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Published in:
The Cerebellum

DOI:
10.1007/s12311-021-01333-9

Publication date:
2021

Invited article for "The Cerebellum" as invited speaker at the SRCA conference

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Compliance with ethical standards:

Conflict of interest: The authors declare to have no conflict of interest.
Funding: This work has been supported by an SRP57 grant by the Vrije Universiteit Brussel awarded to Frank Van Overwalle, Natacha Deroost and Chris Baeken. There is no other funding source.
Ethical approval: This article does not contain any studies with human participants or animals performed by any of the authors.

For appropriate special issue - 11th SRCA symposium

Limitations:
- abstract of 200-280 words = 250
- main text between 2500 and 5500 words = ~3000

Keywords: Crus, action sequencing, social mentalizing, false beliefs, trait inferences, implicit learning, action prediction

Abstract

Recent advances in social neuroscience have highlighted the critical role of the cerebellum and especially the posterior cerebellar Crus in social mentalizing (i.e., theory of mind). Research in the past 5 years has provided growing evidence supporting the view that the posterior cerebellum builds internal action models of our social interactions to predict how other people's actions will be executed, and what our most likely responses to these actions will be. This paper presents an overview of a series of fMRI experiments on novel tasks involving a combination of (a) the learning or generation of chronological sequences of social actions either in an explicit or implicit manner, which (b) require social mentalizing on another person's mental state such as goals, beliefs, and implied traits. Together, the results strongly confirm the central role of the posterior cerebellar Crus in identifying and automatizing action sequencing during social mentalizing, and in predicting future action sequences based on social mentalizing inferences about others. This research program has important implications: It provides for the first time (a) fruitful starting points for diagnosing and investigating social sequencing dysfunctions in a variety of mental disorders which have also been related to cerebellar dysfunctions, (b) provides the necessary tools for testing whether noninvasive neurostimulation targeting the posterior cerebellum has a causal effect on social functioning, and (c) whether these stimulation techniques and training programs guided by novel cerebellar social sequencing insights, can be exploited to increase posterior cerebellar plasticity in order to alleviate social impairments in mental disorders.

What is Social Mentalizing?

In interactions with other people it is crucial to understand the current context, including actions of others, and to predict their upcoming reactions. To do this, we need to infer the "mind" of these other persons, that is, their intentions, preferences, beliefs, and traits, because this allows us to make far better predictions about their responses. The capacity to read the "mind" is termed ***social mentalizing*** or "theory of mind", and is supported by a ***mentalizing network*** in the human brain which encompasses the larger part of the ***default mode network*** (see meta-analyses by Schurz et al., 2014; 2021; Van Overwalle, 2009).

However, to understand and predict the actions of others, it is equally important to put social mentalizing in the appropriate context of past and future actions of others and self, that is, ***action sequences***. A correct sequence of behaviors is required to read others' mind and make social judgments. For example, hitting a person without prior provocation is likely to be considered aggressive, while hitting after being attacked is likely to be judged as protective or defensive. As another example, engaging in a negotiation requires continuously monitoring what other persons say at each moment, to be able to understand what they know, intend and believe, to guess how much concession margin they have, and so anticipate their next moves. Sequence learning is involved in a wide range of human motor, cognitive and social skills, and facilitates efficient and adaptive human behaviors, including social interaction.

Mind reading is supported by several key cortical regions in the ***mentalizing network***, including the ***temporoparietal junction*** (TPJ) mainly responsible for switching one's attention to the other persons' mental state, and the ***medial prefrontal cortex*** (mPFC) mainly subserving judgments about others' stable traits and characteristics (Van Overwalle, 2009). Fehlbaum et al. (2021) documented that these key regions were activated during mentalizing and showed overlapping neural activity across different age categories (i.e., children, adolescents and adults). However, recent research has uncovered that learning and processing of social action sequences is supported by another key brain region in social mentalizing, the ***posterior cerebellum*** (Guell & Schmahmann, 2020; Van Overwalle, Baetens, Mariën, & Vandekerckhove, 2014, 2015). The meta-analysis that systematically described this activity for the first time by Van Overwalle et al. (2014, Tables 2 and S1) reported that the posterior cerebellum was recruited in about 1/3 of neuroimaging studies on social mirroring (i.e., inferring intentions from motions of human body and limbs), event mentalizing (without body parts, including goal-directed shape motions or actions, true and false beliefs, moral judgments and social games, e.g., Gabay, Radua, Kempton, &

Mehta, 2014), and person mentalizing (including traits of self and others), and in more than 3/4 studies on abstract mentalizing (including judgments about social categories, and about past, future and hypothetical events). The present paper highlights and reviews recent evidence demonstrating the crucial function of the posterior cerebellum in detecting and predicting sequences of actions that require social mentalizing (Van Overwalle, Ma, & Heleven, 2020; Van Overwalle, Manto, et al., 2020). Although this brain area was neglected in social neuroscience for a long time, it is becoming increasingly clear that impairments in social mentalizing in a variety of psychiatric disorders (Luyten, Campbell, Allison, & Fonagy, 2020) can be linked to deviations in volume or functionality in the posterior cerebellum, such as in autism (Cauda et al., 2011; D'Mello, Crocetti, Mostofsky, & Stoodley, 2015), depression (Gong et al., 2020), bipolar disorder (Brady et al., 2020) and schizophrenia (Bernard & Mittal, 2015; Brady et al., 2020). Wang, Kloth & Badura (2014) argued that in early life, the cerebellum shapes the function of other brain regions, especially those relating to cognition and affect. Consequently, early cerebellar dysfunction (e.g., at birth) may disrupt the maturation of distant neocortical circuits, resulting in social cognitive impairments such as autism (Courchesne et al., 2001; Limperopoulos et al., 2007).

The Social Function of the Posterior Cerebellum

According to the "***sequence detection hypothesis***" of the cerebellum proposed by Leggio & Molinari (2015), a central function of the cerebellum is to support sequence learning and memories supported by internal models, that underpins not only motor acquisition (Baetens, Firouzi, Van Overwalle, & Deroost, 2020), but also non-motor mental processes involving event sequences. Put in the framework of predictive coding as dominant paradigm of brain functionality in neuroscience, the cerebellum can be conceived as a crucial coprocessor together with the cortex "especially in understanding the computational architecture of perception... action and choice behavior" (Friston et al. 2016). Applying the ***sequence detection hypothesis*** of the cerebellum (Leggio & Molinari, 2015) to social cognition, the function of the cerebellum is to encode social action sequences repeatedly encountered in our interactions with other people, which are rewarding or punitive (De Zeeuw, Lisberger, & Raymond, 2020). This allows people to automatically predict and intuitively execute behaviors in future interactions to attain desired results, and to automatically and rapidly adjust behavioral execution when the actual result is unexpected or undesirable (Leggio et al., 2011). For instance, after learning that feedback best begins with positive comments to appease the listener, people might slowly do this automatically and so make their social interactions more efficient.

The important contribution of the posterior cerebellum to social interaction processes and prediction was demonstrated for the first time in a large-scale meta-analysis of fMRI studies on social cognition by Van Overwalle et al. (2014). Activation in the cerebellum was revealed in about one third of more than 200 studies included in this meta-analysis, involving research on the observation of biological human actions, and mentalizing about other persons' goals, beliefs, personality traits and so on. The most consistent cerebellar activation was found in almost all studies on autobiographic past memories or simulations about future events - which typically involve chronological actions involving the self and others (e.g., recounting one's last summer holiday or fantasizing about an upcoming holiday; Van Overwalle et al., 2014). A recent meta-analysis by Van Overwalle et al. (2020) which examined all studies reporting activation in the posterior cerebellum, showed that the posterior cerebellar Crus 2 appears to be a main site of social mentalizing as opposed to other cognitive (e.g., linguistic, musical) or non-cognitive (e.g., somatosensory, motor) functions. While exploring effective connectivity with dynamic causal modelling across multiple samples involving inferences of traits and stereotypes (Van Overwalle, Van de Steen, & Mariën, 2019) as well as beliefs (Van Overwalle, Van de Steen, van Dun, & Heleven, 2020), it was demonstrated that these social inferences rely on a circuitry of closed loops (i.e., bidirectional connections) between the posterior cerebellar Crus 2 and key cortical areas of the mentalizing network, namely, the cortical temporo-parietal junction, from which unidirectional connections signals are sent to the medial prefrontal cortex. These closed loops imply a strong synchrony between cerebellar and cortical social processing.

Early Work on Social Sequencing

A key ability in social mentalizing is understanding others' ***false*** **beliefs**, which requires distinguishing others' beliefs from one's own (Kampis, Fogd, & Kovács, 2017; Wimmer & Perner, 1983). For example, in a false belief task developed by Saxe, Schulz, & Jiang (2006), a chocolate is moved out of a box and then returned to the same box or moved to another box. Critically, when this happens, a protagonist (i.e., a girl) is oriented toward or away from the boxes. When the girl is oriented toward the boxes, she can see the final location of the chocolate and therefore holds a true belief of reality. Conversely, when the girl is oriented away from the boxes, she cannot see any movements, and therefore holds a false belief of the chocolate's location, based on her latest – but outdated – true belief when she was oriented to the boxes.

As this task demonstrates, identifying action sequences is important for inferring false or true beliefs held by other persons. It is critical to know whether and when the girl actually saw what happened and when not. Although this might seem relatively uncomplicated in this example, in the context of a series of actions and mental state inferences, keeping track of who knows what and when might become quite complex. Some patients with neurological, psychiatric or developmental disorders such as autism show significant impairments on such false belief tasks (Carlsson, Miniscalco, Gillberg, & Åsberg Johnels, 2018), and may therefore be particularly vulnerable during natural social interactions which require to identify and engage in appropriate social sequences.

In earlier work exploring the social sequencing function of the posterior cerebellum, our lab investigated the role of false and true beliefs during action sequences, using (adaptations of) existing tasks. In one of these tasks, events were portrayed using cartoon-like pictures (***Picture Sequencing task***; Langdon & Coltheart, 1999; see **Figure 1**). In a similar task, events were presented in brief sentences (***Verbal Sequencing task*** by Heleven et al., 2019; based on the Faux Pas test by Baron-Cohen et al., 1999). In both tasks, the events were presented in a randomized order, and participants had to put them in a correct chronological order. An fMRI study demonstrated that the posterior cerebellar Crus was recruited more strongly when generating the correct sequence of actions that require mentalizing on other person's true and false beliefs as opposed to actions that involve well-known social routines (e.g., shopping) or mechanical events (e.g., car accident; Heleven et al., 2019). In another study with patients suffering from generalized cerebellar disorders, impairments on these tasks were also stronger when mentalizing about others' false beliefs than about routine social or mechanical events (Van Overwalle, De Coninck, et al., 2019),

Novel Social Sequencing Tasks

To convincingly demonstrate the critical role of the posterior cerebellar Crus in social mentalizing, and to explore its function across a variety of social mentalizing inferences, a series of novel social sequencing tasks were developed (e.g., Heleven, van Dun, & Van Overwalle, 2019; Ma, Pu, et al., 2021; Pu et al., 2020). These tasks combined (a) classic mentalizing inferences ranging from low-level goals to high-level beliefs and traits with (b) detecting, memorizing, or predicting the temporal sequence of the underlying social actions. This critical combination of social mentalizing and sequencing was then typically compared to control conditions involving:

(a) non-social aspects (e.g., involving objects and their characteristics), to investigate the domain-specificity of the posterior cerebellum, and

(b) non-sequential conditions involving selecting actions without sequencing, to investigate the critical role of sequencing.

Figure 2 depicts a number of these tasks involving the combination of sequencing and mentalizing about others' goal-directed intentions (Li et al., 2021) and traits of others (Pu et al., 2020) not only at an explicit level, but also at an implicit level (Ma, Heleven, et al., 2021).

- A ***goal-directed intention*** study (Li et al., 2021; **Figure 2A**) investigated a novel social navigation task where a protagonist — a smurf — is moving step-after-step through a spatial grid in order to reach a desired goal (e.g., a cake, money, etc.). Participants were required to observe, memorize, and subsequently reproduce the trajectory taken by the smurf towards one of many desirable goals, while avoiding obstacles such as trees, plants, and rocks. In the non-social control condition, a ball made exactly the same trajectory, but this was introduced as rolling around on an uneven terrain and stopping at a hole.
- In another study exploring ***trait-implying actions*** of others (Pu et al., 2020; **Figure 2B**), participants were requested to memorize a given sequence of actions performed by a human protagonist described in short sentences all implying the same trait. For instance, giving first a compliment, then buying a present, and next picking up a book for someone; these distinct actions all imply kindness as a trait. In the non-social control condition, objects were described that underwent mechanical movements or changes, and that implied the same characteristic. For example, moving at high speed, being earlier than other vehicles, and arriving in record time all imply the characteristic — fast
- Yet another study (Ma, Heleven, et al., 2021) explored whether ***implicit learning of belief sequences*** might take place. Testing implicit social learning is important, because it has been claimed that the cerebellum is necessary for implicit learning and automatization (Schmahmann, 2019). To investigate this, a novel implicit belief learning task was created, which combined a false belief task (Saxe et al., 2006; Wimmer & Perner, 1983) with a classic serial reaction time (SRT) task for implicit learning (Nissen & Bullemer, 1987). In a classical SRT task, the same sequence of stimuli is repeatedly presented without informing participants about this. Under these conditions of limited awareness, implicit learning is demonstrated by

faster responses after many repetitions of the same sequence (Training Phase), and slower responses when a new sequence is presented (Test Phase).

In the novel ***belief SRT*** task developed by Ma, Heleven, et al. (2021), participants were requested to identify true and false beliefs of two protagonists (e.g., smurfs; see also Özdem et al., 2019). Unbeknownst to them, there was a standard sequence of these true-false beliefs which was repeated over the course of the experiment. Specifically, we used a true-false belief task similar to Saxe et al. (2006) described earlier. Participants saw one of two smurfs, receiving flowers at four fixed locations on top of the screen (**Figure 2C**), and were requested to report how many flowers the smurf thought to have received. When the smurf was oriented toward the screen, he or she could see the flowers and thus held a true belief about the number of flowers. Conversely, when the smurf was oriented away from the screen, he or she could not see any changes and hence held a false belief. In that case, the correct answer was the number of flowers the smurf thought to have receive the last time they held a true belief.

Figure 3 depicts the main fMRI results of these three novel tasks. As can be seen, the critical social sequencing condition showed stronger recruitment in the posterior cerebellar Crus for ***goal-directed intentions*** (Li et al., 2021; **Figure 3A**) and ***trait-implying actions*** of others (Pu et al., 2020; **Figure 3B**) in comparison with non-sequencing control conditions where participants only observed trajectories or read trait sentences without memorizing the trajectory or sentence order. Comparisons against other relevant non-social control conditions (i.e., rolling balls, or sentences describing characteristics of objects rather than persons respectively; see earlier) showed similar activation of the posterior cerebellar Crus. A comparison of the test versus training phase in the ***belief SRT*** task (Ma, Pu, et al., 2021; **Figure 3C**) showed similar recruitment of the posterior cerebellar Crus.

These results convincingly demonstrate that the posterior cerebellar Crus supports explicit memorizing or implicit learning of social actions sequences that require understanding of a protagonist's mental state.

Beyond Action Sequencing: Social Inconsistencies and Sequencing Prediction

To explore other aspects of cerebellar social functioning, we further investigated to what extent the posterior cerebellum goes beyond the mere identification and learning of action sequences as demonstrated by the prior tasks.

- In one study, we explored to what extent the posterior cerebellar Crus might be sensitive to deviations from previously acquired knowledge, not only in sequences, but also in higher-level social information caused by inconsistencies revealed by social mentalizing, such as ***inconsistencies in trait implications*** revealed by inconsistent actions in a person's actions. To investigate this, Pu et al. (2021) slightly modified the previous study by Pu et al. (2020). As in that study, participants were required to memorize the given temporal order of a series of social actions of a protagonist that implied a personality trait. However, not only did all actions of the protagonist imply the same trait (Consistent condition: telling the truth, asking to be fair, returning a lost wallet: implying honesty) as in the previous study, but occasionally, one or two actions implied the opposite trait (Inconsistent condition: telling a lie, asking to cheat: implying dishonesty). Intriguingly, this novel study revealed that trait-inconsistent actions recruited the posterior cerebellar Crus more than trait-consistent actions (**Figure 3D**). This clearly demonstrates that the posterior cerebellar Crus is sensitive to deviations not only from pre-learned sequences, but also at a higher level of social trait mentalizing where it is assumed that humans have stable traits leading to the similar trait-implying behaviors.
- Besides observing actions of others here and now, we also tested the hypothesis that the cerebellum might be a coprocessor in the service of predictive coding (Friston et al. 2016) supporting the prediction of future actions. For example, once mental state inferences are made, this can serve as a basis to anticipate future social encounters and their outcomes to our benefit, which is arguably the ultimate goal of social behavior (Frith & Frith, 2006; Molinari & Masciullo, 2019; Pisotta & Molinari, 2014). Specifically, we investigated how information about a person's mental state (e.g., trait) might help to ***predict his or her future action*** sequences. Haihambo et al. (2021) explored this question by reversing the task logic of the inconsistent trait study by Pu et al. (2021) described above. In this novel study, participants were first given the trait of a protagonist (e.g., Fumak is dishonest), and then they had to select four out of six possible actions that were consistent with the trait information and put them in the correct chronological order (**Figure 4**). The fMRI results confirmed that predicting future actions recruited the posterior cerebellar Crus, in comparison with non-sequential information processing (i.e., only predicting future actions without putting them in

the correct order) or non-social information processing (i.e., making predictions about the state of an object based on its characteristics; **Figure 3E**).

Implications and Future Directions of Research

The prior tasks converge on the conclusion that a major function of the posterior cerebellar Crus involves identifying, learning, or predicting sequences of actions requiring various types of social mentalizing. Hence, research can now be directed to in-depth questions related to the posterior cerebellum and focus on potential (clinical) applications. Some of the most pressing questions for research in the immediate future are:

- What is the causal role of the cerebellar Crus? Although neuroimaging results may demonstrate the role of the posterior cerebellum, this constitutes only correlational evidence, and does not demonstrate its causal impact. To investigate the causal impact of posterior cerebellum functioning on mentalizing, future research might focus on noninvasive neurostimulation (e.g., transcranial direct current stimulation, tDCS, or transcranial magnetic stimulation, TMS; Cattaneo et al., 2021) to measure its modulating impact on mentalizing. So far, only one study has addressed this issue on social sequencing. Heleven et al. (2021) delivered repetitive **TMS** targeting the posterior cerebellum (using 1000 pulses with an intertrain interval of 0.5 s at a frequency of 1 Hz, positioning a double cone coil at 1–2 cm below the cerebellar inion). The authors found that TMS increased the speed at which participants generated the correct sequence of true and false belief events as well as of social routines and non-social events in the Picture Sequencing task described above. Thus, repetitive TMS had a general facilitatory effect on all types of sequences, which was somewhat unexpected.
- Given the generalized effects of TMS on sequence processing observed by Heleven et al. (2021), one may wonder to what extent this can be explained by the possibility that the rTMS pulses may have not only affected the targeted area, but may have spread beyond the posterior cerebellar area. Perhaps more focal stimulation using high definition tDCS might be more selective in facilitating social mentalizing only?
- Can noninvasive cerebellar stimulation facilitate the processing of other mentalizing sequencing judgments besides beliefs such as traits or goals? For this, researchers can turn to the novel social sequencing tasks described earlier.

- With respect to psychological disorders, can we develop diagnostic tools for detecting social sequencing impairments in pathologies that show posterior cerebellar dysfunctions, including autism (Cauda et al., 2011; D'Mello et al., 2015), depression (Gong et al., 2020), bipolar disorder (Brady et al., 2020), schizophrenia (Bernard & Mittal, 2015; Brady et al., 2020) and perhaps others? Even if cerebellar dysfunctions are not causality related to all these disorders, cerebellar involvement may be very relevant. The social sequencing tasks described earlier can be used as a starting point for this diagnostic tool development.
- Can non-invasive cerebellar stimulation be used for these populations in order the improve their impaired mentalizing capabilities? For example, can non-invasive stimulation improve cerebellar plasticity to remediate maladaptive patterns in social, depressive, obsessive-compulsive, or addictive-related thought or action sequences? Encouragingly, several clinical studies have provided initial evidence that cerebellar tDCS might improve cognitive functions and decrease maladaptive thoughts in bipolar depression (Bersani et al., 2015; Dondé, Neufeld, & Geoffroy, 2018; Minichino et al., 2015), obsessive-compulsive disorders (Bation et al., 2016, 2019), and schizophrenia (Escelsior et al., 2019). However, so far, no study has yet addressed social mentalizing dysfunctions.
- Can behavioral therapies focusing on social action sequencing accomplish more improvements on social thinking and skills than therapies focusing only on non-sequential mentalizing?

Conclusion

The sequencing hypothesis of social thinking and automatization sketched above has provided a fruitful ground for conducting neuroimaging research on the social function of the posterior cerebellum. It appears that many social mentalizing inferences, from low-level goals to higher-level traits, as well as explicit and implicit learning of social action sequences, recruit the posterior cerebellar Crus. The theoretical and clinical implications of this work are encouraging. These novel tasks might become very useful for future studies and the development of tools for diagnosing social mentalizing impairments in psychiatric and developmental disorders which involve the posterior cerebellum, such as autism. Non-invasive stimulation of the posterior cerebellum might offer novel ways of exploring the causal function of the posterior cerebellum while thinking about social sequences, and it might also pave the way for novel therapeutic use in clinical populations.

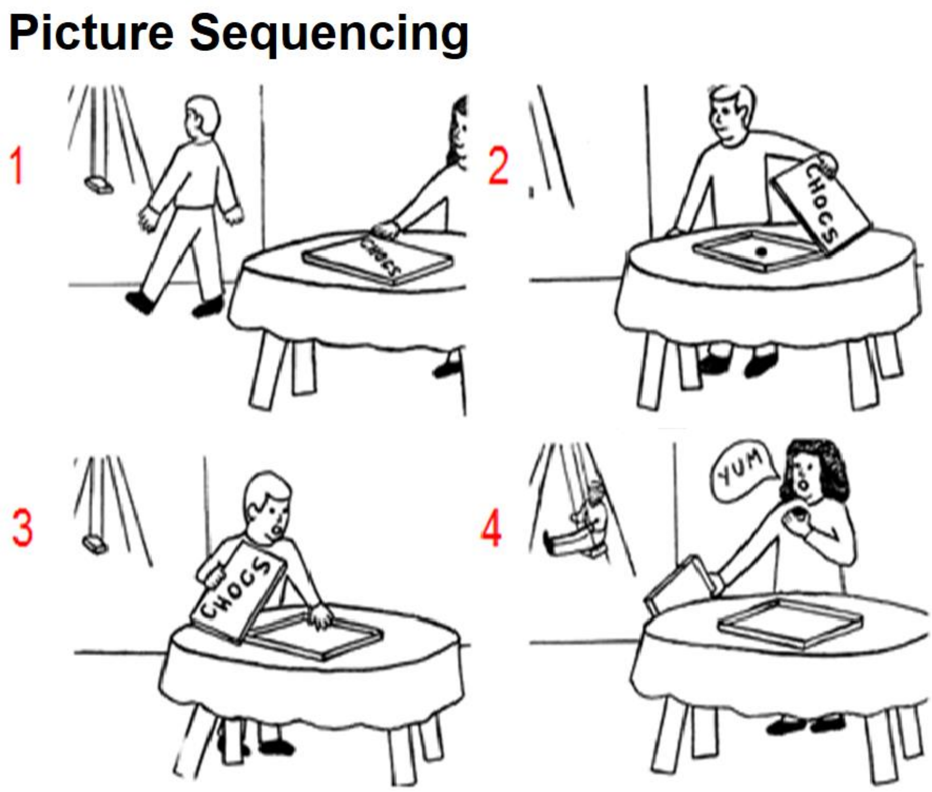

Figure 1: Picture sequencing tasks. An example of a false belief sequence (the correct order is 2 – 1 – 4 – 3; Baron-Cohen, Leslie, & Frith, 1986; Heleven et al., 2019).

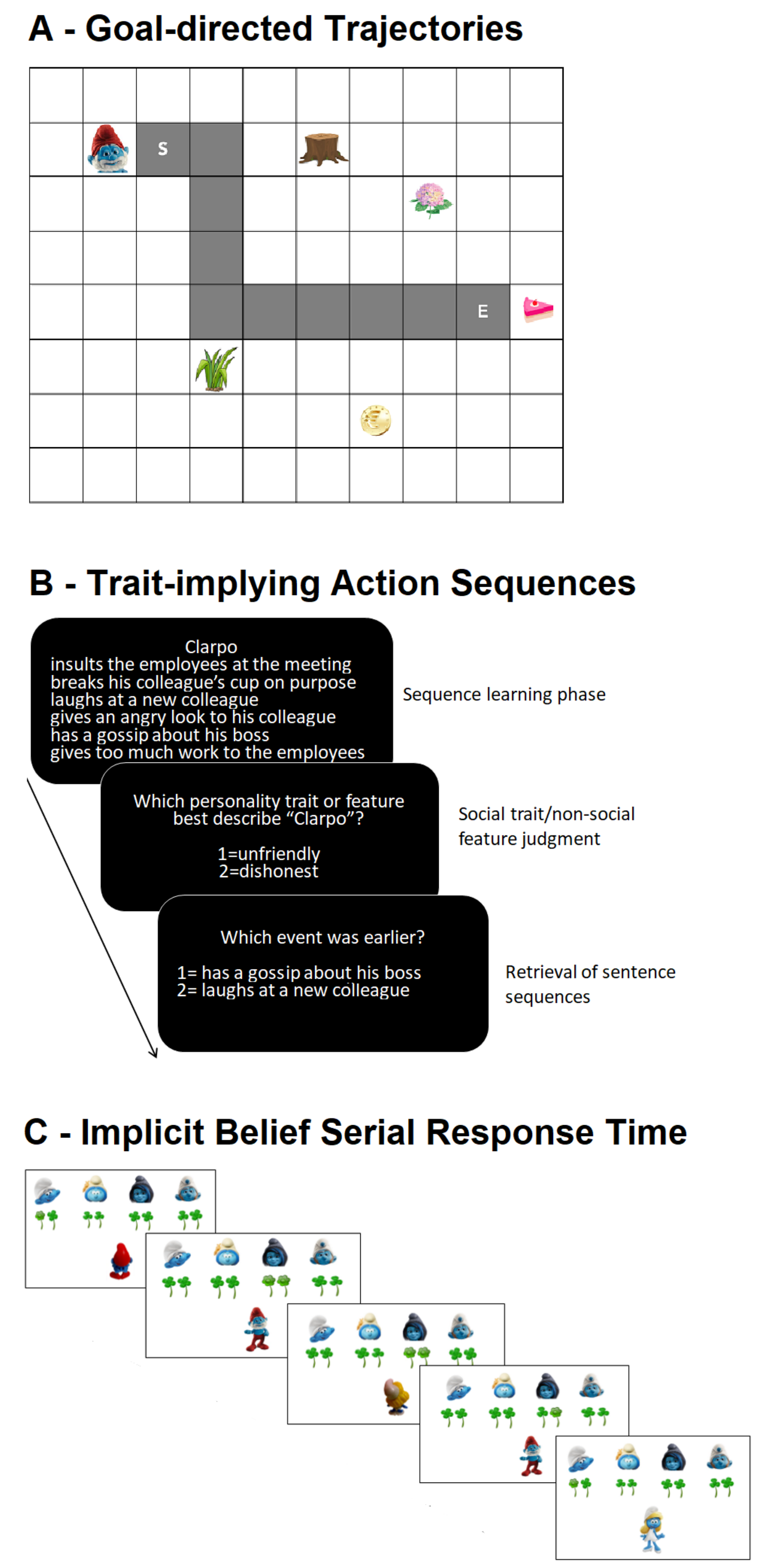
A - Goal-directed Trajectories
S
E
B - Trait-implying Action Sequences
Clarpo
insults the employees at the meeting
breaks his colleague's cup on purpose
laughs at a new colleague
gives an angry look to his colleague
has a gossip about his boss
gives too much work to the employees
Sequence learning phase
Which personality trait or feature best describe "Clarpo"?
1=unfriendly
2=dishonest
Social trait/non-social feature judgment
Which event was earlier?
1= has a gossip about his boss
2= laughs at a new colleague
Retrieval of sentence sequences
C - Implicit Belief Serial Response Time

Figure 2. A – Goal-directed trajectories: An example of a trial depicting a smurf moving along a trajectory from start (denoted by "S") to end ("E") shown in gray (characters and gray not shown to the participants; Li et al., 2021). **B – Trait-implying Action Sequences**: An example of a trial with six sentences implying a pro-social trait of which the order had to be memorized (Pu et al., 2020). **C – Implicit Belief Serial Response Time**: Participants had to answer as fast as possible how many flowers the smurf could see when oriented to the flowers; and when not, how many flowers he or she had seen previously. Unbeknownst to them, there was a fixed order of true and false beliefs held by the smurfs (Ma, Pu, et al., 2021).

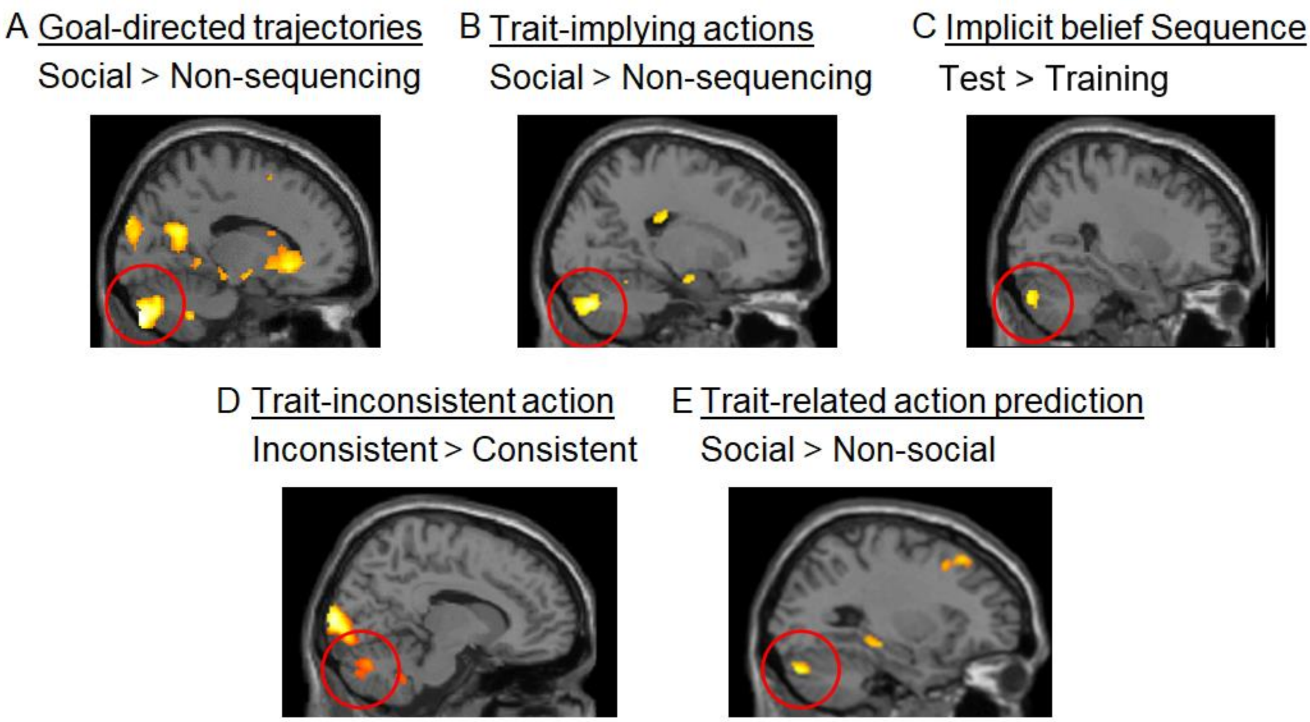

Figure 3. fMRI contrasts for various social sequencing tasks revealing activation in the posterior cerebellum. **A – Goal-directed trajectories** (Li et al., 2021). **B** – **Trait-implying Action Sequences** (Pu et al., 2020). **C** – **Implicit Belief Serial Response Time** (Ma, Pu, et al., 2021). **D – Trait-inconsistent Action Sequences (**Pu et al., 2021)**. E** – **Trait-based Action Prediction (**Haihambo et al., 2021).

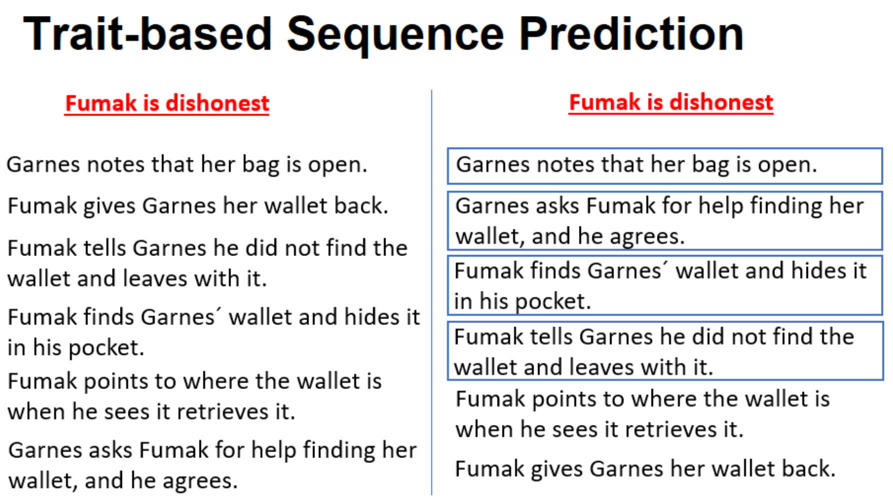

Figure 4: Trait-based Sequence Prediction task. **Left** - An example with the trait of the person presented first on top, and random presentation of the sentences underneath. **Right** - The final correct ordering of the sentences (Haihambo et al., 2021).

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