

Gamma-band activity in the human superior temporal sulcus during mentalizing from nonverbal social cues

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Abstract

The posterior superior temporal sulcus (pSTS) is a key structure for our ability to infer others' mental states based on social cues including facial expressions, body posture, and gestures ("mentalizing"), but the neural mechanisms of this ability remain largely unknown. We recorded electrocorticogram directly from the pSTS in humans to show that enhanced neural oscillations in the gamma frequency range (35–55 Hz) accompany mentalizing. One patient with a lesion in pSTS was tested behaviorally on this task; he was unable to infer a virtual character's preferences from nonverbal social cues. Enhanced coherent gamma oscillations in the patients with intact pSTS may reflect a process by which social signals are bound into a unified representation to support mentalizing. This may be relevant for other social cognitive processes, as well as to the study of autism spectrum disorders, for which both mentalizing deficits and abnormal gamma activity have been reported.

Descriptors: Social cognition, Intracranial EEG, Gamma band, Superior temporal sulcus, Mentalizing

During most of our social interactions, we humans quickly and often accurately assess the desires and motives of those around us, using verbal and nonverbal social cues, including facial expressions, body posture, and gestures (Frith & Frith, 2006). The posterior superior temporal sulcus (pSTS) has been not only identified as a key structure for the perception and interpretation of socially salient bodily or facial cues (Allison, Puce, & McCarthy, 2000; Keysers & Perrett, 2004), but has also been described as a key node of the neural network involved in the ability to infer other person's mental states (Frith & Frith, 2003), also called "mentalizing." Other important structures of this neural network include the medial frontal cortex and temporal poles (Amodio & Frith, 2006; Frith & Frith, 1999). Functional magnetic resonance imaging (fMRI) studies have shown pSTS activation during mentalizing tasks (Brunet, Sarfati, Hardy-Bayle, & Decety, 2003; Gallagher & Frith, 2004; Gallagher et al., 2000; Schulte-Ruther, Markowitsch, Fink, & Piefke, 2007; Völlm et al., 2006), viewing stimuli of other persons' intentions or

expressive gestures and faces (Gallagher & Frith, 2004; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001), viewing animate entities (Castelli, Happe, Frith, & Frith, 2000; Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005), observing other persons' actions (Pelphrey, Adolphs, & Morris, 2004; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004), and viewing biological motion (Bonda, Petrides, Ostry, & Evans, 1996; Grossman & Blake, 2002). Studies of humans with lesions to pSTS show that its structural integrity is necessary for representing others' beliefs in video- and story-based false belief tasks (Aperly, Samson, Chiavarino, & Humphreys, 2004; Samson, Aperly, Chiavarino, & Humphreys, 2004) as well as for discriminating eye gaze direction (Akiyama et al., 2006).

However, the neural mechanisms by which mentalizing is computed within the pSTS and in other brain regions involved remain largely unknown. Functional MRI has a slow temporal resolution and measures blood flow instead of electrophysiological activity, and thus can provide only limited insight into the neural mechanisms that might support mentalizing in the pSTS. A few event-related electroencephalogram (EEG) potential studies have investigated the timing and topographical distribution of mentalizing processes (Liu, Sabbagh, Gehring, & Wellman, 2004; Sabbagh, Moulson, & Harkness, 2004; Sabbagh & Taylor, 2000). For example, Liu et al. recorded EEG during a nonverbal mentalizing task (the false-belief task). The authors found a late ERP component with a left frontal scalp distribution (with a possible generator in the anterior prefrontal cortex) that was associated with a judgment about someone else's beliefs. Decoding

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mental states from facial expressions also recruits fronto-temporal networks (Sabbagh et al., 2004). Although these studies shed some light on the timing and surface topography of electrophysiological activity associated with mentalizing, surface-recorded event-related potentials have poor spatial resolution, and, due to decreased signal-to-noise from conduction through different tissues, it is difficult to resolve relatively high-frequency neural oscillations (i.e., the synchronous and rhythmic firing of cell assemblies). Such oscillations are thought to act as the “glue” that binds neural assemblies at both local and distal levels (Engel & Singer, 2001; von der Malsburg, 1995). In particular, oscillations in the gamma range ($\sim 30\text{--}80$ Hz) are thought to coordinate the timing of both local and distal neural networks (Engel & Singer, 2001; Fries, Nikolic, & Singer, 2007; Jensen & Colgin, 2007; Karakas, Basar-Eroglu, Ozesmi, Kafadar, & Erzen, 2001; Melloni et al., 2007).

We hypothesized that during mentalizing, the pSTS might utilize neural oscillations to coordinate and synchronize incoming signals; this might bind disparate social cues to help form a unified and coherent representation of someone else’s mental state (e.g., Grossmann, Johnson, Farroni, & Csibra, 2007). To examine this hypothesis, we recorded neural activity directly from the pSTS of four patients who had electrodes implanted for presurgical evaluation of epilepsy. Intracranial electrocorticogram (ECoG) provides a rare opportunity to examine cortical activity at a spatial and temporal resolution not provided by noninvasive means. We conducted frequency transforms of intracranial ECoG data recorded while patients were engaged in a mentalizing task, in which they had to infer the preferences of virtual characters from non-verbal social cues (gesture, body posture, facial expression), or, in control conditions, indicate their own preferences or the spatial locations of objects. We also behaviorally tested a patient who had a lesion in the pSTS. These complementary methods provide converging evidence for the necessity and nature of electrophysiological activity within the pSTS for mentalizing.

Thus, we had two primary research goals. The first was to examine the neural mechanisms that are employed by the pSTS during mentalizing. We were particularly interested in the gamma frequency band, but also examined activity in other frequency bands. The second goal was to compare mentalizing to other forms of perspective taking, such as spatial perspective taking. The pSTS has been implicated in both mental (Gallagher & Frith, 2004; Schulte-Ruther et al., 2007; Völlm et al., 2006) and spatial perspective taking (e.g., Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006). This latter research question is also in part derived from the developmental psychology literature: Evidence from developmental (e.g., Flavell, Everett, Croft, & Flavell, 1981; Flavell, Shipstead, & Croft, 1978; Saxe, Carey, & Kanwisher, 2004) and comparative (Povinelli & Eddy, 1996; Tomasello, Call, & Hare, 2003; Tomasello, Carpenter, Call, Behne, & Moll, 2005) psychology suggests a dissociation between the two kinds of perspective taking in terms of developmental/evolutionary trajectories, which would suggest a difference in their neuro-functional bases.

Methods

Patients

Five patients with pharmacoresistant epilepsy participated in the study, four with electrodes implanted over the lateral temporal cortex/inferior parietal cortex (see Figure 3, below, for localization of electrodes) (patients GS: female, 29 years old; NB: male,

56 years old; HR: female, 56 years old, LU: male, 54 years old), and one with a lesion in the pSTS (patient AA: male, 26 years old; see Supplemental Figure S1 for localization of the lesion). Recordings were performed at the Department of Epileptology, University of Bonn, Germany, and were approved by the local ethics committee. No seizure occurred in any of the patients during the 24 h preceding the experiment. The location of electrode placement was made entirely on clinical grounds. The electrodes reported here were not identified as positive seizure origins in any of the patients.

Electrode Selection and Localization

To select an electrode from each patient, we examined the task-induced (i.e., baseline-corrected) gamma power across all trials in all conditions and selected the electrode with maximal gamma power for further analyses. This selection procedure thus identified electrodes that covered cortex with maximal task-related gamma activity and was blind to task condition. This approach of anatomical constraints and hypothesis-independent functional identification is commonly used, especially in cases of strong *a priori* hypotheses regarding particular anatomical regions (Axmacher et al., 2007; Fell et al., 2001; Mormann et al., 2005). This is an appropriate approach because (1) the number of electrodes is large compared to the number of patients; (2) due to interpatient variability in electrode placement and functional cortical anatomy, it is not possible to use only an anatomical selection procedure; and (3) this reduces the possibility of type I errors because we are not searching for the effect of interest from among all possible electrodes (some patients had electrodes over additional regions outside the pSTS). In Figure 3, below, we display the implantation electrode schema and selected electrode (electrode with red arrow) for each patient. Note that the chosen electrodes are roughly in the same location across patients, even though our selection procedure was blind to anatomical location. These locations can be compared with a meta-analysis of published neuroimaging studies of biological motion provided in Figure 3 of Allison et al. (2000). Based on previous neuroimaging and intracranial findings, it appears as if mentalizing engages regions throughout the pSTS (Allison et al., 2000; David et al., 2008). We note that others have used the terms “pSTS” and “temporal-parietal-junction (TPJ)” synonymously (Aichhorn et al., 2006; Castelli et al., 2000), despite suggestions of a functional differentiation (Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Saxe, 2006). Because we did not have a sufficient number of patients with electrodes over the TPJ, delineating possible functional dissociations was not possible. We use the term “pSTS” because it is anatomically descriptive and thus adequate with respect to our actual study. Along a similar vein, because of the small number of patients, possible hemisphere differences were not examined (e.g., Pelphrey, Singerman, Allison, & McCarthy, 2003).

The electrical signal picked up by the electrodes is largely but not entirely locally generated; because the amplitude of field potentials decays with the inverse square of distance (Morris & Luders, 1985), a neural generator 1 cm away from the electrode will contribute about 0.01% of a generator 0.1 cm away.

Task

Patients sat comfortably in a chair in an ECoG testing room designed to monitor ECoG and other biophysical signals. The experiment was run on a laptop computer using Presentation software and was placed on a movable table in front of the

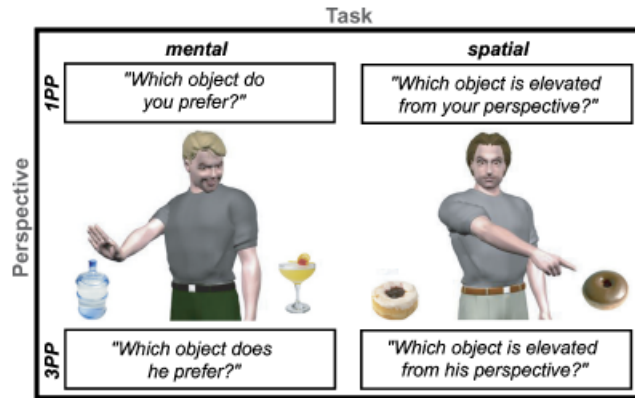


Figure 1. Overview of task.

patients approximately 60 cm in front of the patient. The laptop was equipped with a parallel trigger cable, which delivered square wave pulses to the ECoG recording device and provides milli-second precision about experiment event timing.

The experiment was conducted in four sessions, separated by brief rest periods. There were four experimental conditions, each repeated twice per session. Each session contained 72 trials. During each trial, a stimulus was displayed for 4000 ms followed by a 1000 ms intertrial interval. Instructions were shown for 6 s at the beginning of each session. Subjects practiced the task during an introductory session before data recordings. Stimuli were designed using Poser (Version 6, Curious Labs, Inc.), Photo Objects (Vol. 1, Hemera Technologies, Inc.), and Adobe Photoshop CS (Version 8.0.1, Adobe Systems, Inc.). The stimuli depicted a virtual character (“avatar”) surrounded by two different objects of the same object category (Figure 1). Object categories were chosen randomly (food, animals, tools, clothes, etc.). The objects showed a subtle difference in position, with one object located higher compared to the other object. Avatars expressed preferences to one of the two objects by combinations of different facial expressions (positive, negative, neutral), gestures (positive, negative, no gesture), and body positions (turned toward or away from the object, neutral position).

Patients were asked to perform two different tasks from two different perspectives (i.e., 2×2 factorial design). During the mentalizing task, the patients indicated the object they themselves preferred (mental first-person perspective; *1PP mental*) or the object the avatar preferred (mental third-person perspective; *3PP mental*). The use of face, gesture, or body stimuli as explicit operationalizations of mental perspective taking or mentalizing is common and established (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001; Gallagher & Frith, 2004; Schulte-Ruther et al., 2007). During the visual-spatial task, the patients indicated the elevated object from their own visual-spatial perspective (*1PP spatial*) or the avatar’s perspective (*3PP spatial*). During 3PP spatial, patients were instructed to perform a mental transformation of their own spatial egocentric perspective onto the avatar’s spatial perspective (Blanke & Arzy, 2005; Blanke et al., 2005; Parsons, 1987; Vogeley & Fink, 2003). Note that 3PP spatial involved a viewer rotation, which is different from object rotation (Vogeley & Fink, 2003; Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999). During the 3PP mental condition, patients were asked to indicate the object as seen from their own perspective in order not to confound 3PP mental with 3PP

spatial. This operationalization had the advantage of testing mental and spatial perspective taking without changing visual input: Stimuli were the same for all four conditions and thus differed only by their instructions. The instructions were: “Which object is elevated from your perspective?” (*1PP spatial*), “Which object is elevated from his perspective?” (*3PP spatial*), “Which object do you prefer?” (*1PP mental*), and “Which object does he prefer?” (*3PP mental*) (Figure 1). All responses involved left–right judgments and were indicated by pressing a corresponding mouse button. Correct responses were counter-balanced and systematically varied with respect to the side of object elevation and avatars’ preferences.

Operationally, we define “mentalizing” as the process of extracting the avatar’s preference for one of the two objects, which must be inferred based on the avatar’s facial expression, body posture, and gesture, and which together constitute a global impression of the avatar’s preference. Mental states (intentions, beliefs, desires, thoughts, etc.) can be expressed in many different ways (e.g., prosody, eye gaze, gestures, language). Here we focused on nonverbal, socially salient signals, namely facial expression, gestures, and body orientation, all of which convey a virtual character’s predilection for a given object in the environment. The use of faces, gestures, and body position as stimulus material is a common and established operationalization of mentalizing (e.g., Baron-Cohen et al., 2001; Gallagher & Frith, 2004; Schulte-Ruther et al., 2007; Völlm et al., 2006). In the critical mentalizing condition—*3PP mental*—the salience of the character’s preference depended on the congruence of facial expression, gesture, and body position and was not homogenous or uniform throughout; thus, it was not possible to solve the task by attending to only one feature or other simple rule-based strategies (also see Discussion).

Behavioral Analyses

Behavioral data were analyzed using the Statistical Package for the Social Sciences (SPSS for Windows; Version 12.0). Dependent variables were reaction times (RT) and accuracy (percentage of correct responses). It was not possible to determine accuracy for the *1PP mental* condition, as responses reflected subjective preferences. To account for outliers in RTs, we calculated the median RT for each condition epoch (which appeared twice in each session) and then averaged across sessions. Patient AA asked not to complete the fourth session; thus, his data include the first three sessions only (216 trials in total). The percentage of correct answers was averaged across sessions for each participant. To assess whether accuracy deviated from chance levels within each patient, we used binomial probability distributions. The null hypothesis was that correct answers were given with a probability of 0.5. The binomial probability distribution provides cumulative probabilities for each number of correct answers. This test allowed us to examine the performance of individual patients in each condition. We used the function `binopdf.m` in the Matlab statistics toolbox. To test for differences in RTs or accuracy between conditions (i.e., reflecting task difficulty) that could account for differences in neural activity, the Wilcoxon’s matched pairs test was computed.

ECoG Recording and Analyses

Depth ECoG recordings were referenced to linked mastoids, recorded at a sampling rate of 1000 Hz, band-pass filtered (0.01 Hz [6 dB/octave] to 300 Hz [12 dB/octave]) and digitally decimated to 500 Hz off-line. All analyses and illustrations were conducted

in Matlab 6.5, utilizing software written by the authors. Time-frequency decomposition was conducted via wavelet analysis, in which the ECoG time series was convolved with a set of complex Morlet wavelets, defined as a Gaussian-windowed complex sine wave: $e^{i2\pi ft} e^{-t^2/(2\sigma^2)}$. t is time and f is frequency, which increased from 3 to 100 Hz in 70 logarithmically spaced steps. σ defines the width of each frequency band and was set according to $5/(2\pi f)$. 5 corresponds to the number of wavelet cycles and provided a good trade-off between time and frequency resolution. We also explored other values, ranging from 3 to 10; the resulting time-frequency maps were similar for values in this range. After convolution of the wavelet with the ECoG, power was defined as the modulus of the resulting complex signal $Z[t]$ (power time series: $p(t) = \text{real}[z(t)]^2 + \text{imag}[z(t)]^2$). The baseline was defined as average frequency power from -400 to -200 ms prior to the onset of each trial. This was done to avoid potential overlap of wavelets covering pre- and poststimulus activity; the results were similar when using a -200 - to 0 -ms baseline. Finally, task-induced power time courses were normalized by converting the baseline-corrected signal to a decibel (dB) scale ($10 * \log_{10}[\text{task/baseline}]$); this allows a direct comparison of effects across frequency bands.

Statistics

To compare oscillation power across conditions, we used a “tiling” method, in which activity differences between conditions were assessed within specified time-frequency tiles (i.e., windows). The idea is that under the null hypothesis of no differences between conditions, there is an equal number of pixels (where one pixel is one point in time-frequency space) with negative and positive values. If the conditions differ significantly from each other, the distribution of pixels will not be uniform about zero, but instead will be shifted to the left or right, depending on which condition elicits more oscillation power. Thus, we calculated the difference between conditions (e.g., 3PP mental vs. 3PP spatial) at each pixel, averaged across patients, and then tested whether the distribution of pixels in each time-frequency region was different from that expected by the null hypothesis of no differences between conditions, using a binomial distribution test. We used the following frequency bands (in hertz): 4–8 (theta), 8–13 (alpha), 13–33 (beta), 35–55 (gamma), 60–90 (upper gamma). We used the following time bands (in seconds): 0–1, 1–2, 2–3, 3–4. This tiling method is appropriate because of the large number of time-frequency space pixels compared to the number of patients. To control for Type I errors, we used a false-discovery-rate map-wise corrected threshold (Genovese, Lazar, & Nichols, 2002) of $p < .01$ across tiles. Because the number of possible statistical comparison exceeds the number of patients, we focus on the results that are of a priori theoretical interest and motivation.

Results

Behavioral Performance

The four patients with intact pSTS performed well on the task, with high accuracy in all conditions (Figure 2). This pattern of performance was similar to what we have observed in healthy control subjects in a separate study (David et al., 2008). For patient AA (suffering from a pSTS lesion), accuracy was significantly above chance in both 3PP spatial and 1PP spatial (binomial test, $p < .01$). However, this was not the case during the 3PP mental condition ($p = .446$; see blue line in Figure 2). Thus, performance was disproportionately poor when he had to infer

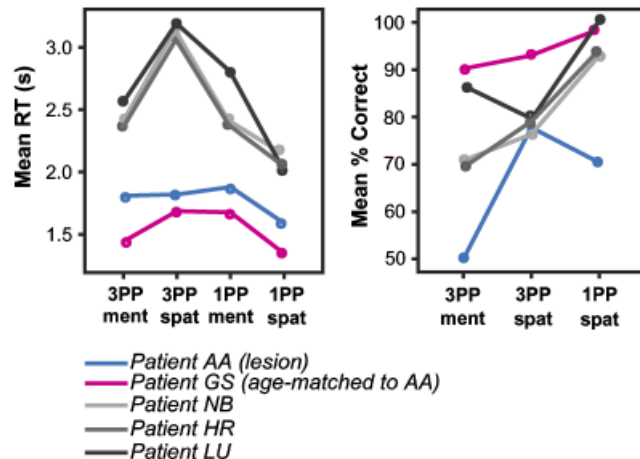


Figure 2. Behavioral performance. Percent correct is not displayed for the 1PP mental condition because it involved a subjective judgment about which object the patients preferred. Patient AA (27 years) is plotted against the age-matched patient GS (28 years) and the three older patients (54–56 years).

the avatar’s preference. Reaction time was not significantly different between patient AA and the other patients (Mann Whitney U test, $p > .10$), demonstrating that all patients were engaged in the task to a similar degree of cognitive demand (Figure 2). Neither RTs nor accuracy differed significantly among conditions (Wilcoxon matched pairs test, $p > .07$ for all pairwise comparisons).

Time-Frequency Analyses

The behavioral findings confirm that structural integrity of the pSTS is necessary for correctly inferring the preferences of other individuals (Samson et al., 2004). We next examined the ECoG of the other four patients to gain insight into what neural processes within the pSTS might support mentalizing. As discussed in the Methods section, we chose one electrode from each patient according to an anatomical/functional selection procedure. Interestingly, the electrodes that exhibited maximum gamma activity were in nearly the same pSTS region in all four patients (Figure 3). The location of these electrodes is also similar to those reported in other related intracranial ECoG, functional MRI, and surface ECoG studies (Allison et al., 2000; Blanke & Arzy, 2005; Gobbini et al., 2007; Sabbagh et al., 2004).

In all experiment conditions, we observed significant task-induced increases in gamma oscillation power (especially around 35–55 Hz) throughout the entire trial, as well as decreases in alpha/beta oscillation power (5–20 Hz; Figure 4a). The commonalities across conditions are not surprising, considering we designed the experiment such that stimuli were the same across all conditions.

The most relevant conditions to compare in terms of mentalizing are the 3PP mental versus 3PP spatial conditions; in both conditions, the patients needed to think about the task from the avatar’s point of view, but only during 3PP mental trials did the patients need to mentalize and infer the avatar’s preference. The 3PP mental condition was associated with significantly (FDR-corrected $p < .01$) enhanced gamma activity (35–55 Hz) throughout the entire trial, as well as suppressed alpha activity (8–12 Hz) and suppressed upper gamma activity (60–90 Hz) toward the end of the trial (Figure 4b,c). The differences in lower gamma remained significant until the end of the trial (4 s) and thus are not

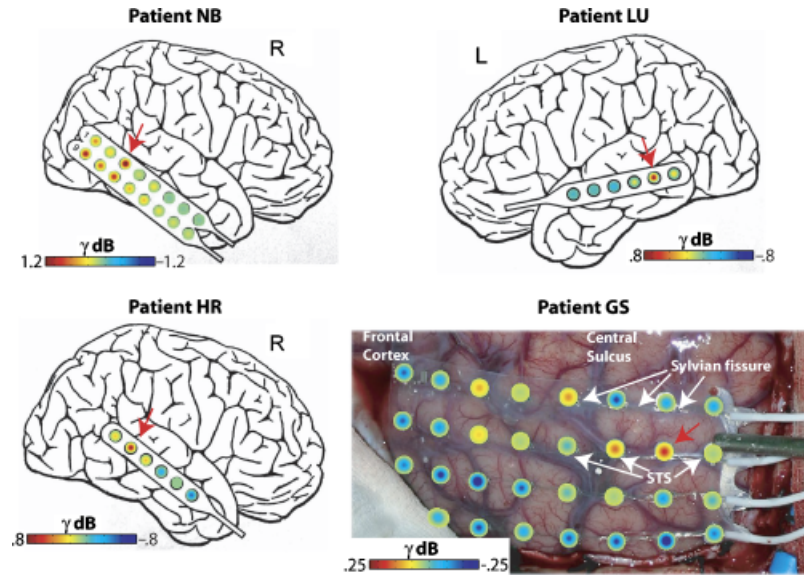


Figure 3. Topographical distribution of task-related (averaging over all conditions) gamma oscillation (30–90 Hz) power. Red arrows point to electrodes used for statistical analyses and plotting. An intra-operative picture was available only for patient GS.

likely due to early visual or motor processes. There was a modest increase in gamma power during 1PP mental compared to 1PP spatial conditions, but this was not statistically significant over time and frequency (Supplemental Figure S2).

Discussion

The primary goal of the present study was to investigate the electrophysiological mechanisms in the pSTS that might support mentalizing (the ability to infer mental states of others) from nonverbal social cues. Results demonstrated significantly increased neural oscillations in the gamma frequency range in the pSTS associated with this mentalizing task. In concordance with

this main result, one patient with a lesioned pSTS was selectively impaired in mentalizing.

The human pSTS region has been anatomically described as the cortex within the STS and including cortices on surfaces of the adjacent superior and middle temporal gyri as well as angular gyrus (e.g., Pelphrey et al., 2004). Several authors have associated activity (measured through functional MRI) in the pSTS with tasks related to the detection of animate entities (Blakemore et al., 2003; Castelli et al., 2000; Schultz et al., 2005), nonverbal mentalizing (Brunet et al., 2003), and perception of expressive faces (Narumoto et al., 2001) or expressive gestures (Gallagher & Frith, 2004). All of these tasks, including our own, used stimuli that implicated the perception of social cues and the interpretation of such cues for the understanding of other people's behavior

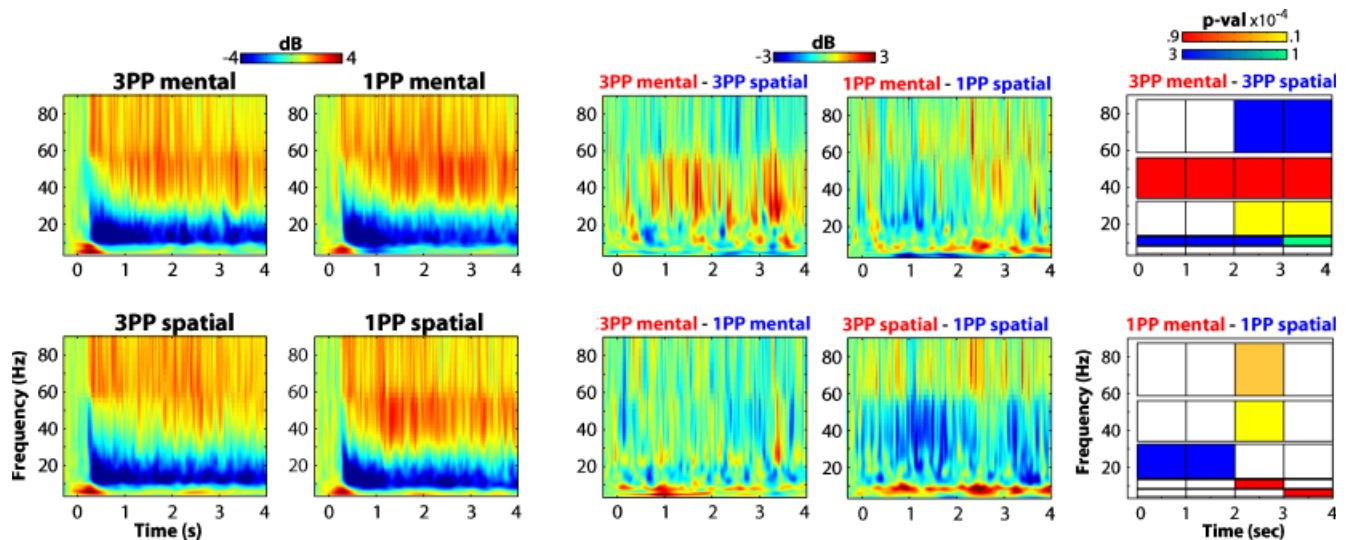


Figure 4. ECoG oscillation power results from pSTS of four patients. a: Task-induced changes in oscillatory power over time (x-axis) and frequency (y-axis). b: Differences in oscillation power between conditions. c: Regions in time-frequency space in which significantly enhanced (red/yellow) and suppressed (blue/green) activity was observed during mentalizing (3PP mental compared with 3PP spatial). Other statistical contrasts are displayed in the Supplemental Information.

and mental states. Based on available research, it seems that one important function of the pSTS is the analysis of higher representational and socially relevant signals by decoding changeable aspects of visual social information such as of body orientation, gestures, or faces that may convey another person's mental states such as intentions, preferences, or beliefs.

These data provide novel evidence for the role of gamma oscillations in the pSTS for mentalizing during social cognition. Gamma oscillations were present during all trial types, but were significantly more pronounced during 3PP mental trials. Oscillations are largely driven by rhythmic interneuron activity, which helps coordinate spike timing (Mann & Paulsen, 2007), thus synchronizing neurons into functional assemblies, or neural networks, which might help form complex representations or transfer and control the flow of information (Benucci, Frazor, & Carandini, 2007; Fries et al., 2007; Rubino, Robbins, & Hatsopoulos, 2006; Singer, 1999; Steriade, 2006). In terms of pSTS gamma activity, all task conditions induced increased gamma activity compared to the pretask baseline. Thus, gamma activity appears to play an important role in the functioning of this region in general. However, there was significantly enhanced gamma activity during 3PP mental condition compared to its control condition, 3PP spatial. This difference appears stronger during 3PP than during 1PP conditions, because the analogous statistical comparison (1PP mental vs. 1PP spatial) yielded only one significant tile in the gamma range and no significant suppression of alpha activity. These differences in gamma activity cannot be accounted for by differences in the difficulty of conditions, because the patients' performance between conditions did not significantly differ (e.g., RTs were relatively largest for 3PP spatial, whereas accuracy was relatively poorest for 3PP mental).

We suggest that this increased gamma band activity reflects a neural mechanism by which mentalizing is supported. By this mechanism, visually complex and socially salient signals may converge in the pSTS; coherent gamma oscillations may help unite these signals into a coherent representation that allows for reasoning about other people's mental states. This proposal links findings from the pSTS to animal research implicating gamma activity in binding sensory representations (Engel & Singer, 2001; von der Malsburg, 1995) and is consistent with previous studies that have demonstrated increased gamma activity during socially relevant situations, for example in babies viewing faces that are looking directly at them (Grossmann et al., 2007).

In addition to changes in gamma power, we observed changes in the alpha band that mirrored the gamma effects but in the opposite direction. Alpha suppression was particularly associated with mentalizing about others: There was more suppression for 3PP mental than for 1PP mental, as well as more suppression for 3PP mental compared to 3PP spatial. The significant alpha suppression may be functionally related to mu rhythm activity: Mu suppression has been implicated in the mirror neuron system and biological motion perception (Bernier, Dawson, Webb, & Murias, 2007; Oberman et al., 2005; Oberman, Ramachandran, & Pineda, 2008; Ulloa & Pineda, 2007). However, the term "mu" generally refers to activity over motor and sensory-motor electrodes (Babiloni et al., 1999; Muthukumaraswamy & Johnson, 2004), so we cannot determine whether the alpha suppression corresponds to motor-related mu activity. Another possibility is that the alpha suppression was related to posterior alpha suppression as seen in EEG studies. This alpha suppression has been interpreted to reflect the engagement of complex cognitive processes (Klimesch, Sauseng, & Hanslmayr, 2007). Posterior alpha

activity is thought to originate in relatively posterior occipital regions such as striate and extrastriate cortex (Lind, Flor-Henry, & Koles, 1999; Lopes da Silva, 2004; Michel, Lehmann, Henggeler, & Brandeis, 1992), but some source localization studies have also identified possible contributors in posterior temporal cortex (Liljestrom, Kujala, Jensen, & Salmelin, 2005; Lin et al., 2004).

Our lesion data complemented the ECoG findings: The condition with the largest increases in gamma power (3PP mental) was associated with patient AA's most severe impairment. Neither the age-matched patient GS (who demonstrated almost perfect performance) nor the older but gender-matched patients LU and NB showed this drastic drop in performance. The present finding is comparable to previous case studies that reported belief-reasoning—but no executive function or working memory deficits—associated with lesions in the TPJ (which is in close proximity to the pSTS; Samson et al., 2004) and deficits in eye gaze discrimination due to a lesion of pSTS itself (Akiyama et al., 2006). Thus, the present finding adds to recent research supporting the idea that pSTS is necessary for some aspects of mentalizing (Brunet et al., 2003; David et al., 2008; Gallagher & Frith, 2004; Gallagher et al., 2000; Schulte-Ruther et al., 2007; Völlm et al., 2006), and together with the intracranial ECoG results suggests that pSTS gamma may be a critical neural mechanism underlying this important social process.

Previous studies of mentalizing processes using surface EEG recordings have demonstrated that activity distributed over fronto-temporal electrode sites is associated with inferring others' beliefs and reading others' facial expressions (Liu et al., 2004; Sabbagh & Taylor, 2000; Sabbagh et al., 2004). In some cases, this activity was estimated to be generated in the middle temporal and orbitofrontal cortices (Sabbagh et al., 2004). In these studies, oscillations were not assessed, although based on our findings and those of Grossmann and colleagues (2007), one might imagine that these event-related potential differences were accompanied by enhanced gamma oscillation power. Two important strengths of intracranial ECoG are the increased spatial resolution and the increased signal-to-noise ratio; these strengths provide the opportunity to localize high frequency oscillations in the cortex (e.g., Figure 3).

These findings have implications for the interpretation of the blood-oxygen-level dependent (BOLD) response often seen in functional MRI studies of mentalizing and related social cognitive processes. Previous studies have shown a correlation between the BOLD response and gamma oscillation power, measured through local field potentials (Lachaux et al., 2007; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Logothetis & Pfeuffer, 2004; Viswanathan & Freeman, 2007), optical imaging (Allen, Pasley, Duong, & Freeman, 2007), and surface ECoG (Foucher, Otzenberger, & Gounot, 2003; Laufs et al., 2003). Although we did not measure these same patients in the task with fMRI, the localization is consistent with related previous studies (Castelli et al., 2000; Gallagher & Frith, 2004; Saxe et al., 2004; Schultz et al., 2005), and with our own previous study, which used the same task in healthy controls and found similar patterns of activation to what we observed in our gamma range (David et al., 2008). We also found that oscillation power in the alpha range (8–12 Hz) showed the opposite pattern of results to gamma; this is also in accordance with previous findings that the BOLD response correlates negatively with alpha power (Brookes et al., 2005; Laufs et al., 2003). Thus, it appears that the pSTS BOLD response in mentalizing tasks reflects both increased gamma and suppressed alpha activity at the same time, among other neurobiological processes that might contribute to the BOLD response.

We acknowledge some limitations of the current study. First, we had only four patients with intracranial ECoG data and only one lesioned patient. However, behavioral results were similar to those of healthy control subjects in the same task, despite differences between the studies in age, health, and methodology (previously functional MRI) (David et al., 2008), suggesting that the ECoG results are generalizable to broader populations. Although in surface EEG or magnetoencephalography (MEG) studies, 10 or more subjects typically are required for adequate signal-to-noise, the superior signal-to-noise and spatial resolution of intracranial ECoG means that fewer subjects are needed for reliable results. For example, in previous reports of intracranial ECoG activity during mentalizing, only one patient was tested (Allison et al., 2000; Blanke et al., 2005). Second, we did not take systematic postexperiment mood ratings, although anecdotally, all patients including AA did not appear ill tempered or incapable of performing the task. Thus, AA's significantly impaired performance (no different than chance levels) during the 3PP mental condition compared to his better-than-chance performance and relatively fast RTs in the other conditions demonstrates a disproportionate difficulty with the 3PP mental condition. This is also in line with several previous reports that have linked pSTS lesions in impaired social cognitive functions including mentalizing (Akiyama et al., 2006; Apperly et al., 2004; Samson et al., 2004). Third, we report activity only from the pSTS, but it is likely that other brain regions played critical roles in this task. For example, as discussed above, neuroimaging literature demonstrates a role of the anterior medial prefrontal cortex in social cognitive processes. Collectively, the pSTS, TPJ, and medial frontal cortex form a neural "mentalizing network" (Frith & Frith, 2003). Indeed, the assumption of a network is strongly supported by evidence on anatomical connectivity in the monkey (Amodio & Frith, 2006; Barbas, Ghashghaei, Dombrowski, & Rempel-Clower, 1999; Carmichael & Price, 1996). We report data only from pSTS because of restrictions in electrode placement, which are made entirely on clinical grounds.

Although in theory it would be possible to perform the 3PP spatial task by first computing the first-person perspective and then inverting the response, patients were specifically instructed

to perform a mental own body transformation. Reaction time data do not favor the alternative hypothesis: Inverting a response should be easier than computing a spatial perspective transformation, and yet reaction times were generally longest for the 3PP spatial condition. Thus, although we cannot definitively rule out whether patients used this strategy, the explicit instructions plus reaction time patterns support the idea that patients performed a mental transformation instead of simply inverting left and right responses. Relatedly, the 3PP spatial condition may have involved an inhibitory cognitive component to suppress an automatic response to the ipsilateral visual stimulus while activating the correct response. This inhibition is inherent in all situations in which one takes another person's perspective (Frith & de Vignemont, 2005; Vogeley & Fink, 2003). However, such inhibitory processes likely also exist during the 3PP mental condition. That is, when judging another person's preferences (3PP mental), one must suppress his or her own personal preferences (Frith & de Vignemont, 2005). Whether and how closely these two expressions of cognitive control are matched could be debated and is outside the scope of this report, but to the extent that they are similar, they were subtracted out in the analyses.

In conclusion, we have demonstrated that significant increases in gamma oscillations and decreases in alpha oscillations in the human pSTS accompany mentalizing about others' preferences as expressed by nonverbal cues. These findings might also be relevant to related processes such as the interpretation of others' facial or gestural expressions, gaze, or body orientation and biological or intentional motion. It previously has been suggested that the pSTS may be especially relevant for processing changeable and movable aspects of socially relevant stimuli that convey an intention or another mental state (Pelphrey et al., 2004). The pSTS, and specifically increased gamma oscillatory activity within the pSTS, may provide critical support for the analysis of socially relevant signals. Finally, our findings may also be relevant to the study of autism spectrum disorders, for which mentalizing deficits, abnormal gamma activity, and hypofunctionality in the pSTS have been reported (Boddaert et al., 2004; Brock, Brown, Boucher, & Rippon, 2002; Brown, Gruber, Boucher, Rippon, & Brock, 2005; Frith & Happe, 2005).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Intra-operative photograph of lesion in patient AA.

Figure S2. Statistics for all comparisons, each thresholded using a FDR map-wise correction level of $p < .01$. Note that some of these data are identical to what is displayed in Fig. 4b; the data are replotted here for ease of comparison.

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