Who you gonna call? TMS-induced inhibition of the left premotor cortex acts as a Bayesian Ghost Buster by altering illusory social perception

Charline Peylo[1], Elisabeth Sterner[1], Yifan Zeng[1], the EMPRA students[1§] and Elisabeth V. C. Friedrich[1]*

[1]Department of Psychology, Research Unit Biological Psychology, Ludwig-Maximilians-University Munich, Leopoldstr. 13, 80802 Munich, Germany

[§]EMPRA students in alphabetical order:
Annika Bingger
Gabriel Engelhardt
Viola Gnam
Marie Gottmann
Christof Leininger
Zdislava Lukasova
Keno Mersmann
Ada Özbey
Liisbeth Pirn
Jacob Riecke
Sarah Schellnast
Gina Marie Schowe
Dominik Weidenhöfer
Jasmin Wunderatzke
Nele Wunner

*** Corresponding author:**
Elisabeth V. C. Friedrich
Research Unit Biological Psychology, Department of Psychology, LMU Munich
Leopoldstr. 13, 80802 Munich, Germany
Email: elisabeth.friedrich@psy.lmu.de
Phone: +49 (0) 89 / 2180 6159
Fax: +49 (0) 89 / 2180-3125

Acknowledgments
We would like to thank Imme Zillekens, Leonhard Schilbach, Cristina Becchio and Atesh Koul for providing the experimental task and advice during setup and analysis. Moreover, our thanks goes to Paul Sauseng for providing valuable advice throughout the study. This study was funded by a DFG grant to E.V.C.F. (FR 3961/1-1).

Abstract

Prior experiences help us to navigate social interactions. Communicative actions from one person are used to predict another person's response. However, in some cases, these predictions can outweigh the processing of sensory information and lead to illusory social perception such as believing to see two people interact, although in real, there is only one person present. This phenomenon was referred to as seeing a Bayesian ghost.

In this pre-registered study, we used a two point-light agents design. One agent was well-recognizable and performed either a communicative or individual gesture. The other agent either was blended into a cluster of noise dots and responded to this gesture or it was entirely replaced by noise dots. The participants had to indicate the presence or absence of the masked agent. Before the task, we applied either inhibitory non-invasive brain stimulation over the left premotor cortex (i.e., real TMS) or sham TMS as control condition.

As expected, participants had more false alarms (i.e., Bayesian ghosts) in the communicative than individual condition in the sham TMS session and this difference between conditions vanished in the real TMS session. In contrast to our hypothesis, the general level of false alarms increased (rather than decreased) in the real TMS session for both conditions.

These findings confirm that the premotor cortex is causally linked to the illusory social perception of a Bayesian ghost, which is likely due to disrupted action predictions and of clinical significance.

Keywords:
Continuous Theta Burst Stimulation (cTBS), action prediction, interpersonal predictive coding, point-light agents, dyadic social interaction, communicative gestures

Introduction

Our prior expectations affect our perception of others' actions in social interactions. For example, you see your friend sticking out his hand to a woman as if he would like to shake hands and introduce himself. Due to your prior experience, you expect the woman to respond to the handshake. The use of prior experience to anticipate the interaction partner's response action is called interpersonal predictive coding (Manera et al., 2011a, b; von der Lühe et al., 2016). Usually, interpersonal predictive coding helps us to handle complex social situations, but sometimes it can also lead to erroneous perception. Imagine in our example above that you are in a dark and smoky club when you see your friend trying to introduce himself to the woman. When you see the woman sticking out her hand too, you might have an illusion of them shaking hands when in fact the woman was just grabbing her drink and did not respond to your friend at all. This example should illustrate that our top-down expectations can be so strong that they overwrite our sensory information in ambiguous situations and lead us to perceive something or even someone who is not present. This phenomenon was called "seeing a Bayesian ghost" in previous work (Friedrich et al., 2022a; Manera et al., 2011b; von der Lühe et al., 2016). We use this term to describe an illusory perception of a person responding to a communicative gesture from another person due to prior expectations. The goal of this study was to investigate if there is a causal relationship between premotor activation and the occurrence of the Bayesian ghost.

We used an experimental design developed by Manera and colleagues (2011b) including two point-light agents (Figure 1; Friedrich et al., 2022a, b; Manera et al., 2011b; Zillekens et al., 2019). The agents are humans represented by moving lights that are attached to their major joints. Point-light displays are perceived as biological motion and can be used to investigate social interactions (Neri et al., 1998; Pavlova, 2012). In the current experimental design, agent A was well-recognizable and performed either a communicative or individual gesture. Agent B was blended into a cluster of noise dots and was either present (signal trials) or absent (noise trials). The participants' task was to indicate whether they saw agent B in the cluster of noise dots or not. Previous studies using the same experimental design showed that communicative gestures, in contrast to individual actions, facilitated the perception of a second agent (Friedrich et al., 2022b; Manera et al., 2011b; Zillekens et al., 2019).

Based on the same experimental design, Friedrich and colleagues (2022a) defined the Bayesian ghost as a false alarm response in the communicative noise trial. These are trials, in which agent A performed a communicative gesture and the participants indicated to see agent B although it was not present in the cluster of noise dots. The behavioral results showed that participants made more false alarms (i.e., participants indicated that agent B was present although it was absent) in the communicative than in the individual condition and the opposite was true for correct rejections (i.e., participants indicated correctly that agent B was absent). On the neural level, false alarms were compared to correct rejections within the communicative noise trials. The results demonstrated that activation of the left premotor cortex during the observation of agent A's communicative gesture predicted the occurrence of the Bayesian ghost in the later time segment. Importantly, the premotor activation was very specific for this early time segment of the task, in which agent A was observed and the predictions for agent B's response were formed. During the actual appearance of the Bayesian ghost (i.e., when participants watched the cluster of noise dots

and indicated the presence or absence of agent B), more posterior regions in the sensorimotor cortex and adjacent parietal regions were activated.

The involvement of the premotor cortex in generating action predictions is supported by studies showing that the sensorimotor cortex is active when expecting a predictable action (Kilner et al., 2004; Krol et al., 2020; Maranesi et al., 2014; Urgesi et al., 2010) and does not rely on visual input to generate mental representations of intended motions (Cisek & Kalaska, 2004; Umiltà et al., 2001). Moreover, non-invasive brain stimulation with transcranial magnetic stimulation (i.e., TMS) of different parts of the premotor cortex led to a change from reactive to predictive action strategies (Cattaneo & Parmigiani, 2021).

The use of TMS makes it possible to identify causal relations between brain areas and functions (Walsh & Cowey, 2000). Depending on the specific TMS protocol, the effects of TMS can be excitatory or inhibitory, and short or long lasting (di Lazzaro et al., 2011; Hallett, 2007; Huang et al., 2005). Continuous Theta Burst Stimulation (cTBS) is a repetitive TMS protocol (i.e., many pulses are applied repeatedly), which can inhibit the motor cortex for up to an hour (Huang et al., 2005). Inhibiting the left premotor cortex with repetitive TMS was shown to impair the detection of biological motion (van Kemenade et al., 2012), action understanding (Michael et al., 2014) and action prediction (Brich et al., 2018; Stadler et al., 2012).

These findings led us to our hypothesis that the premotor cortex is causally linked to the occurrence of the Bayesian ghost. To test this, we used offline cTBS to inhibit the left premotor cortex right before participants started the experimental task. In a different session, we applied sham TMS to the left premotor cortex as control condition in a within-subject design with randomized session order.

If the premotor cortex really is causally linked to the occurrence of the Bayesian ghost, we expect that inhibition of the left premotor cortex with cTBS will disrupt the processes involved in the formation of the Bayesian ghost. This might lead to a reduction in the number of false alarms in the communicative condition. Thus, in the real TMS session, there should be no difference between the number of false alarms in the communicative condition (because predictions are disrupted) and the individual condition anymore (because no predictions are possible in the first place). In contrast, in the sham TMS session, we expect to replicate the results from the study of Friedrich and colleagues (2022a): Participants should make more false alarms in the communicative condition (because predictions are made about agent B's response action) than in the individual condition (because no predictions are possible).

Methods

Pre-registration

The experiment was pre-registered on Open Science Framework (https://osf.io/4fvns/?view_only=22773756c68c4d47b7ed27a25f3219ce).

Participants

An a-priori power analysis was performed with G*Power 3.1 (Faul et al., 2009) to determine the sample size for a repeated-measures ANOVA with $\alpha=0.05$ and a power of $1-\beta=0.8$. Previous TMS literature reported effect sizes of d = 0.9 - 1.2 (Basil et al., 2017; Lapenta et al., 2022; Michael et al., 2014; Stadler et al., 2012; van Kemenade et al., 2012). Yet we suggest such effect sizes may be overestimated due to rather small sample sizes tested in these studies. As a conservative estimation, an effect size of d = 0.7 (f = 0.35) was used, and resulted in a minimal sample size of 19 participants.

We recruited 21 young, healthy participants. All of them were right-handed, had normal or correct-to-normal vision, no diagnosis of neurological or psychiatric disorders, no history of medication intake and were not pregnant. In addition, all fulfilled the TMS safety criteria in line with Rossi and colleagues (2009). Two participants were excluded: For one participant the real TMS session had to be abandoned due to a fire alarm; and the other one failed to perform significantly above chance level in the sham TMS session (same criteria as in Friedrich and colleagues (2022a)). The remaining 19 participants (5 male and 14 female) were on average 21.6 (SD = 3.7) years old and obtained a mean Autism Spectrum Quotient of 14.1 (SD = 5.0; Baron-Cohen et al., 2001), which is indicative of a control group without clinically significant levels of Autism Spectrum Disorder. The participants gave written informed consent prior to the study and received course credits as compensation. The study was conducted under the approval of the LMU Munich Faculty 11 ethics committee and in accordance with the Declaration of Helsinki. The participants had no information about the different stimulation protocols (i.e., whether the TMS application was excitatory, inhibitory or sham) during the experiment.

Experimental Task

We used the same experimental task as the one in Friedrich and colleagues (2022a). It was programmed with Matlab R2016a (The MathWorks, Inc., Natick, Massachusetts, United States) and Psychophysics Toolbox (Version 3.0.14; Brainard & Vision, 1997; Kleiner et al., 2007; Pelli & Vision, 1997).

The visual stimuli were presented on a 1280 × 1024 monitor with a refresh rate of 60 Hz. The video included two point-light agents, which were each defined by 13 moving dots and were displayed on the two sides of the gray screen (Figure 1). Agent A performed actions that either revealed an intention to communicate (communicative condition: asking to squat down, asking to look at the ceiling, asking to sit down) or not (individual condition: turning around, sneezing, drinking). These gestures were chosen from the Communicative Interaction Database (Manera et al., 2010). Agent B performed actions responding to agent A's gesture (i.e., squatting down, looking at the ceiling, sitting down). Agent B was blended into a cluster of spatio-temporally scrambled moving noise dots in half of the trials (signal trials). In the other half of the trials, it was entirely replaced by noise dots (noise trials). The dots of agent B were presented using a limited life-time technique (for more detail, see Friedrich et al., 2022a, b; Manera et al., 2011b; Zillekens et al., 2019). The participants' task was to indicate whether agent B was present or absent in the cluster of noise dots.

Each trial began with a blank screen for an inter-trial interval of 1.5-3 s and was followed by a 1 s fixation cross indicating the subsequent position of agent A on the left or right side of the screen, which was counterbalanced. Then, agent A was presented together with the cluster of moving dots. If agent B was present in the cluster of dots, its response action was delayed between 1267-1567ms. Depending on the specific action, the videos lasted for 3600-4300ms. Participants were asked to first passively observe agent A and then, to watch the cluster of noise dots. They should decide as fast and accurate as possible whether agent B was present or absent and indicate their choice by pressing the dedicated Yes or No key on a keyboard (keys were counterbalanced between yes and no responses). Participants had to respond while the video with the point-light agent(s) was still on-going. As we stimulated the left premotor cortex, we asked all participants to make their choice with the left hand.

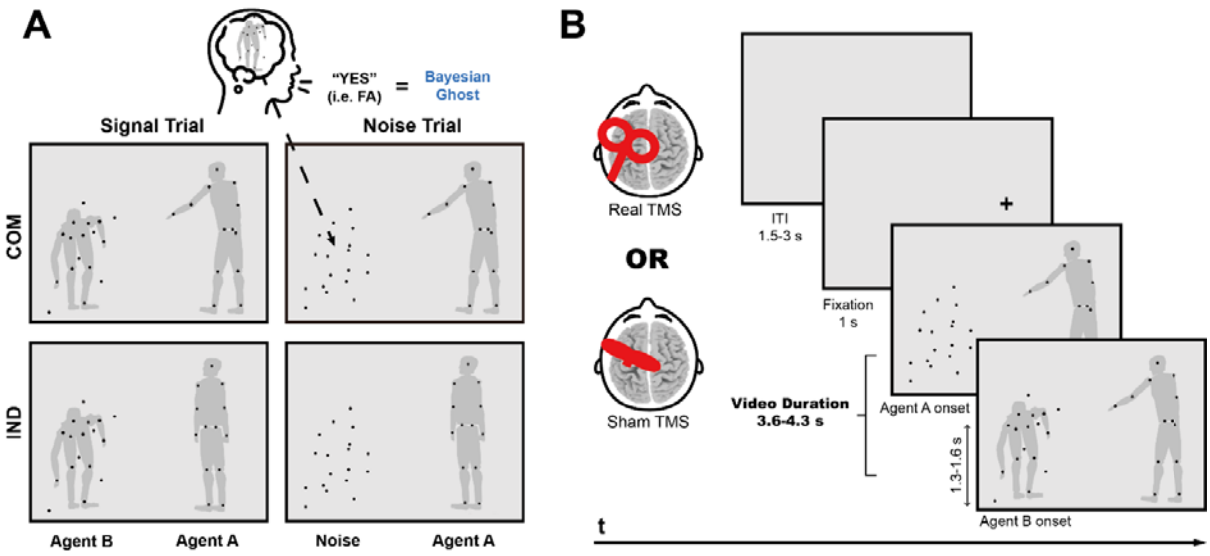

Figure 1. Experimental design (adapted from Friedrich et al., 2022a, b and Zillekens et al., 2019)**. (A) Task conditions:** Agent A performed either a communicative (COM) or an individual (IND) gesture. Agent B performed a gesture in response of agent A. Half of the trials were signal trials, where agent B was blended into a cluster of randomly moving noise dots. In the other half of the trials, agent B was entirely replaced by the noise dots (noise trial). The task of the participants was to report the presence or absence of agent B. The Bayesian ghost is defined as a false alarm (FA) in the communicative noise trials. Please note that the gray silhouettes only serve illustration purposes and were not visible for the participants. **(B) Timing:** The main experiment was divided into two sessions on two separate days. In each session, participants received either offline real or sham TMS. Following the TMS application, participants performed the task. Each trial was initiated with a jittered intertrial interval (ITI) between 1.5 - 3 s, followed by a 1 s fixation cross indicating the subsequent location of agent A. Then, the video displaying agent A and the cluster of dots (with or without agent B) started. Although, agent B was present from the beginning of the video, its response action was delayed between 1.3 -1.6 s. Participants were required to make a response as long as the video was still on-going. The video duration dependent on the specific action and was between 3.6 -4.3 s long. Please note that the gray silhouettes again only serve illustration purposes and were not visible for the participants. COM, communicative condition; IND, individual condition; FA, false alarm; ITI, intertrial interval.

TMS Apparatus

We delivered continuous Theta Burst Stimulation (cTBS) offline via a Mag&More PowerMag Research 100 TMS stimulator (Mag&More®) with a 7 cm figure-eight coil (Mag&More®). We first determined the active motor threshold over the left primary motor cortex. Participants maintained a voluntary flexion of their right wrist while actively stretching out their fingers. Single pulses were delivered to their left primary motor cortex with increasing intensity until a motor response was observable in exactly 3 out of 6 trials. For the actual cTBS, the coil was moved from the primary motor cortex 1.5 cm in the anterior direction and placed on the premotor cortex. We followed the cTBS protocol described by Huang and colleagues (2005). The stimulation was set to an intensity of 80% of the individual active motor threshold. The active motor threshold was on average 45% of the maximal stimulator output. We applied a 40 s continuous train, including bursts of three pulses at 50 Hz repeating every 200 ms (600 pulses in total). The sham TMS session followed the same procedure. The only difference between the sham and real TMS session was that the coil was tilted by 90 degrees in an upright position so that no effect on the brain was induced while retaining the clicking sound.

Procedure and Study Design

Each participant took part in two sessions on different days. In one session real TMS and in the other one sham TMS was applied in counterbalanced order between participants. Before the experiment, participants were asked to sign the informed consent, fill out the Autism Spectrum Quotient (Autism Research Center; Baron-Cohen et al., 2001) and the Edinburgh Handedness Inventory (Veale, 2013).

At the beginning of both sessions, we determined the active motor threshold of each participant to define the stimulation intensity used for the real or sham TMS application. Similarly, we individualized the task difficulty in both sessions with a pre-test including 108 trials of an established procedure (Friedrich et al., 2022a, b; Manera et al., 2011b; Zillekens et al., 2019): Participants were asked to identify the presence or absence of agent B, which was blended into a cluster of noise of either 5, 20, or 40 dots. We fitted the response curve with a cumulative Gaussian function and obtained the number of dots corresponding to an average performance of 70%. This served as the individually adapted number of noise dots in the main experimental task.

Then, real or sham TMS – depending on the session - was applied offline right before participants performed the main experimental task (Figure 1B). At the end of the last session of the experiment, participants were asked to fill out a questionnaire to indicate whether they experienced the TMS applications as excitatory, inhibitory or sham.

Data Analysis and Statistics

First, we analyzed the questionnaire about the experienced effects of TMS application and compared the two TMS sessions in terms of performance (percent correct) and the number of noise dots needed to achieve the desired accuracy of 70%. For this purpose, we computed a two-sided dependent *t* test (for the normally distributed percent correct) and a two-tailed Wilcoxon signed-rank test (for the non-normally distributed number of noise dots) together with their Bayesian equivalents (using a default Cauchy prior of 0.707).

Afterwards, we performed the pre-registered 2x2x2 repeated-measures ANOVA (https://osf.io/4fvns/?view_only=22773756c68c4d47b7ed27a25f3219ce) for the number of responses with factors 'TMS' (real vs. sham), 'condition' (communicative vs. individual) and 'response' (false alarm vs. correct rejection). To account for the non-normality and presence of outliers in some of the above variables (which could potentially bias the ANOVA's results), and to further explore our hypothesis that inhibition of the left premotor cortex through real TMS reduces the difference between the communicative and the individual condition in the number of false alarms, we performed three additional Wilcoxon signed-rank tests and their Bayesian equivalents (using a default Cauchy prior of 0.707 and a Markov Chain Monte Carlo algorithm with 1000 samples). These follow-up tests contrasted the number of false alarms in the communicative and the individual condition separately for sham and real TMS, as well as the condition difference (COM – IND) between the two types of TMS. Because we expected (a) significantly more false alarms in the communicative than in the individual condition when applying sham TMS, (b) no such difference after applying real TMS and hence (c) a significant reduction of this condition difference following real compared to sham TMS, the first and last test were one-tailed and the second test was two-tailed. FDR correction was used to account for multiple comparisons. All statistical tests were performed using JASP 0.16.4 (JASP Team, 2022) and the corresponding data was plotted in the Spyder 4.1.5 environment (Spyder Developer Team, 2020) for Python 3.7.3 (Van Rossum & Drake, 2009) using custom-written scripts and the open-source packages Matplotlib 3.3.2 (Hunter, 2007) and NumPy 1.19.2 (Harris et al., 2020).

Results

In order to make sure that participants were blind to the effects of the TMS application, at the end of the study we asked them how they had experienced stimulation in the sessions. For the real TMS session, seven participants thought an excitatory TMS has been applied, three thought it had been inhibitory and nine had taken it as sham. For the sham TMS session, three and four participants guessed excitatory and inhibitory, respectively, whereas twelve participants correctly took it as sham. No one guessed the TMS effects in both sessions correctly.

Overall, participants performed equally well in both TMS sessions (sham: M=72.52%, SD=9.23%; real: M=71.51%, SD=9.44%; $t(18)=0.42$, $p=.682$, $d=0.096$; $BF_{01}=3.90$) and required an equal amount of noise dots to achieve the desired average accuracy of approximately 70% (sham: M=18.00, Mdn=14.00, SD=14.08; real: M=22.32, Mdn=14.00, SD=28.00; $z=-0.04$, $p=.983$, $r_{rb}=-.012$; $BF_{01}=4.20$).

The pre-registered 2x2x2 repeated-measures ANOVA for the number of responses with factors 'TMS' (real vs. sham), 'condition' (communicative vs. individual) and 'response' (false alarm vs. correct rejection) yielded a highly significant but trivial main effect of factor 'response' ($F(1,18)=17.96$, $p<.001$, $\eta^2_p=.499$): As predicted based on the targeted 70% average accuracy, participants made overall more correct rejections (M=41.72, SD=13.13) than false alarms (M=20.71, SD=10.08). In addition to this main effect, we observed a significant interaction between factors 'condition' and 'response' ($F(1,18)=7.75$, $p=.012$, $\eta^2_p=.301$), indicating a larger numerical advantage of correct rejections over false alarms in

the individual condition (Δ*M*=23.63, Δ*SD*=22.73) than in the communicative condition (Δ*M*=18.40, Δ*SD*=21.24). The predicted three-way interaction between factors 'TMS', 'condition' and 'response' did not reach statistical significance ($F(1,18)=2.17$, $p=.158$, $\eta^2_p=.108$), nor did any of the other effects (all $p \geq .124$). Descriptive statistics underlying the absent three-way interaction however suggested that the difference between the number of false alarms in the communicative and the individual condition might have been reduced following real compared to sham TMS (sham: Δ*M*=3.90, Δ*SD*=6.84; real: Δ*M*=0.63, Δ*SD*=4.83), as originally predicted. And so was the condition difference between the number of correct rejections albeit to a smaller degree (sham: Δ*M*=-4.05, Δ*SD*=6.98; real: Δ*M*=-1.90, Δ*SD*=4.90). The results are summarized in Figure 2.

To further explore our hypothesis that inhibition of the left premotor cortex through real TMS reduces the difference between the number of false alarms in the communicative and the individual condition, we contrasted the number of false alarms in the communicative and the individual condition separately for sham and real TMS. Additionally, we made a comparison of this condition difference (COM – IND) between the two types of TMS. For these comparisons, we performed three additional Wilcoxon signed-rank tests and their Bayesian equivalents. In line with our hypotheses and previous results, in the sham TMS session, we observed significantly more false alarms in the communicative condition (*M*=21.16, *Mdn*=21.00, *SD*=12.21) than in the individual condition (*M*=17.26, *Mdn*=15.00, *SD*=11.32; $z=2.20$, $p=.045$, $r_{rb}=.591$; $BF_{10}=9.72$). Importantly, this condition difference was absent after applying real TMS (communicative: *M*=22.53, *Mdn*=22.00, *SD*=9.76; individual: *M*=21.90, *Mdn*=21.00, *SD*=11.34; $z=0.54$, $p=.600$, $r_{rb}=.142$; $BF_{01}=3.43$) and significantly reduced compared to sham TMS (sham: Δ*M*=3.90, Δ*Mdn*=3.00, Δ*SD*=6.84; real: Δ*M*=0.63, Δ*Mdn*=2.00, Δ*SD*=4.83; $z=1.87$, $p=.048$, $r_{rb}=.516$; $BF_{10}=2.08$). It should be noted, however, that this decreased condition difference following real compared to sham TMS was primarily driven by an increase in the number of false alarms in the individual condition (Δ*M*=4.63, Δ*Mdn*=4.00, Δ*SD*=7.82), rather than by the predicted decrease in the number of false alarms in the communicative condition (Δ*M*=1.37, Δ*Mdn*=-1.00, Δ*SD*=9.30).

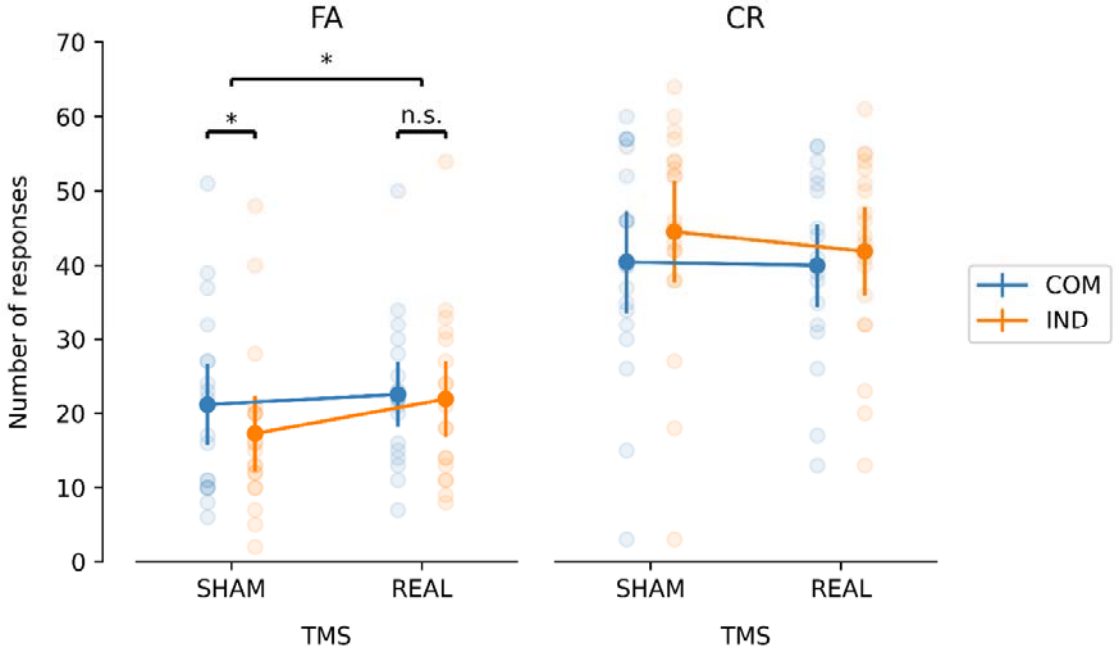

Figure 2. Real TMS eliminates the condition difference (COM-IND) for false alarms seen in sham TMS. Number of false alarms (FA; left column) and correct rejections (CR; right column) as a function of condition (communicative: COM vs. individual: IND) and TMS session (sham vs. real). Translucent dots represent the sampling distribution and opaque dots with error bars represent the sample mean and its 95% confidence interval. Asterisks highlight statistical significance at $p < .05$, whereas non-significant differences with $p \geq .05$ are abbreviated with n.s.

Discussion

Bayesian ghost is causally linked to premotor cortex

This pre-registered study aimed to investigate if the occurrence of the Bayesian ghost is causally linked to premotor activation. In a within-subject design, we used real TMS (cTBS) versus sham TMS to inhibit the left premotor cortex offline before participants performed a point-light agent discrimination task. Although most of the participants distinguished the sham TMS from the real TMS application, only three out of 19 participants thought that the real TMS was inhibitory. Moreover, none of the participants indicated the effect of both sessions correctly. Thus, we can assume that our experimental manipulation was successful. In the sham TMS session, we could replicate the findings of Friedrich and colleagues (2022a): After seeing a communicative gesture of agent A, participants saw a Bayesian ghost (i.e., indicated by a false alarm in the communicative noise trial) more often than in the individual condition. In the real TMS session, the difference between the communicative and individual condition in the number of false alarms vanished. Thus, real TMS affected the processes underlying the illusory social perception of a second agent. We can therefore accept our hypothesis that the premotor cortex really is causally related to perceiving the Bayesian ghost. This result is also in line with previous studies showing that the premotor cortex is involved in action predictions (Brich et al., 2018; Cattaneo & Parmigiani, 2021; Cisek & Kalaska, 2004; Kilner et al., 2004; Krol et al., 2020; Maranesi et al., 2014; Stadler et al., 2012; Umiltà et al., 2001; Urgesi et al., 2010)

Real TMS leads to an increase rather than a decrease in false alarms

In contrast to our hypothesis, real TMS descriptively increased the number of false alarms in both conditions, the individual and the communicative one. As we inhibited the left premotor cortex with TMS, we expected that we impair the generation of predictions in the communicative condition and thus false alarms will decrease to the level of the individual condition, in which no predictions were possible in the first place. However, the inhibition of the left premotor cortex led descriptively to an increase in false alarms in both conditions. In the following paragraphs, we discuss different explanations for this result.

One explanation could be that real TMS generally increases the noise level, which might have led to more false alarms in the real than the sham TMS session. This explanation is in line with the findings of van Kemenade and colleagues (2012) who reported a similar post-TMS increase in false alarms for detecting a noise-masked agent. Moreover, several studies suggested that TMS generates neural noise (Miniussi et al., 2010; Ruzzoli et al., 2010;

Schwarzkopf et al., 2011). Injecting low-level noise may raise the probability of detection by randomly pushing some of the weak signals above the threshold (Moss et al., 2004). In the noise trials of the present study, the movement of the random noise dots might be accidentally boosted by neural noise and erroneously interpreted as a body motion. Consequently, more false alarms were made.

Since the premotor cortex is not only associated with action prediction but also with action perception (Candidi et al., 2008; Caspers et al., 2010; Cross et al., 2009; Wheaton et al., 2004), another possible explanation for the increase in the number of false alarms following real TMS might be a disturbance in the perception of agent A rather than a disruption in the prediction of agent B. If real TMS decreased the participants' ability to distinguish between the communicative and individual gestures (i.e., creating a situation of uncertainty) and biased them into mistaking individual for communicative ones, then that might explain why participants made more false alarms following real TMS (especially in the individual condition). In line with this reasoning, it has been shown that social judgements like emotion identification are adversely affected by uncertainty (Clarke et al., 2005) and that perceptual ambiguity can be associated with a bias towards social interpretations (Salge et al., 2020; Varrier & Finn, 2022). The opposite effect, however, can sometimes be observed as well (Vanrie et al., 2004). It should also be noted that participants were familiarized with the different gestures at the beginning of each session and that the set from which the stimuli in the present study originated has previously been shown to yield a high accuracy in communicative gesture identification and discrimination (Manera et al., 2010). Therefore, a TMS-induced disturbance in the prediction of agent B might provide a more plausible explanation for the increase in false alarms following TMS than a disrupted perception of agent A.

A disturbance in the prediction of agent B due to real TMS does not necessary imply that predictions could not be generated at all. It is also possible, that predictions were still generated following real TMS, but that an increased prediction error was induced in both conditions. That would mean, that the predictions were not accurate and biased towards false positives in both conditions. Stadler and colleagues (2012) as well as Brich and colleagues (2018) reported more prediction errors and less prediction accuracy, respectively, when inhibiting the left premotor cortex with TMS.

Another aspect to consider is that the premotor cortex is not the only region involved in action prediction and also not isolated within the brain but strongly interconnected with other areas. Also the parietal cortex was identified as core region for action predictions (Fontana et al., 2012). The premotor cortex and the parietal cortex are strongly interconnected and both are involved in action prediction (Balser et al., 2014; Ptak et al., 2017; Schubotz, 2007) by supporting predictive functions in the absence of visual input (Stadler et al., 2012). If the premotor cortex is inhibited, we could speculate that parietal areas are missing important input and thus produce erroneous output like illusory perception. This speculation is supported by the results of Friedrich and colleagues (2022a) who suggested that the superior parietal region was involved in creating the illusion in absence of actual biological motion. Also in clinical studies, the superior parietal cortex was found to show impaired functional connectivity (Schilbach et al., 2016; Tarasi et al., 2021) and altered brain structures (Cachia et al., 2014; Delli Pizzi et al., 2014) in individuals with symptoms of hallucinations.

We cannot determine with certainty which of these explanations is the real cause of the increase in false alarms after real TMS in both conditions. But it is also important to note, that this increase in false alarms caught our attention because it was in contrast to what we expected, however, it remains a mere descriptive phenomenon of our data.

Premotor cortex involvement in Bayesian ghosts most likely includes - but is not limited to - action prediction

In this study, the premotor cortex was inhibited offline with cTBS, which means that a virtual lesions was set before the participants started with the experimental task and this virtual lesion should have lasted for the whole session (Huang et al., 2005). The experimental task is rather complex and each trial consists of different parts, which can be divided into three time segments (Friedrich et al., 2022b): First, participants were watching agent A's gesture and in case of a communicative gesture, they generated predictions for agent B's response action. Second, they focused on the cluster of noise dots and tried to detect agent B among them. Third, they decided, whether they see agent B or not and indicated their choice with a button press. The inhibition of the premotor cortex could have different influences on this range of processes.

In the first time segment, an inhibited premotor cortex could have led to an impaired perception of agent A's gesture (i.e., participants were not able any more to discriminate between individual and communicate gesture; also see above). This idea is supported by the study of Michael and colleagues (2014) who showed that participants were less accurate in recognizing pantomimed actions after inhibiting the respective area in the premotor cortex. Thus, inhibiting the premotor cortex decreased performance in action understanding.

Another possibility is that participants could still recognize agent A's gesture correctly but failed to generate or maintain (correct) predictions based on its communicative gesture. Premotor cortex activation was found to be especially involved in the initial phase of action prediction, i.e., to initiate the generation of predictions (Stadler et al., 2012; Urgesi et al., 2010). This is in line with the EEG study of Friedrich and colleagues (2022a) showing that premotor activation in the first time segment predicted the occurrence of the Bayesian ghost, which appeared in a later time segment. During the appearance of the Bayesian ghost, more posterior regions were activated. However, an inhibited premotor cortex could also influence the ability to observe biological motion in the cluster of noise dots in this later time segment (Fadiga et al., 2005).

As we used offline TMS, we cannot conclude which aspect(s) of the tasks were exactly targeted, but it is likely to be more than one.

Limitations

As already mentioned in the section above, our experimental design targeted multiple cognitive processes from biological motion perception, over gesture discrimination to action prediction; all of which are critical at different points in time and potential explanations for our results. Since our offline application of TMS most likely induced a general rather than a time- and thus process-specific inhibition of the premotor cortex, the question of the mechanism

underlying our findings remains open to discussion. Moreover, it should be noted that only the exploratory tests but not the planned ANOVA yielded significant effects of TMS on task performance. A potential reason for this difference is that the follow-up tests focused only on the number of false alarms (in line with the definition of a Bayesian ghost as an illusory percept of a non-existent second agent; i.e., a false alarm), whereas the ANOVA also included the number of correct rejections. The rationale behind this was to match the methods between the current experiment and the preceding study by Friedrich and colleagues (2022b), allowing for a direct comparison between our results and the ones in support of premotor cortical involvement in the occurrence of a Bayesian ghost. However, since the number of correct rejections was neither central to our hypotheses, nor to the effect size estimation underlying our a-priori power analysis, this factor might have just added more variance to the model without providing additional explanatory power. This might have led to a smaller overall effect size than what we had anticipated based on the false alarm literature alone and hence to a lower statistical power. The exploratory tests on just the number of false alarms as central element of our hypotheses, in contrast (and despite the reduced power in non-parametrical testing), provided significant and anecdotal to moderate evidence that the illusory social perception of a Bayesian ghost indeed depends on the premotor cortex.

Conclusions and relevance of the findings

Our findings show that the premotor cortex is causally linked to the illusory social perception of a Bayesian ghost, which is likely due to disrupted action predictions. However, future studies are needed to apply TMS online to target the different processes involved in this complex task (Friedrich et al., 2022b). Then, we could determine more precisely the role of the premotor cortex in interpersonal predictive coding and the phenomenon of the Bayesian ghost.

Our findings are also of clinical significance. An over-reliance on predictions was associated with schizophrenic symptoms, whereas an under-reliance on predictions was associated with Autism Spectrum Disorder (Tarasi et al., 2021). Moreover, illusory perception is a symptom of a variety of psychiatric disorders and mental health conditions; and so is impairment in social functioning. Identifying the brain regions responsible for generating action predictions in a social context and for producing illusory social perception is a central aspect to understand mental disorders better and consequently to find better treatment options.

References

Balser, N., Lorey, B., Pilgramm, S., Stark, R., Bischoff, M., Zentgraf, K., Williams, A. M., & Munzert, J. (2014). Prediction of human actions: expertise and task-related effects on neural activation of the action observation network. *Human Brain Mapping*, *35*(8), 4016–4034. https://doi.org/10.1002/HBM.22455

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger Syndrome/High-Functioning Autism, Males and Females, Scientists and Mathematicians. In *Journal of Autism and Developmental Disorders* (Vol. 31, Issue 1).

Basil, R. A., Westwater, M. L., Wiener, M., & Thompson, J. C. (2017). A Causal Role of the Right Superior Temporal Sulcus in Emotion Recognition From Biological Motion. *Open Mind*, *2*(1), 26–36. https://doi.org/10.1162/OPMI_A_00015

Brainard, D. H., & Vision, S. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433–436.

Brich, L. F. M., Bächle, C., Hermsdörfer, J., & Stadler, W. (2018). Real-time prediction of observed action requires integrity of the dorsal premotor cortex: Evidence from repetitive transcranial magnetic stimulation. *Frontiers in Human Neuroscience*, *12*, 101. https://doi.org/10.3389/FNHUM.2018.00101/BIBTEX

Cachia, A., Amad, A., Brunelin, J., Krebs, M. O., Plaze, M., Thomas, P., & Jardri, R. (2014). Deviations in cortex sulcation associated with visual hallucinations in schizophrenia. *Molecular Psychiatry 2014 20:9*, *20*(9), 1101–1107. https://doi.org/10.1038/mp.2014.140

Candidi, M., Urgesi, C., Ionta, S., & Aglioti, S. M. (2008). Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions. *Https://Doi.Org/10.1080/17470910701676269*, *3*(3–4), 388–400. https://doi.org/10.1080/17470910701676269

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, *50*(3), 1148–1167. https://doi.org/10.1016/J.NEUROIMAGE.2009.12.112

Cattaneo, L., & Parmigiani, S. (2021). Stimulation of different sectors of the human dorsal premotor cortex induces a shift from reactive to predictive action strategies and changes in motor inhibition: A dense transcranial magnetic stimulation (tms) mapping study. *Brain Sciences*, *11*(5). https://doi.org/10.3390/brainsci11050534

Cisek, P., & Kalaska, J. F. (2004). Neural correlates of mental rehearsal in dorsal premotor cortex. *Nature*, *431*(7011), 993–996. https://doi.org/10.1038/NATURE03005

Clarke, T. J., Bradshaw, M. F., Field, D. T., Hampson, S. E., & Rose, D. (2005). The perception of emotion from body movement in point-light displays of interpersonal dialogue. *Perception*, *34*(10), 1171–1180. https://doi.org/10.1068/p5203

Cross, E. S., Kraemer, D. J. M., Hamilton, A. F. de C., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the Action Observation Network to Physical and Observational Learning. *Cerebral Cortex*, *19*(2), 315–326. https://doi.org/10.1093/CERCOR/BHN083

Delli Pizzi, S., Franciotti, R., Tartaro, A., Caulo, M., Thomas, A., Onofrj, M., & Bonanni, L. (2014). Structural Alteration of the Dorsal Visual Network in DLB Patients with Visual

Hallucinations: A Cortical Thickness MRI Study. *PLOS ONE*, *9*(1), e86624. https://doi.org/10.1371/JOURNAL.PONE.0086624

di Lazzaro, V., Dileone, M., Pilato, F., Capone, F., Musumeci, G., Ranieri, F., Ricci, V., Bria, P., Iorio, R. di, de Waure, C., Pasqualetti, P., & Profice, P. (2011). Modulation of motor cortex neuronal networks by rTMS: Comparison of local and remote effects of six different protocols of stimulation. *Journal of Neurophysiology*, *105*(5), 2150–2156. https://doi.org/10.1152/JN.00781.2010/ASSET/IMAGES/LARGE/Z9K0051107170001.JPEG

Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. Current opinion in neurobiology, 15(2), 213-218.

Faul, F., Erdfelder, E., Buchner, A., & Lang, A. G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160. https://doi.org/10.3758/BRM.41.4.1149/METRICS

Fontana, A. P., Kilner, J. M., Rodrigues, E. C., Joffily, M., Nighoghossian, N., Vargas, C. D., & Sirigu, A. (2012). Role of the parietal cortex in predicting incoming actions. *NeuroImage*, *59*(1), 556–564. https://doi.org/10.1016/J.NEUROIMAGE.2011.07.046

Friedrich, E. V. C., Zillekens, I. C., Biel, A. L., O'Leary, D., Seegenschmiedt, E. V., Singer, J., Schilbach, L., & Sauseng, P. (2022a). Seeing a Bayesian ghost: Sensorimotor activation leads to an illusory social perception. *IScience*, *25*(4), 104068. https://doi.org/10.1016/j.isci.2022.104068

Friedrich, E. V. C., Zillekens, I. C., Biel, A. L., O'Leary, D., Singer, J., Seegenschmiedt, E. V., Sauseng, P., & Schilbach, L. (2022b). Spatio-temporal dynamics of oscillatory brain activity during the observation of actions and interactions between point-light agents. *European Journal of Neuroscience*, *August 2022*, 1–23. https://doi.org/10.1111/ejn.15903

Hallett, M. (2007). Transcranial Magnetic Stimulation: A Primer. *Neuron*, *55*(2), 187–199. https://doi.org/10.1016/J.NEURON.2007.06.026

Harris, C. R., Millman, K. J., Van Der Walt, S. J., Gommers, R., Virtanen, P., Cournapeau, D., ... & Oliphant, T. E. (2020). Array programming with NumPy. *Nature*, *585*(7825), 357-362.

Harris, J. A., Clifford, C. W. G., & Miniussi, C. (2008). The functional effect of transcranial magnetic stimulation: signal suppression or neural noise generation? *Journal of Cognitive Neuroscience*, *20*(4), 734–740. https://doi.org/10.1162/JOCN.2008.20048

Huang, Y. Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2005). Theta burst stimulation of the human motor cortex. *Neuron*, *45*(2), 201–206. https://doi.org/10.1016/j.neuron.2004.12.033

Hunter, J. D. (2007). Matplotlib: A 2D graphics environment. *Computing in science & engineering*, *9*(03), 90-95.

JASP Team (2023). JASP (Version 0.17)[Computer software].

Kilner, J. M., Vargas, C., Duval, S., Blakemore, S. J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience*, *7*(12), 1299–1301. https://doi.org/10.1038/nn1355

Kleiner, M., Brainard, D., & Pelli, D. (2007). *What's new in Psychtoolbox-3?*

Krol, M. A., Schutter, D. J. L. G., & Jellema, T. (2020). Sensorimotor cortex activation during anticipation of upcoming predictable but not unpredictable actions. *Social Neuroscience*, *15*(2), 214–226. https://doi.org/10.1080/17470919.2019.1674688

Lapenta, O. M., Valasek, C. A., Vieira, S. M. G., & Boggio, P. S. (2022). Reading Point-Light Walkers and Amorphous—A TMS Study. *Psychology and Neuroscience*, *15*(2), 198–209. https://doi.org/10.1037/PNE0000273

Manera, V., Becchio, C., Schouten, B., Bara, B. G., & Verfaillie, K. (2011a). Communicative interactions improve visual detection of biological motion. *PLoS ONE*, *6*(1). https://doi.org/10.1371/journal.pone.0014594

Manera, V., del Giudice, M., Bara, B. G., Verfaillie, K., & Becchio, C. (2011b). The second-agent effect: Communicative gestures increase the likelihood of perceiving a second agent. *PLoS ONE*, *6*(7), 1–7. https://doi.org/10.1371/journal.pone.0022650

Manera, V., Schouten, B., Becchio, C., Bara, B. G., & Verfaillie, K. (2010). Inferring intentions from biological motion: A stimulus set of point-light communicative interactions. *Behavior Research Methods*, *42*(1), 168–178. https://doi.org/10.3758/BRM.42.1.168

Maranesi, M., Livi, A., Fogassi, L., Rizzolatti, G., & Bonini, L. (2014). Mirror neuron activation prior to action observation in a predictable context. *Journal of Neuroscience*, *34*(45), 14827–14832. https://doi.org/10.1523/JNEUROSCI.2705-14.2014

Michael, J., Sandberg, K., Skewes, J., Wolf, T., Blicher, J., Overgaard, M., & Frith, C. D. (2014). Continuous Theta-Burst Stimulation Demonstrates a Causal Role of Premotor Homunculus in Action Understanding. *Psychological Science*, *25*(4), 963–972. https://doi.org/10.1177/0956797613520608/ASSET/IMAGES/LARGE/10.1177_0956797613520608-FIG2.JPEG

Miniussi, C., Ruzzoli, M., & Walsh, V. (2010). The mechanism of transcranial magnetic stimulation in cognition. *Cortex*, *46*(1), 128–130. https://doi.org/10.1016/J.CORTEX.2009.03.004

Moss, F., Ward, L. M., & Sannita, W. G. (2004). Stochastic resonance and sensory information processing: a tutorial and review of application. *Clinical Neurophysiology*, *115*(2), 267–281. https://doi.org/10.1016/J.CLINPH.2003.09.014

Neri, P., Morrone, M. C., & Burr, D. C. (1998). Seeing biological motion. *Nature 1998 395:6705*, *395*(6705), 894–896. https://doi.org/10.1038/27661

Pavlova, M. A. (2012). Biological Motion Processing as a Hallmark of Social Cognition. *Cerebral Cortex*, *22*(5), 981–995. https://doi.org/10.1093/CERCOR/BHR156

Pelli, D. G., & Vision, S. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Perini, F., Cattaneo, L., Carrasco, M., & Schwarzbach, J. v. (2012). Occipital Transcranial Magnetic Stimulation Has an Activity-Dependent Suppressive Effect. *Journal of Neuroscience*, *32*(36), 12361–12365. https://doi.org/10.1523/JNEUROSCI.5864-11.2012

Ptak, R., Schnider, A., & Fellrath, J. (2017). The Dorsal Frontoparietal Network: A Core System for Emulated Action. *Trends in Cognitive Sciences*, *21*(8), 589–599. https://doi.org/10.1016/J.TICS.2017.05.002

Rossi, S., Hallett, M., Rossini, P. M., Pascual-Leone, A., Avanzini, G., Bestmann, S., Berardelli, A., Brewer, C., Canli, T., Cantello, R., Chen, R., Classen, J., Demitrack, M., di

Lazzaro, V., Epstein, C. M., George, M. S., Fregni, F., Ilmoniemi, R., Jalinous, R., … Ziemann, U. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, *120*(12), 2008–2039. https://doi.org/10.1016/J.CLINPH.2009.08.016

Ruzzoli, M., Abrahamyan, A., Clifford, C. W. G., Marzi, C. A., Miniussi, C., & Harris, J. A. (2011). The effect of TMS on visual motion sensitivity: an increase in neural noise or a decrease in signal strength? *Journal of Neurophysiology*, *106*(1), 138–143. https://doi.org/10.1152/JN.00746.2010

Ruzzoli, M., Marzi, C. A., & Miniussi, C. (2010). The neural mechanisms of the effects of transcranial magnetic stimulation on perception. *Journal of Neurophysiology*, *103*(6), 2982–2989. https://doi.org/10.1152/jn.01096.2009

Salge, J. H., Pollmann, S., & Reeder, R. R. (2020). Anomalous visual experience is linked to perceptual uncertainty and visual imagery vividness. *Psychological Research 2020 85:5*, *85*(5), 1848–1865. https://doi.org/10.1007/S00426-020-01364-7

Schilbach, L., Hoffstaedter, F., Müller, V., Cieslik, E. C., Goya-Maldonado, R., Trost, S., Sorg, C., Riedl, V., Jardri, R., Sommer, I., Kogler, L., Derntl, B., Gruber, O., & Eickhoff, S. B. (2016). Transdiagnostic commonalities and differences in resting state functional connectivity of the default mode network in schizophrenia and major depression. *NeuroImage: Clinical*, *10*, 326–335. https://doi.org/10.1016/J.NICL.2015.11.021

Schubotz, R. I. (2007). Prediction of external events with our motor system: towards a new framework. *Trends in Cognitive Sciences*, *11*(5), 211–218. https://doi.org/10.1016/J.TICS.2007.02.006

Schütz-Bosbach, S., & Prinz, W. (2007). Prospective coding in event representation. *Cognitive Processing*, *8*(2), 93–102. https://doi.org/10.1007/S10339-007-0167-X/METRICS

Schwarzkopf, D. S., Silvanto, J., & Rees, G. (2011). Stochastic Resonance Effects Reveal the Neural Mechanisms of Transcranial Magnetic Stimulation. *Journal of Neuroscience*, *31*(9), 3143–3147. https://doi.org/10.1523/JNEUROSCI.4863-10.2011

Silvanto, J., Muggleton, N. G., Cowey, A., & Walsh, V. (2007). Neural adaptation reveals state-dependent effects of transcranial magnetic stimulation. *The European Journal of Neuroscience*, *25*(6), 1874–1881. https://doi.org/10.1111/J.1460-9568.2007.05440.X

Spyder Developer Team (2020) https://www.spyder-ide.org/. Accessed 8 August 2021

Stadler, W., Ott, D. V. M., Springer, A., Schubotz, R. I., Schütz-Bosbach, S., & Prinz, W. (2012). Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. *Frontiers in Human Neuroscience*, *6*(FEBRUARY 2012), 1–11. https://doi.org/10.3389/fnhum.2012.00020

Tarasi, L., Magosso, E., Ricci, G., Ursino, M., & Romei, V. (2021). The directionality of fronto-posterior brain connectivity is associated with the degree of individual autistic traits. *Brain Sciences*, *11*(11). https://doi.org/10.3390/brainsci11111443

Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron*, *31*(1), 155–165. https://doi.org/10.1016/S0896-6273(01)00337-3

Urgesi, C., Maieron, M., Avenanti, A., Tidoni, E., Fabbro, F., & Aglioti, S. M. (2010). Simulating the future of actions in the human corticospinal system. *Cerebral Cortex*, *20*(11), 2511–2521. https://doi.org/10.1093/cercor/bhp292

van Kemenade, B. M., Muggleton, N., Walsh, V., & Saygin, A. P. (2012). Effects of TMS over Premotor and Superior Temporal Cortices on Biological Motion Perception. *Journal of Cognitive Neuroscience*, *24*(4), 896–904. https://doi.org/10.1162/JOCN_A_00194

Van Rossum, G., Drake, F.L. (2009). *Python 3 reference manual*. CreateSpace, Scotts Valley

Vanrie, J., Dekeyser, M., & Verfaillie, K. (2004). Bistability and Biasing Effects in the Perception of Ambiguous Point-Light Walkers. *Http://Dx.Doi.Org/10.1068/P5004*, *33*(5), 547–560. https://doi.org/10.1068/P5004

Varrier, R. S., & Finn, E. S. (2022). Seeing Social: A Neural Signature for Conscious Perception of Social Interactions. *Journal of Neuroscience*, *42*(49), 9211–9226. https://doi.org/10.1523/JNEUROSCI.0859-22.2022

Veale, J. F. (2013). Edinburgh Handedness Inventory – Short Form: A revised version based on confirmatory factor analysis. *Http://Dx.Doi.Org/10.1080/1357650X.2013.783045*, *19*(2), 164–177. https://doi.org/10.1080/1357650X.2013.783045

Vilidaite, G., & Baker, D. H. (2018). Psychophysical measurement of the effects and non-effects of TMS on contrast perception. *Brain Stimulation*, *11*(4), 956–957. https://doi.org/10.1016/j.brs.2018.04.005

von der Lühe, T., Manera, V., Barisic, I., Becchio, C., Vogeley, K., & Schilbach, L. (2016). Interpersonal predictive coding, not action perception, is impaired in autism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1693). https://doi.org/10.1098/RSTB.2015.0373

Walsh, V., & Cowey, A. (2000). Transcranial magnetic stimulation and cognitive neuroscience. *Nature Reviews. Neuroscience*, *1*(1), 73–80. https://doi.org/10.1038/35036239

Wheaton, K. J., Thompson, J. C., Syngeniotis, A., Abbott, D. F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *NeuroImage*, *22*(1), 277–288. https://doi.org/10.1016/J.NEUROIMAGE.2003.12.043

Zillekens, I. C., Brandi, M. L., Lahnakoski, J. M., Koul, A., Manera, V., Becchio, C., & Schilbach, L. (2019). Increased functional coupling of the left amygdala and medial prefrontal cortex during the perception of communicative point-light stimuli. *Social Cognitive and Affective Neuroscience*, *14*(1), 97–107. https://doi.org/10.1093/scan/nsy105