



Research report

Understanding communicative actions: A repetitive TMS study

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ABSTRACT

Despite the ambiguity inherent in human communication, people are remarkably efficient in establishing mutual understanding. Studying how people communicate in novel settings provides a window into the mechanisms supporting the human competence to rapidly generate and understand novel shared symbols, a fundamental property of human communication. Previous work indicates that the right posterior superior temporal sulcus (pSTS) is involved when people understand the intended meaning of novel communicative actions. Here, we set out to test whether normal functioning of this cerebral structure is required for understanding novel communicative actions using inhibitory low-frequency repetitive transcranial magnetic stimulation (rTMS). A factorial experimental design contrasted two tightly matched stimulation sites (right pSTS vs left MT+, i.e., a contiguous homotopic task-relevant region) and tasks (a communicative task vs a visual tracking task that used the same sequences of stimuli). Overall task performance was not affected by rTMS, whereas changes in task performance over time were disrupted according to TMS site and task combinations. Namely, rTMS over pSTS led to a diminished ability to improve action understanding on the basis of recent communicative history, while rTMS over MT+ perturbed improvement in visual tracking over trials. These findings qualify the contributions of the right pSTS to human communicative abilities, showing that this region might be necessary for incorporating previous knowledge, accumulated during interactions with a communicative partner, to constrain the inferential process that leads to action understanding.

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1. Introduction

Human referential communication involves selecting behaviors that allow an addressee to recognize the communicative intentions of those behaviors (Levelt, 1989; Levinson, 2006). In everyday communication, we largely exploit pre-established shared symbols built in a common language to make those intentions accessible to our interlocutors. Yet, even within such a conventional symbol system, those intentions still need to be inferred from multiple semantic ambiguities present in every utterance (Levinson, 2006). This study aims at characterizing a neural mechanism that supports the inferential processes required for human referential communication (Cutica, Bucciarelli, & Bara, 2006; Noordzij et al., 2009; Sabbagh, 1999).

Given that human referential communication rides on a large background of pragmatic inferences, several authors have started to study these inferential abilities under situations in which shared symbols are not available and their occurrence can be experimentally controlled (Galantucci & Garrod, 2011; de Ruiter et al., 2010). This work has shown that the right posterior superior temporal sulcus (pSTS) is an important element of the cerebral system supporting human referential communication, both for communicators generating novel signals as well as for addressees trying to decode those signals (Cleret de Langavant et al., 2011; Gao, Scholl, & McCarthy, 2012; Mashal, Faust, Hendler, & Jung-Beeman, 2007; Noordzij et al., 2009, 2010). However, it remains to be seen whether unperturbed functioning of pSTS is necessary for inferring the intentions of communicative behaviors, in particular when those intentions cannot be retrieved on the basis of conventional symbols. Here, we address this issue by temporarily disrupting neural function in the right pSTS by using low-frequency repetitive transcranial magnetic stimulation (rTMS), in the context of a task requiring participants to infer the meaning of novel referential communicative behaviors. We aim at qualifying the nature of the right pSTS contributions to communicative inferences by analyzing the alterations caused by a transient interference with neural activity in this region, as compared to those evoked by a control task, or after inhibition of a control region.

The involvement of the right pSTS in establishing a novel referential communicative system is one among several contributions associated with this region, including the perception of biological motion and goal directed actions, moral judgments, and mental state attribution (Arfeller et al., 2013; Bahnemann, Dziobek, Prehn, Wolf, & Heekeren, 2010; Grossman, Battelli, & Pascual-Leone, 2005; Shultz, Lee, Pelphrey, & McCarthy, 2011). This heterogeneity might reflect superficial differences of an underlying unitary function. The right pSTS might generate predictions based on the integration of current sensory stimuli with domain-independent priors (Jakobs et al., 2012; Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005), as suggested by its involvement with predictions pertaining to different domains [e.g., body schema (Blanke et al., 2005; Grossman et al., 2005), gravity (Bosco, Carrozzo, & Lacquaniti, 2008), and beliefs (Young, Camprodon, Hauser, Pascual-Leone, & Saxe, 2010)]. Although this predictive function could be an instance of a

general Bayesian inference mechanism (Friston, 2010; Friston, Kilner, & Harrison, 2006), the pSTS appears to be distinctively able to construct predictions based on information from several different categories. This property appears particularly well suited for handling the domain-independent abductions that are required when producing and interpreting novel symbols (Fodor, 2000; Quine, 1960). We reasoned that those predictions could capture (1) sensory predictions based on statistical regularities of the sensory stimuli experienced by the participants, as implied in some accounts of human communication (Iacoboni, 2005; Schippers, Roebroek, Renken, Nanetti, & Keysers, 2010; Tognoli, Lagarde, DeGuzman, & Kelso, 2007; Turesson & Ghazanfar, 2011); (2) conceptual predictions based on semantic conventions, as established by the participants during the experiment (Schultz et al., 2005; Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009; Young et al., 2010); or (3) conceptual predictions based on a dynamic context shared among communicators, as determined by the trial-by-trial adjustments of the participants to the intended meaning of the stimuli (Menenti, Pickering, & Garrod, 2012). The first possibility would suggest that rTMS over the right pSTS alters performance across different tasks that use the same timeseries of sensory stimuli. The second possibility would suggest rTMS-related alterations that are a function of the overall level of proficiency in a communication task. We indexed proficiency as the number of correct responses per unit time [Efficiency (Machizawa & Driver, 2011; Nixon, Lawton-Craddock, Tivis, & Ceballos, 2007; Townsend & Ashby, 1983; Woltz & Was, 2006)]. The third possibility would suggest rTMS-related alterations that depend on the recent history of communicative interactions of the participants. We indexed these dynamic adjustments in communicative proficiency as the rate of change in Efficiency over trials (Efficiency Rate).

In this study, participants' abilities to comprehend novel communicative actions were quantified in a controlled and validated experimental setting; the Tacit Communication Game (TCG; Fig. 1A) (Blokpoel et al., 2012; Newman-Norlund et al., 2009; de Ruiter et al., 2010). In this interactive task, two players are asked to recreate a spatial configuration of two simple geometrical shapes (one for the Communicator and one for the Addressee) on a digital game board. Crucially, this spatial configuration is shown to the Communicator only (trial epoch 1 in Fig. 1A). This requires the Communicator to convey, and the Addressee to comprehend, the position and orientation of the Addressee's shape. The only means the players had to communicate is with an unconventional tool, namely by moving their simple geometrical shape. Different pairs of participants solve these novel communicative problems in different ways (Blokpoel et al., 2012; de Ruiter et al., 2010), an indication that pairs mutually converge on a common solution from a potentially infinite set of possible arbitrary solutions (van Rooij et al., 2011). This feature of the task makes it possible to isolate adjustments in communicative performance driven by the recent history of interactions between participants from overall variations in communicative performance, and their interaction with stable cognitive traits. Those traits are an important source of inter-subject variance in communicative abilities. For instance,

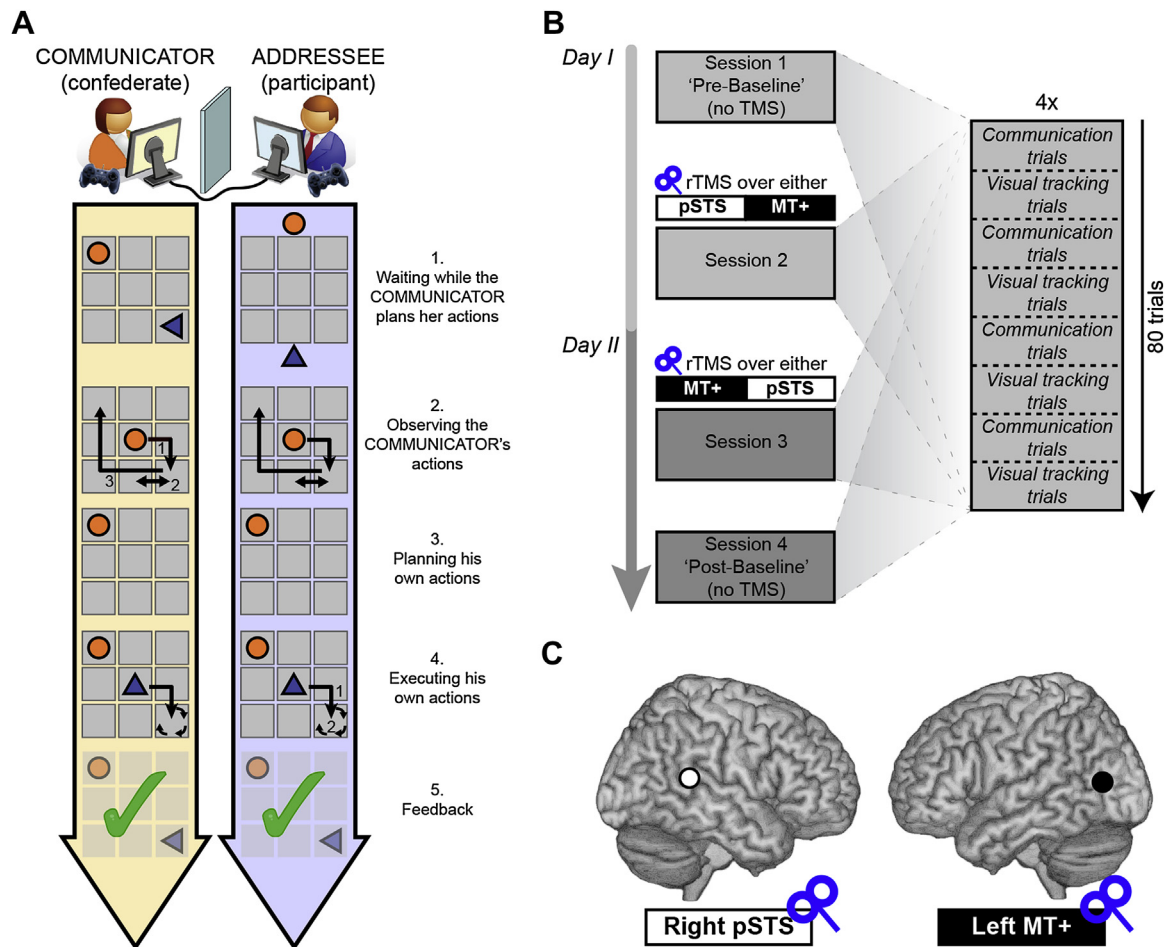


Fig. 1 – Task setup. (A) Example communication trial in which both players had to jointly reproduce a spatial configuration of two tokens presented to the first player in turn only, i.e., the Communicator (epoch 1). A participant, the Addressee, had to infer from the Communicator's actions (epoch 2, orange token, starting at the center) where and how to position his token (blue). During a visual tracking trial involving the same sequence of events (not shown), the participant viewed identical actions but with the instruction to determine the grid location last visited twice or rotated at by his co-player. (B) The experiment consisted of four sessions spread over 2 separate days. Participants received TMS at 1 Hz for 20 min just prior to task performance in sessions 2 and 3. The order of stimulation sites was counterbalanced across participants. Each session encompassed 80 trials organized by type (Communication, Visual tracking) into eight blocks of 10 trials and with the order counterbalanced across participants. (C) Whole-brain visualization of stimulation sites; right pSTS [white dot, MNI coordinates: (50, -42, 14)] and left MT+ [black dot (-43, -70, 10)].

Addressee's performance on the Raven's progressive matrices test (Raven, 1989, 2000) predicts how quickly a communicative pair establishes novel shared symbols (Volman, Noordzij, & Toni, 2012). Accordingly, we used this psychometric index to characterize the inferential processes supported by the right pSTS during referential communication. Namely, Addressees with high Raven's scores might more readily use abstract relations to quickly generate novel analogical mappings between observed actions and their communicative intentions (Blokpoel et al., 2012; Carpenter, Just, & Shell, 1990; Volman et al., 2012). We reasoned that if rTMS over right pSTS influences Addressees' ability to quickly grasp novel communicative meanings according to recent communicative interactions (see Hypothesis #3 above), then Addressees with high Raven's scores might

be particularly impaired by rTMS-induced cerebral alterations.

Specificity of the rTMS intervention was ensured by controlling for the communicative relevance of the stimuli and for the cerebral location of the intervention, across four different experimental sessions. Functionally, we assessed the effects of rTMS during a visual tracking task that used exactly the same timeseries of stimuli shown during the communication task, but with no communicative requirements. Anatomically, we contrasted the effects of stimulating the right pSTS with those evoked by stimulating a contiguous homotopic region involved in integrating position information when viewing moving objects [left MT+ (Bosco et al., 2008; Maus, Ward, Nijhawan, & Whitney, 2013)], a function required for processing the stimuli used during the communication and the visual tracking tasks.

2. Materials and methods

2.1. Participants

Thirteen right-handed healthy adults (18–28 years, mean = 22, seven women) with normal or corrected-to-normal vision participated in this study. Participants were screened for contra-indications of TMS and gave written informed consent according to the institutional guidelines of the local ethics committee (Committee on Research Involving Human Subjects, Region Arnhem-Nijmegen, The Netherlands). They received written instructions for each experimental task and were either offered a financial payment or given credits toward completing a course requirement as a compensation for their participation.

2.2. Experimental design

Participants performed two tasks: a communication task and a visual tracking task. The task that the participants were currently performing was indicated throughout the relevant trials on the participants' screen. Each task involved two players, i.e., a participant and a co-player, two geometrical shapes ("tokens"), and two hand-held game controllers. In both tasks the participants observed the movements of the co-player's token, namely horizontal translations, vertical translations or 90° clockwise rotations on a visually presented 3 × 3 digital grid (the "game board"). The co-player was facing another 19 inch monitor in the same sound-proof experimental room. The participants and the co-player were not otherwise allowed to interact with each other.

During the communication trials both players had to jointly reproduce a spatial configuration of two tokens presented to the co-player only (trial epoch 1 in Fig. 1A). The participant observed the communicative actions of the co-player, the Communicator, to infer the target position and orientation of his token (epoch 2). A yellow bar signaled the end of the Communicator's movements and indicated that the participant's turn had started. The participant (the Addressee) had unlimited time to plan his actions (but was instructed to plan as fast as possible, epoch 3). After pressing the start button, the participant had 5 sec to move his token from the center grid position toward the inferred target position and orientation (epoch 4). When the participant pressed the start button again (and within a maximum movement time of 5 sec), feedback was presented to both players to indicate whether they had jointly reproduced the target configuration (epoch 5).

During the visual tracking trials, the participant observed the token's movements on the grid, as during the communication trials. However, the participant was told that in these tracking trials the co-player was instructed to move across predetermined grid locations. The task of the participant was to move his token to the grid location last visited twice by the co-player before she completed her movements. Grid locations where the co-player rotated her token twice were also considered as "visited twice". After moving to the grid location last visited twice, the participants were asked to rotate their token twice on that location. If the co-player had not visited or

rotated at any location twice during her movements, the participant had to visit the center grid location and rotate twice. After 5 sec or when he pressed the start button, feedback was presented to indicate whether the participant had successfully completed the trial according to the task instructions.

Unbeknownst to the participants, the co-player was a confederate that was only pretending to control her token with the game controller. In fact, during both tasks the co-player actions were identical, namely pre-recorded token movements reproducing frequently used strategies identified in previous studies involving this task setting (Blokpoel et al., 2012; Noordzij et al., 2009; de Ruiter et al., 2010). For instance, in case the Communicator's token was orientation specific (i.e., a rectangle or triangle, but not a circle), the Communicator went to the Addressee's target position, rotated her token to indicate the target orientation of the Addressee's token, and then moved to her own target position completing her part of the target configuration. In case her token was a circle, the Communicator first went to the Addressee's target position and briefly waited. Then she wiggled a couple of times (e.g., repeating the number 2 action in trial epoch 2 – Fig. 1A) to indicate the target orientation of the Addressee's token, and then moved to her own target position. Occasionally, she did not wiggle when such an action was redundant given a situation in which the target orientation matched that of the begin orientation of the receiver token.

An experiment consisted of four sessions (Fig. 1B) spread over 2 separate days (~2 weeks separation) and lasted about 5 h in total. An initial familiarization block preceded the two sessions on the first day (~35 min) and another familiarization block those on the second day (~5 min). Each session encompassed 80 trials (~15 min) organized by type (Communication, Visual tracking) into eight blocks of 10 trials (Fig. 1B). The participants alternated between the two types on a block-by-block basis with the order counterbalanced across participants. Two sessions with no prior stimulation were used to determine pre-stimulation and post-stimulation baselines. These sessions took place ~1 h before session 2 and ~1 h after session 3 respectively. The participants received low-frequency rTMS over right pSTS or left MT+ (~20 min, Fig. 1C) just prior to task performance in sessions 2 and 3 which were recorded on separate days. For each participant the moment of the two TMS interventions was matched for the time of the day (± 1.5 h). The order of stimulation site was counterbalanced across participants.

2.3. TMS protocol

The pulses were administered offline, i.e., prior to task performance, to induce a temporally stable and task-independent modulation of local cortical processing efficiency. The stimulation sites in the right pSTS and left MT+ were selected on the basis of the peak voxel (group contrast, Communicative > Non-Communicative) reported in a previous fMRI study with the communication task [right pSTS, MNI coordinates: (50, -42, 14) (Noordzij et al., 2009)], and on the basis of the mean spatial location reported in a cytoarchitectonic analysis of the human extrastriate cortex [left MT+ (-43, -70, 10) (Malikovic et al., 2007)]. Restricting the stimulation of

this control area to the opposite hemisphere as our experimental site of interest minimizes the possibility of cortical spread across stimulation sites as a result of the repetitive stimulation (Paus et al., 1997).

High-resolution anatomical images were acquired using an MP-RAGE sequence on a separate day (176 slices, TE/TR = 3.68/2.25 sec, voxel size $1 \times 1 \times 1$ mm). These images were spatially normalized to standard MNI space using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK) and used to calibrate a frameless stereotactic system (BrainSight, Rogue Research Inc.), linking each participant's structural scan and stimulation sites. By means of neuronavigation the TMS coil was positioned over the relevant brain location (either right pSTS or left MT+). TMS was then delivered using a biphasic Magstim Super Rapid Stimulator (Magstim Company Ltd., Whitland, UK), using a figure-of-eight coil with a diameter of 70 mm. We applied a 20 min train of repetitive low-frequency (1 Hz) stimulation at 60% maximum stimulator output (Grossman et al., 2005). Previous studies have shown that 1 Hz stimulation temporarily reduces metabolic activity by 5–30% (Mottaghy et al., 2002; Valero-Cabre, Payne, & Pascual-Leone, 2007) and excitability of the cortex within the stimulated area (Boroojerdi, Prager, Muellbacher, & Cohen, 2000).

2.4. Cognitive traits

A recent study (Volman et al., 2012) shows that the ability of a pair of communicators to establish novel shared symbols is predicted by the Communicator's score on the Need for Cognition Scale [NCS; (Cacioppo, Petty, & Kao, 1984)] and by the Addressee's score on the Raven's progressive matrices test (Raven, 1989, 2000). The score on the Raven test is a non-verbal measure of fluid reasoning, in which participants solve up to 36 problem items with increasing difficulty in 20 min. Each item of this test consists of three series of three images. The last of the three series lacks the third image and has to be filled out by the participant choosing from one of eight options. Solving problems in the Raven test is thought to capture cognitive processes related to encoding and inferring regularities in the test items. This test is thought to distinguish individuals on their ability to induce abstract relations and to handle a large set of problem-solving goals in working memory (Carpenter et al., 1990). Accordingly, we reasoned that if rTMS over right pSTS influences Addressees' ability to quickly grasp novel communicative meanings according to recent communicative interactions (see Hypothesis #3 in Introduction), then Addressees with high Raven's scores might be particularly impaired by rTMS-induced cerebral alterations. Namely, Addressees with high Raven's scores might more readily use abstract relations to generate novel mappings between observed actions and their communicative intentions (Blokpoel et al., 2012; Carpenter et al., 1990; Volman et al., 2012). Participants' Raven's scores were therefore expected to account for a significant portion of inter-individual variability in task performance during the communication trials (Volman et al., 2012), both before and after rTMS. To assess the specificity of the cognitive traits captured by the Raven, we also asked the Addressees tested in this experiment to complete the Need for Cognition questionnaire [NCS; (Cacioppo et al., 1984), translated in Dutch], a personality

questionnaire consisting of 18 statements targeting participants' intrinsic motivation to solve cognitive challenges. The psychometric assessments were completed by the participants on the second day, between the third and fourth sessions.

2.5. Data analysis

Planning times and accuracies on both tasks were recorded by Presentation software (Neurobehavioral Systems, Albany, CA, USA) and analyzed offline using custom MATLAB code (MathWorks, Natick, MA, USA). Participants' planning time was defined as the interval in seconds starting after the Communicator's movement interval and ending when the participant pressed the start button (epoch 3 in Fig. 1A). Accuracy refers to the percentage of successfully accomplished trials. In order to consider the combined effects of both measures of task performance, we used Efficiency [i.e., Accuracy/Planning time; see (Machizawa & Driver, 2011; Nixon et al., 2007; Townsend & Ashby, 1983; Woltz & Was, 2006)] and Efficiency Rate [$d(\text{Efficiency})/d(\text{trials})$]. Efficiency increases with greater accuracies and smaller planning times and it indicates the number of correct responses per unit time. Efficiency Rate indicates the rate of change in Efficiency over trials, i.e., the benefits from task experience gained during preceding trials in a session, calculated as the beta value of a linear regression of Efficiency across the 40 task-specific trials of each experimental session. To ensure that the data adheres to the assumption of normality, we filtered the planning times and accuracies (which is a binomial measure) with a moving average of seven trials prior to estimating the regression. This approach allows a robust estimate of the overall (linear) trend across an experimental session that is sensitive to sustained changes in performance rather than single-trial errors. A positive rate indicates an improvement in task performance over trials.

We analyzed the effect of experimental manipulations on Efficiency and Efficiency Rate in two steps. First, we tested whether participants improved their performance in either task over the course of the experiment. Showing changes in performance between the pre- and post-stimulation baseline sessions excludes that floor or ceiling effects prevent the detection of rTMS-related effects in task performance in the intervening stimulation sessions (Fig. 1B). Accordingly, the effects of Task (Communication, Visual tracking) and Time (Pre-, Post-stimulation baseline) on Efficiency were estimated using a 2×2 repeated-measures analysis of variance (ANOVA). Second, we tested whether rTMS over the right pSTS influenced overall task performance (Efficiency) and within-session changes in task performance (Efficiency Rate). In order to avoid spurious differences between sessions with and without rTMS intervention, we focused this analysis on sessions 2 and 3, i.e., sessions with prior rTMS intervention. Accordingly, the effects of Task (Communication, Visual tracking) and TMS site (pSTS, MT+) on Efficiency and Efficiency Rate were estimated using a 2×2 repeated-measures analysis of covariance (ANCOVA). The covariates in this analysis considered the inter-subject variance accounted for by the order of stimulation (e.g., session 2: pSTS; session 3: MT+; or viceversa) and cognitive traits (i.e., mean-centered

psychometric scores on Raven and NCS, see Section 2.4). By adding the interaction terms between the covariates and the within-subject variables to the model we test whether the hypothesized within-subject interaction between Task and TMS site is affected by each subject covariates scores (Anstey et al., 2007; Delaney & Maxwell, 1981). The significant results ($p < .05$) are reported.

3. Results

Prior to any stimulation participants were able to successfully accomplish each task well above chance level (conservative estimate of chance level over nine game board locations: 11%). The percentage of correct responses at pre-stimulation baseline was $85 \pm 3\%$ and $86 \pm 3\%$ (mean \pm standard error of the mean) for the communication task and the visual tracking task respectively.

We compared task performance before and after the rTMS intervention (pre-baseline and post-baseline sessions, see Fig. 1) to assess the presence of overall learning effects. A repeated-measures ANOVA on Efficiency revealed main effects of Task [Communication, Visual tracking: $F_{(1,12)} = 5.2$, $p = .042$, effect size partial $\eta^2 = .30$] and Time [Pre-, Post-stimulation baseline: $F_{(1,12)} = 25.1$, $p < .001$, partial $\eta^2 = .68$]. These results indicate that the visual tracking task (mean Efficiency over both baseline sessions: .85), was more difficult than the communication task (mean Efficiency: .96), and that the participants became more proficient over the course of the experiment (see Fig. 2). Crucially, there was no interaction effect between Task and Time factors on the Efficiency index. This finding suggests that the overall learning rates from initial baseline (session 1) to final learned performance (session 4) of the two tasks are well comparable. This result allows for an unbiased assessment of whether Efficiency and Efficiency Rate during task learning (sessions 2 and 3) are affected by TMS perturbation.

We then assessed the influence of rTMS-induced cerebral alterations on the level of task performance during sessions 2 and 3, as captured by the measure of Efficiency, and on the

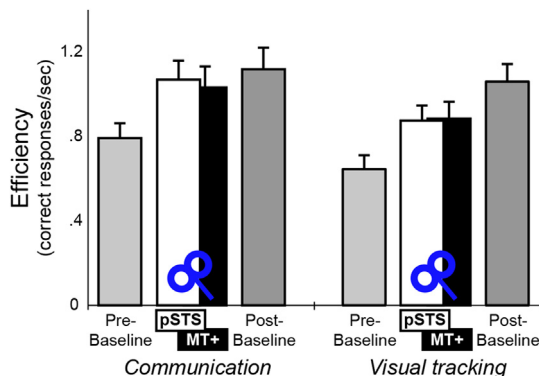


Fig. 2 – Group results for Efficiency on the communication and visual tracking task. Participants became more proficient at each task over the course of the experiment. There was no interaction of Task and TMS site (right pSTS, left MT+). Error bars indicate 1 standard error of the mean.

ability to benefit from task experience gained during preceding trials in a same session, as captured by the Efficiency Rate. A repeated-measures ANCOVA on Efficiency (covariates: order of stimulation site, Raven and NCS scores) revealed a main effect of Task (Communication, Visual tracking), $F_{(1,9)} = 11.8$, $p = .008$, partial $\eta^2 = .57$, and an interaction effect of TMS site (pSTS, MT+) and stimulation order, $F_{(1,9)} = 8.0$, $p = .020$, partial $\eta^2 = .47$. These results indicate that the two tasks differed in complexity also in the rTMS sessions, and that the order of rTMS intervention (session 2: pSTS; session 3: MT+; or vice-versa) had a strong impact on mean performance across both tasks.

Importantly, following TMS to the pSTS, there was less improvement over trials (smaller Efficiency Rate) in the communicative setting than following TMS to MT+ or over visual tracking trials, $F_{(1,9)} = 6.4$, $p = .032$, partial $\eta^2 = .42$. Thus, the interaction between Task (Communication, Visual tracking) and TMS site (pSTS, MT+) did not have an effect on Efficiency (Fig. 2), but it did have an effect on the Efficiency Rate (see Fig. 3A). Furthermore, this interaction effect was affected by a participant's score on the Raven test, as indicated by an interaction of Task, TMS site, and Raven, $F_{(1,9)} = 5.6$, $p = .042$, partial $\eta^2 = .39$. There were no other statistically significant main or interaction effects, all $p > .12$.

In a post-hoc analysis of the simple effects constituting this interaction we observed a strong negative association between the Raven test score and the Efficiency Rate at the communication task, $r_s = -.695$, $p = .008$, but not at the visual tracking task following TMS over pSTS, $r_s = .169$, $p = .6$ (see Fig. 3B), as indicated by Spearman's rank-order correlation. Further post-hoc exploration of the relation between Raven's scores and performance in both tasks indicated that there was a statistically significant positive correlation between the Raven test score and the Efficiency Rate at the communication task during the pre-stimulation baseline, $r_s = .657$, $p = .015$. This result indicates that individuals that quickly grasped novel communicative meanings according to recent communicative interactions before receiving rTMS, were also most affected by rTMS over pSTS during the communication task. There were no other significant correlations between the Raven and the Efficiency Rate, or the Efficiency, across any of the other sessions.

4. Discussion

This study was designed to investigate whether a functionally intact right pSTS is necessary for understanding the intention of novel communicative actions. We used an experimental setting where an Addressee needs to disambiguate communicative and instrumental components of the movements of a communicative partner, and find a relation between the communicator's movements and their meaning. Mimicking the movements of the communicative partner (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Tognoli et al., 2007) or following low-level statistical regularities in the stimulus material (Pickering & Garrod, 2004) are not viable options for solving this task. Rather, the absence of pre-existing conventions encourages the Addressee to use higher-order conceptual structures when inferring meaning from the

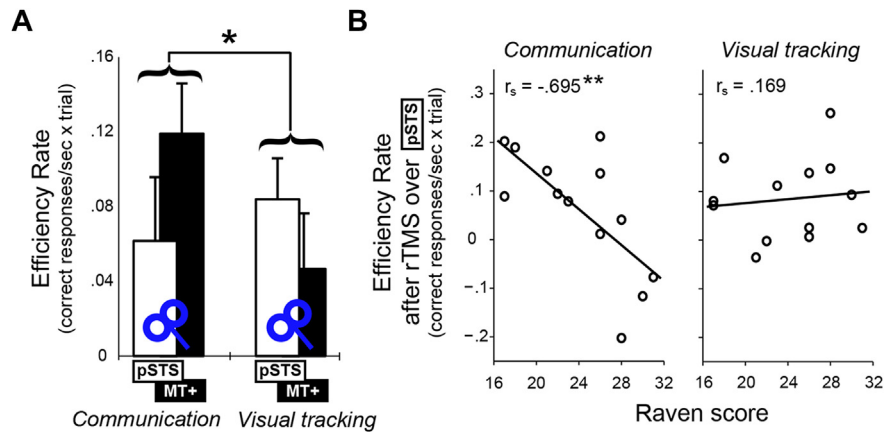


Fig. 3 – Group results for Efficiency Rate on the communication and visual tracking task. (A) Efficiency Rate on the communication and visual tracking task with prior rTMS. A positive rate indicates an improvement in task performance over trials. Asterisk (*) indicates a significant interaction between Task (Communication, Visual tracking) and TMS site (right pSTS, left MT+) on the Efficiency Rate ($p < .05$). Error bars indicate 1 standard error of the mean. (B) Scatter plots of individuals' Raven's score against Efficiency Rate during performance of the communication and the visual tracking task, following rTMS over right pSTS. Black line: least-square regression line; r_s : Spearman rank correlation coefficient; ** $p < .01$.

observed movements (van Rooij et al., 2011). We targeted the right pSTS given that previous studies indicated increased metabolic activity in this region when subjects made those communicative inferences (Noordzij et al., 2009). There are two main results. First, rTMS over the right pSTS reduced participants' ability to improve their task efficiency during the course of the communicative interactions. This impairment of Efficiency Rate was functionally and anatomically specific. Functionally, the impairment occurred in relation to corresponding effects in a visual tracking task that used exactly the same sequences of stimuli. Anatomically, the impairment occurred in relation to rTMS effects on a contiguous homotopic temporal region (left MT+). Second, the magnitude of the rTMS effect over right pSTS was particularly strong in those Addressees with high Raven's scores. The analogical movement-meaning mappings established by those participants might be less sensitive to the continuously changing surface structure of the communicative problems (Volman et al., 2012). This observation suggests that alterations of the right pSTS are particularly disruptive for those participants that under normal circumstances process the movements of their communicative partner according to abstract relations. Taken together, these observations indicate that the contribution of the right pSTS to communicative inferences is dynamic and conceptual in nature. This finding qualifies the suggestion that the right pSTS integrates current sensory stimuli with internalized contextual priors (Jakobs et al., 2012; Schultz et al., 2005), by showing that this region is involved in updating higher-order predictions on sensory material according to the recent history of communicative interactions.

4.1. Interpretational issues

It could be argued that the significant within-session effect on communicative performance (as indexed by the Efficiency Rate) should have given rise to a detectable between-sessions effect on Efficiency, i.e., reduced Efficiency between pre- and

post-stimulation baseline sessions. However, this subtle effect is likely lost in the large between-sessions variance (partly owing to the order of stimulation site) and unspecific improvements in efficiency across sessions. Accordingly, we cannot completely exclude that the pSTS plays a role in specifying predictions based on invariant meanings of the communicative stimuli (see Hypothesis #2 in Introduction).

The analyses focused on those sessions preceded by rTMS interventions and with comparable tasks experience. The differential effects observed between pSTS and MT+ stimulation on performance of the communication and visual tracking task raise the question of how the stimulation effects compare to a sham or null baseline session involving the same experience with the tasks. The existing baseline sessions (sessions 1 and 4) cannot be used for this comparison, given that these were not matched for experience with the tasks. An additional (fifth) session without rTMS might have been included in the experimental design, but we refrained from doing so given that it is debatable whether a null or a sham session can provide an interpretable control for TMS studies (Dräger, Breitenstein, Helmke, Kamping, & Knecht, 2004). For instance, incidental effects of TMS (stimulation noise, somatosensation on the head) have been found to influence task performance in multiple ways (Duecker & Sack, 2013). Future experiments using neurostimulation techniques with more selective sham controls [e.g., transcranial direct current stimulation; (O'Shea et al., 2013)] might be able to better address this issue.

It could be argued that the strong improvements in performance of the communication task during the first experimental session (pre-stimulation baseline) caused participants with relatively high Raven's score to reach a performance ceiling. Accordingly, the relative alteration of their communicative behavior in the subsequent session would be a consequence of that performance ceiling, rather than of the rTMS intervention. Two observations argue against this possibility. First, task performance continued to improve in the

post-stimulation baseline (session 4, see Fig. 2). Second, if participants with high Raven scores were at ceiling level after the first session, while participants with relatively low Raven scores still had room for improvement on the communication task, then there should have been a negative relation between the Raven scores and Efficiency Rate when MT+ was stimulated. In fact, this relation was absent, and there were clear improvements in communicative performance across the group when MT+ was stimulated. Accordingly, the disruption in communicative performance observed in participants with high Raven's scores is more consistent with the notion that alterations of the right pSTS are particularly disruptive for those participants that under normal circumstances process the movements of their communicative partner according to abstract relations.

It could be argued that the relative decline in Efficiency Rate of the communication task after rTMS over pSTS is unspecific, since a similar decline was observed in the visual tracking task after rTMS over MT+. In fact, this finding reinforces the notion that pSTS effects are specifically tuned to sensory stimuli processed in a communicative framework, since the two tasks used exactly the same stimuli. By the same token, this finding emphasizes that MT+ is also involved in predicting stimulus characteristics (and changes thereof) relevant for the visual tracking task (Beintema & Lappe, 2002; Sterzer, Haynes, & Rees, 2006), for instance movement patterns that can be used to predict which grid location is visited twice (see Fig. 1).

4.2. Relevance for human communication

Although the current findings were obtained under experimental conditions that purposely limited the availability of pre-existing shared symbols among communicators, we believe that this work is relevant for understanding the contribution of the right pSTS to a fundamental property of human communication, namely how humans rapidly create those shared symbols from scratch (Evans & Levinson, 2009; Tomasello, 2008). The ability to quickly build new semiotic conventions and re-configure existing ones emerges at different levels of human communication, from infants learning a language without access to the local communicative conventions, to adults disambiguating semantic relations according to pragmatic cues (van Berkum, van den Brink, Tesink, Kos, & Hagoort, 2008; Egidi & Caramazza, 2013). Even during a simple conversation, we continuously update and sharpen conceptual predictions on sensory material according to the recent history of the communicative interaction (Menenti et al., 2012). The present findings increase our understanding of the neural mechanisms of human communication by showing that the right pSTS, in contrast to MT+, is necessary for continuously adjusting those priors according to the recent history of interactions of the communicators, over and above the statistical regularities of the sensory stimuli experienced by the participants (that are also present in the control task). This suggests that human communicative abilities operate on conceptual inferences, rather than sensorimotor brain-to-brain couplings (Hasson et al., 2012), and that those conceptual inferences are continuously updated. This suggestion fits well with the temporal dynamics of neural

activity observed in this region, namely context-dependent neuronal upregulation emerging already before the occurrence of communicative stimuli, and further transient responses to incoming visual information (Stolk et al., 2013). It remains to be seen whether the right pSTS supports the dynamic updating of communicative inferences also when communication relies on linguistic material with strongly established semantic conventions (van Ackeren, Casasanto, Bekkering, Hagoort, & Rueschemeyer, 2012; Mitchell, Ames, Jenkins, & Banaji, 2009; Willems et al., 2010).

5. Conclusion

This study uses rTMS to investigate the necessity and nature of the contributions of the right pSTS to human communication. General task performance was not affected by rTMS, whereas task learning was disrupted depending on the interaction of TMS site and Task. Namely, rTMS over pSTS led to a diminished ability to improve action understanding on the basis of recent communicative history, while rTMS over MT+ perturbed improvement of visual tracking. These findings qualify the contributions of the right pSTS to human communicative abilities, showing that this region might be necessary for incorporating previous knowledge, accumulated during interactions with a communicative partner, to constrain the inferential process that leads to action understanding.

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