94.13 ± 3.25
RT (sec)	1.13 ± 0.30	1.10 ± 0.26	0.88 ± 0.19	0.94 ± 0.18

Note: Reproduction accuracy = number of correct steps divided by the total steps for each trajectory. Reproduction RT = time for reproducing the whole trajectory or time to answer the goal / endpoint question. No reproduction task was included in the two Non-sequencing conditions.

Table 3. Whole-brain analysis during the observation of the trajectories with memorizing (Sequencing) or without memorizing (Non-Sequencing)

Contrasts and Anatomical Label	*MNI coordinate*			*Voxels*	*max t*
	x	*y*	*z*		
Social Sequencing > Non-social Sequencing					
L Cerebellum (Crus I)	-10	-72	-26	140	4.82
L Cerebellum (VII)	-8	-76	-40		4.14
R Middle Frontal Gyrus	42	32	22	751	5.11*
R Angular Gyrus, including TPJ °	34	-60	48	565	4.55
R Inferior Parietal Lobule, including aIPS °	44	-48	42		4.25
R Fusiform Gyrus	26	-76	-2	444	4.75
Social Sequencing < Non-social Sequencing					
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Social Sequencing > Social Non-sequencing					
L Cerebellum (Crus II)	-14	-86	-40	1041	7.23***
L Cerebellum (Crus I)	-18	-72	-30		6.43***
L Cerebellum (Crus II)	-16	-80	-34		6.42***
R Cerebellum (Crus II)	14	-86	-38	454	4.82
R Cerebellum (Crus I)	22	-70	-36		4.47
R Cerebellum (Crus I)	30	-84	-32		4.36
R Middle Orbital Gyrus, including mPFC °	2	58	-2	331	4.72
R Inferior Frontal Gyrus (p. Triangularis)	56	28	26	486	4.76
R Superior Frontal Gyrus	28	26	52	648	5.04*
Thalamus: Temporal	2	-8	8	8313	6.49***
L Middle Temporal Gyrus, including TPJ °	-62	-54	16	1941	6.44***
L Middle Occipital Gyrus	-42	-78	34	263	5.70**
L Cuneus, including PCun °	-8	-92	22	2017	6.21***
Social Sequencing < Social Non-sequencing					
L Cerebellum (IV-V)	-20	-52	-22	1633	12.38***
L Cerebellum (IV-V)	-8	-56	-14		8.12***
L Cerebellum (VI)	-4	-64	-18		7.33***
R Cerebellum (VI)	26	-56	-22	795	6.23***
L Cerebellum (VIII)	-18	-60	-50	258	8.02***
L Cerebellum (VIII)	-30	-52	-52		5.39*
L Cerebellum (VIII)	-32	-44	-48		3.86
R Insula Lobe	48	6	4	230	6.07**
L Precentral Gyrus, including PMC °	-58	4	30	265	6.80***
L Rolandic Operculum	-44	-2	10	291	6.71***
R Putamen	28	-2	2	145	5.15*
L Posterior-Medial Frontal, including SMA °	-4	-4	56	1351	7.92***
L Precentral Gyrus	-36	-10	60	562	6.46***
R Rolandic Operculum	52	-20	20	174	5.84**
R Precentral Gyrus	38	-20	56	2868	13.01***
L Postcentral Gyrus, including aIPS °	-38	-34	46	3265	8.58***
Non-social Sequencing > Non-social Non-sequencing					
R Cerebellum (Crus II)	20	-80	-34	363	5.02*
R Cerebellum (Crus II)	14	-88	-38		4.48
Lobule VIIA Crus II	-14	-84	-44	348	4.98†
L Cerebellum (Crus II)	-18	-78	-36		4.64
L Cerebellum (Crus II)	-22	-88	-38		4.08
R Superior Frontal Gyrus	14	46	52	216	4.71
R Inferior Frontal Gyrus (p. Triangularis)	54	36	12	421	5.69**
L Inferior Frontal Gyrus (p. Triangularis)	-54	32	4	129	5.09*
L Middle Cingulate & Paracingulate Gyri	-4	-32	48	786	4.82
L Lingual Gyrus	-8	-44	2	758	5.90**
L Middle Temporal Gyrus, including TPJ °	-62	-58	2	12051	7.84***

L Calcarine Gyrus	-8	-64	14	226	4.22
L Cuneus, including PCun °	0	-82	36	228	4.55
Non-social Sequencing < Non-social Non-sequencing					
L Cerebellum (IV-V)	-18	-50	-24	2446	9.99***
L Cerebellum (VI)	-6	-62	-14		7.45***
L Cerebellum (VIII)	-16	-62	-48		7.37***
L Posterior-Medial Frontal, including SMA °	-6	6	52	962	7.94***
L Precentral Gyrus, including PMC °	-52	2	30	421	7.26***
L Precentral Gyrus	-28	-8	54	718	6.33***
R Precentral Gyrus	38	-22	56	3775	11.18***
L Postcentral Gyrus, including aIPS °	-34	-34	40	4220	8.15***
L Middle Occipital Gyrus	-40	-74	6	135	4.38
R Middle Occipital Gyrus	28	-88	6	181	5.53**
L Middle Occipital Gyrus	-26	-90	10	232	5.89**
Social Non-sequencing > Non-social Non-sequencing					
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Social Non-sequencing < Non-social Non-sequencing					
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Notes: Coordinates refer to the MNI (Montreal Neurological Institute) stereotaxic space. Whole-brain and ROI analysis threshold at voxel-wise uncorrected $p < 0.001$ with voxel extent ≥ 10, with cluster-wise FWE corrected $p < 0.05$. Only the highest peaks of each cluster are shown, except for the cerebellum and significant ROIs. L = left, R = right.

† $p < .10$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$ (peak FWE corrected).

° $p < 0.001$ cluster-level FWE corrected using a small volume correction of a sphere with 15 mm radius and centered around *a priori* MNI coordinates in Table 1. These are also listed in Table 5. mPFC = Medial prefrontal cortex, TPJ = Temporo-parietal junction, PCun = Precuneus, PMC = Premotor cortex, aIPS = Anterior intraparietal sulcus, SMA = Supplementary motor area.

Table 4. Whole-brain analysis during observation (with memorizing: Sequencing) and reproduction of the trajectories

Contrasts and Anatomical Label	*MNI coordinate*			*Voxels*	*max t*
	x	*y*	*z*		
Social Sequencing: Reproduction > Observation					
L Cerebellum (VI)	-24	-52	-22	14431	15.41***
L Cerebellum (VI)	-6	-64	-14		11.07***
R Middle Frontal Gyrus	32	44	28	183	5.13*
L Middle Frontal Gyrus	-36	40	34	307	4.97
L Rolandic Operculum	-46	-2	8	2635	10.35***
L Precentral Gyrus, including PMC °	-56	8	34		6.62***
L Precentral Gyrus	-32	-12	64	424	8.97***
R Precentral Gyrus	38	-20	54	11891	18.07***
L Inferior Parietal Lobule, including aIPS °	-44	-28	46	3938	10.39***
Social Sequencing: Reproduction < Observation					
R Superior Medial Gyrus	4	50	50	1510	5.21*
R Superior Frontal Gyrus	24	4	50	171	5.13*
R Precentral Gyrus, including PMC °	40	4	42	129	4.32
L Postcentral Gyrus	-46	-20	62	126	5.45*
R Superior Parietal Lobule	16	-58	62	145	6.38***
L Precuneus	-14	-60	62	260	5.79**
R Middle Temporal Gyrus	46	-64	6	2511	8.75***
R Middle Temporal Gyrus, including TPJ °	54	-64	12		6.5***
L Middle Occipital Gyrus	-40	-68	6	1020	6.86***
Non-social Sequencing: Reproduction > Observation					
L Cerebellum (IV-V)	-20	-52	-20	14071	17.15***
L Cerebellum (VI)	-32	-48	-28		12.14***
R Lingual Gyrus	6	-68	6		11.72***
R Cerebellum (VIII)	16	-66	-52	155	6.71***
R Cerebellum (VIII)	20	-58	-54		3.47
R Cerebellum (VIII)	30	-50	-50	101	6.12***
L Middle Frontal Gyrus	-38	40	30	291	4.45
L Precentral Gyrus, including PMC °	-60	6	24	1928	9.37***
L Precentral Gyrus	-36	-10	62	402	8.67***
R Thalamus	16	-20	8	2065	8.23***
R Precentral Gyrus	38	-20	56	7333	17.55***
L Inferior Parietal Lobule	-46	-28	46	3736	9.68***
L Postcentral Gyrus, including aIPS °	-48	-34	56		8.96***
Non-social Sequencing: Reproduction < Observation					
L Cerebellum (Crus II)	-20	-84	-34	376	5.14*
R Cerebellum (Crus II)	28	-84	-36	224	4.95
R Cerebellum (Crus II)	18	-86	-36		4.57
R Medial Orbital Gyrus, including mPFC °	2	56	-4	4021	6.08***
R IFG (p. Triangularis)	54	36	2	487	5.34*
L IFG (p. Orbitalis)	-22	34	-10	412	4.60
R Superior Frontal Gyrus	24	2	54	122	4.82
L Superior Frontal Gyrus	-20	0	54	103	5.14*
R Fusiform Gyrus	40	-8	-32	1084	6.70***
L Postcentral Gyrus	-46	-20	62	441	5.94**
L Para Hippocampal Gyrus	-32	-36	-12	210	7.06***
L Precuneus	-2	-54	34	692	4.48
L Superior Parietal Lobule	-18	-56	62	1150	7.30***
R Middle Temporal Gyrus	42	-62	10	3446	9.18***
R Middle Temporal Gyrus, including TPJ °	58	-60	16		7.23***
L Middle Occipital Gyrus	-40	-68	6	3817	8.72***
Reproduction phase: Social Sequencing > Non-social Sequencing					

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Reproduction phase: Social Sequencing < Non-social Sequencing						
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Notes: Coordinates refer to the MNI (Montreal Neurological Institute) stereotaxic space. Whole-brain and ROI analysis threshold at voxel-wise uncorrected $p < 0.001$ with cluster-wise FWE corrected $p < 0.05$, with voxel extent ≥ 10. Only the highest peaks of each cluster are shown, except for the cerebellum and significant ROIs. L = left, R = right. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$ (peak FWE corrected).
° $p < 0.001$ cluster-level FWE corrected using a small volume correction of a sphere with 15 mm radius and centered around *a priori* MNI coordinates in Table 1. These are also listed in Table 5. mPFC = Medial prefrontal cortex, TPJ = Temporoparietal junction, PMC = Premotor cortex, aIPS = Anterior intraparietal sulcus

Table 5. Overview of the regions of interest and their activation as predicted by their functionality

Functional Domain		Social Sequencing		Social Mentalizing			Action Observation			Spatial Memory
Function / Region of interest (ROI) Contrast	Hypothesis	Crus II	Crus I	mPFC	TPJ	PCun	PMC	aIPS	SMA	PHG
Observation Phase: Social Sequencing vs. control conditions										
Social Sequencing > Non-social Sequencing	✓	×	✓	×	✓	×	✓	✓	✓	✓
Social Sequencing < Non-social Sequencing	×	×	×	×	×	×	×	×	×	×
Social Sequencing > Social Non-sequencing	✓	✓	✓	✓	✓	✓	✓	×	×	✓
Social Sequencing < Social Non-sequencing	×	×	×	×	×	×	✓	✓	✓	×
Observation Phase: Non-Social Sequencing / Social Non-sequencing vs. other control conditions										
Non-social Sequencing > Non-social Non-sequencing	(✓)	✓	×	✓	✓	✓	×	×	×	✓
Non-social Sequencing < Non-social Non-sequencing	×	×	×	×	×	×	✓	✓	✓	×
Social Non-sequencing > Non-social Non-sequencing	×	×	×	×	×	×	×	×	×	×
Social Non-sequencing < Non-social Non-sequencing	×	×	×	×	×	×	×	×	×	×
Reproduction Phase vs. Observation Phase										
Social Sequencing: Reproduction > Observation	?	✓	×	×	×	×	✓	✓	✓	×
Social Sequencing: Reproduction < Observation	?	×	×	✓	✓	✓	✓	×	×	✓
Non-social Sequencing: Reproduction > Observation	?	×	×	×	×	×	✓	✓	✓	×
Non-social Sequencing: Reproduction < Observation	?	✓	×	✓	✓	✓	✓	×	×	✓
Reproduction Phase: Social Sequencing vs. control condition										
Social Sequencing > Non-social Sequencing	?	×	×	×	×	×	×	×	×	×
Social Sequencing < Non-social Sequencing	?	×	×	×	×	×	×	×	×	×

Note. ROIs activated in different contrasts, using spheres with centers listed in Table 1 and a radius of 10 mm for Cerebellar Crus I & II and PHG, and 15 mm for mentalizing (mPFC, TPJ, precuneus) and action observation networks (PMC, aIPS, SMA). Hypothesis: activation assumed to be ✓ = present, (✓) = weakly present, × = absent, ? = no prediction; Activation in ROI: ✓ = in at least one hemisphere, × = in no hemisphere. mPFC = medial prefrontal cortex, TPJ = temporo-parietal junction, PCun = precuneus, PMC = premotor cortex, aIPS = anterior intraparietal cortex, SMA = supplementary motor area, PHG= parahippocampal gyrus.

Figure 1. Experimental stimuli and procedure. (A) The task involved an 8 by 10 grid. Shown in grey (not visible for the participants) are easy and hard trajectories from the Social and Non-social conditions. Each trajectory started at any possible cell in the grid, except for the bordering and center cells. The smurf / ball moved from the starting point to an endpoint at a fixed pace (400 ms per step). S, starting point; E, endpoint. In these examples, Papa smurf ended at the cake; and the ball ended at the same location. (B) In the Sequencing conditions, participants were instructed to observe and memorize the trajectories carefully (Observation phase), and then to reproduce the same movements with direction buttons (1 = up, 2 = down, 3 = left, 4 = right; Reproduction phase). Afterwards, the goal/endpoint question was administered. In the Non-sequencing conditions, everything was similar, except that the Reproduction phase was omitted.

Figure 2. Top: Sagittal and Transverse views of the contrasts during the Observation Phase shown at an uncorrected threshold of $p < 0.001$. **Middle:** Activation in the posterior cerebellum of the same contrasts shown on a SUIT flatmap (King et al., 2019) at an uncorrected threshold of $p < 0.001$. The contrasts between Social Sequencing vs. Non-social Sequencing (A), and with Non-sequencing condition (B) strongly activate Crus I and/or II in the mentalizing network, while the analogous contrast between Non-social Sequencing and Non-sequencing condition (C) activate this area in Crus II less so. **Bottom:** SUIT flatmap atlas showing the cerebellar lobules from (King et al., 2019) and functional networks from (Buckner et al., 2011). Warm colors (shades of orange and yellow) on flatmaps correspond to positive brain activation.

Figure 3. Top: Sagittal and Transverse views of the contrasts between the Reproduction and Observation shown at an uncorrected threshold of $p < 0.001$. **Bottom:** Activation in the posterior cerebellum of the same contrast shown on a SUIT flatmap (King et al., 2019) at an uncorrected threshold of $p < 0.001$. The contrasts between Observation > Reproduction in both Social and Non-social Sequencing condition strongly activate Crus I and/or II in the mentalizing network (A - C).