Social gating of sensory information during ongoing communication

Silke Anders [a,*], Yana Heussen [a], Andreas Sprenger [a], John-Dylan Haynes [b,1], Thomas Ethofer [c,d,1]

[a] *Department of Neurology, Universität zu Lübeck, Lübeck, Germany*
[b] *Bernstein Center for Computational Neuroscience Berlin, Charité-Universitätsmedizin, Berlin, Germany*
[c] *Department of Psychiatry, University of Tübingen, Tübingen, Germany*
[d] *Department of Biomedical Magnetic Resonance, University of Tübingen, Tübingen, Germany*

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ABSTRACT

Social context plays an important role in human communication. Depending on the nature of the source, the same communication signal might be processed in fundamentally different ways. However, the selective modulation (or "gating") of the flow of neural information during communication is not fully understood. Here, we use multivoxel pattern analysis (MVPA) and multivoxel connectivity analysis (MVCA), a novel technique that allows to analyse context-dependent changes of the strength interregional coupling between ensembles of voxels, to examine how the human brain differentially gates content-specific sensory information during ongoing perception of communication signals. In a simulated electronic communication experiment, participants received two alternative text messages during fMRI ("happy" or "sad") which they believed had been sent either by their real-life friend outside the scanner or by a computer. A region in the dorsal medial prefrontal cortex (dmPFC) selectively increased its functional coupling with sensory-content encoding regions in the visual cortex when a text message was perceived as being sent by the participant's friend, and decreased its functional coupling with these regions when a text message was perceived as being sent by the computer. Furthermore, the strength of neural encoding of content-specific information of text messages in the dmPFC was modulated by the social tie between the participant and her friend: the more of her spare time a participant reported to spend with her friend the stronger was the neural encoding. This suggests that the human brain selectively gates sensory information into the relevant network for processing the mental states of others, depending on the source of the communication signal.

Introduction

In modern society, humans are not only confronted with various communication signals sent by other humans, but also with a multitude of anonymous signals transmitted by electronic communication devices and the media. Despite their physical similarity, these communication signals might encode very different information, and might require very different processing, depending on the source. Suppose, for example, a person hearing a narrator in the radio and his best friend talking about a car accident that happened that morning. When listening to the radio, the listener is presumably primarily interest in the news. In contrast, when listening to his friend, the listener might try to understand how his friend felt when observing the accident. Thus, just as effective processing of signals from the physical world requires some form of sensory gating (e.g. Knight et al., 1999), effective processing of social signals might require some form of "social gating" that selectively relays information from socially relevant sources to higher stages of neural processing.

Recent advances in application of multivariate pattern-recognition algorithms in neuroimaging (Haynes and Rees, 2006; Kriegeskorte et al., 2006; Norman et al., 2006) have enabled researchers to investigate the processing of communication signals in the human brain at the level of content-specific neural representations. This research has shown that auditory and visual communication signals are parsed into content-related and source-related features early in the processing stream (Formisano et al., 2008; Ethofer et al., 2009; Fox et al., 2009). However, it is currently unknown how such content-specific sensory information is relayed to higher processing stages that enable social cognition.

A longer line of research has shown that when people interact with or make inferences about other people neural activity increases in a neural network (often referred to as "mentalizing network") that includes the medial prefrontal cortex (mPFC), precuneus and the temporo-parietal junction (TPJ) (Frith and Frith, 2003; Gallagher and Frith, 2003; Mitchell, 2009). This increase of neural activity has often been interpreted as reflecting activation of cognitive processes required during social cognition, such as directing attention towards mental

* Corresponding author at: Universität zu Lübeck, Department of Neurology, Ratzeburger Alle 160, 23538 Lübeck, Germany. Fax: +49 451 500 6097.
E-mail address: silke.anders@neuro.uni-luebeck.de (S. Anders).
[1] These authors contributed equally.

states (Gallagher and Frith, 2003; Kampe et al., 2003) or projecting oneself into a different physical or mental world (Mitchell, 2009). Interestingly, a first study using multivoxel pattern analysis to investigate mPFC function provided evidence that the mPFC might not only support specific social cognitive processes, but might also encode content-specific information of communication signals at a supra-modal level (Peelen et al., 2006).

Here, we use a simulated communication experiment to examine how the human brain selectively gates sensory information of communication signals into neural networks that enable social cognition. Participants were made believe that they were receiving two alternative short text messages ("happy" or "sad") from their real-life friend outside the scanner, or from a computer. In order to separate sender-dependent modulation of the flow of neural information from any modulatory effects that might be due to different response requirements, participants were not required to respond to their friends. To map the selective gating of the flow of neural information in the receiver's brain, we first used multivoxel pattern analysis (MVPA, Haynes and Rees, 2006; Kriegeskorte et al., 2006; Norman et al., 2006) to identify brain regions where the sensory content of text messages was encoded independent of the perceived sender, and then searched for brain regions that changed their functional coupling with these sensory-content encoding regions in a sender-dependent manner. For the latter step we used multivoxel connectivity analysis (MVCA), a novel technique that allows to analyse context-dependent changes of the strength of interregional functional coupling between ensembles of voxels.

Materials and methods

Participants

Twenty female participants with no record of neurological or psychiatric disorders were recruited from the Universität zu Lübeck. Participants were asked to bring one of their female friends as communication partner ("sender") to the imaging session. All participants gave written consent before participation and the study was approved by the local Ethics committee (Universität zu Lübeck, Lübeck). Data sets of two participants were later excluded because when explicitly asked after the experiment (see below) they reported doubts that the text messages they had received during imaging had actually been sent by their friend. The final data set consisted of data from 18 participants (age range 19–28 years, mean 22.1 years, 16 right-handed, 2 left-handed). Participants had first met their friend at school (N = 3), university (N = 9), leisure activities (N = 2) or on other occasions (N = 4). At the time of the study, participants had known their friend for an average of 3.4 years (range 6 months to 15 years). To ensure that participants were a representative sample of the population with regard to interpersonal traits all participants were asked to complete a German 16-item version of the *Interpersonal Reactivity Index* (IRI, Davis, 1983), the *Saarbrücker Persönlichkeitsfragebogen* (SPF, http://bildungswissenschaften.uni-saarland.de/personal/paulus/homepage/files/SPF-IRI-_V6.1.pdf). Participants' scores deviated less than one standard deviation (SD) from the norm of their German age reference group (Normentabellen des SPF, http://bildungswissenschaften.uni-saarland.de/personal/paulus/empathy/Normen.pdf, November 21, 2011) on all four subscales (empathic concern, mean = 3.5, SD = 0.6, norm 3.6; fantasy, mean = 3.5, SD = 0.8, norm 3.6; perspective taking, mean = 3.5, SD = 0.6, norm 3.7; personal distress, mean = 2.5, SD = 0.8, norm 2.8).

Cover story

Participants and their friends were told a cover story in order to create an experimental situation in which participants believed they were receiving short text messages sent by either their friend or a computer. Upon arrival in the lab, participants and their friends were informed

that the goal of the study was to investigate the neural mechanisms of short text message communication. They were told that the task of the participant's friend (the "sender") would be to judge the affective state (*happy* or *sad*) of a number of persons, based on photographs of their faces, and to convey each of her decisions by a text message to the participant inside the scanner (the "receiver"). They were then shown the first two trials of a fake experimental set-up in which photographs appeared on a computer screen and, after the "sender" had entered her decision on a keyboard, the corresponding German text message ("*glücklich*" [happy] or "*traurig*" [sad]) appeared on a second screen. They were further told that, on a random basis, photographs would not be evaluated by the participant's friend but by a computer equipped with software for automatic analysis of facial expressions, which would then return the corresponding message to the participant. Finally, participants were told that in some runs the colour of the letters would indicate who had sent the message (i.e. green letters, *friend*; blue letters, *computer*; counterbalanced across participants) while in other runs all messages would be printed in grey letters. The latter runs were part of a different study and data of these runs were not analysed in the current study. The cover story was chosen to ensure that text messages perceived as being sent by the participant's friend and text messages perceived as being sent by the computer were highly similar with regard to (i) visual features, (ii) object of reference (an unknown third person), (iii) content (the third person's affective state, *happy* or *sad*) and (iv) response requirements (participants were not required to respond to the putative sender). Please note that this cover story was intended to allow the identification of visual areas that encode content-specific sensory information during text-message communication, and not to induce widespread empathic responses in the receiver's brain that are typically observed when participants observe an intimate's affective state (e.g. Anders et al., 2011). To ensure that participants attended to the text messages they were asked to indicate by button press after each message who they believed had sent that message. In fact, text messages were presented in a predefined order and the participant's friend was asked to perform an unrelated behavioural experiment while waiting for the participant. To maintain the illusion of the cover story, an error message instead of a text message appeared in a dummy trial after the first third of runs had been completed, and the experimenter suggested to the participant that her friend might have had hit an invalid key on the keyboard and that there would be a short delay because this had to be fixed.

Experimental procedure

Functional image acquisition was divided into sixteen runs. During each run, eight coloured text messages, balanced across the four sender-content combinations (*friend-happy*, *friend-sad*, *computer-happy*, *computer-sad*) (odd runs, 1-3-5-7-9-11-13-15), or twelve grey text messages, balanced across the two contents (*happy* and *sad*) (even runs, 2-4-6-8-10-12-14-16), were presented for 1000 ms each in randomized order. After a delay (2 s or 3.5 s) a response mapping screen appeared for 300 ms (two arrow heads, one pointing to the left and one pointing to the right, one labelled with the friend's first name and the other labelled with "PC"), indicating the participant to convey her response by a response button in her left or right hand, respectively (Fig. 1). Two alternative response mapping screens were used, one with the left and the other with the right arrow head labelled with the participant's first name. Response mapping screens were balanced across the four sender-content combinations and presented in randomized order for each sender-content combination. This way, the participant's decision and subsequent motor response were decoupled. Each trial terminated with a variable inter-trial interval (8.7 to 13.2 s, varying in steps of 1.5 s). Text messages and response mapping screens were presented through MRI-compatible video goggles (VisuaStim, Resonance Technology, Northridge CA, USA) and stimulus presentation and response logging was controlled with Cogent (Wellcome Laboratory of
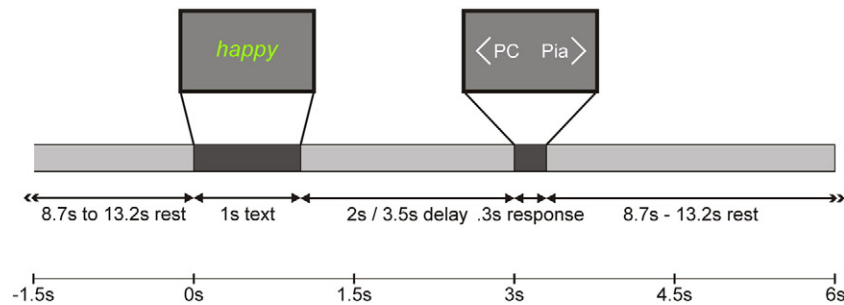
Fig. 1. Experimental design. Text messages ("*happy*" or "*sad*") printed in green or blue letters were presented for 1 s. After a delay of 2 s or 3.5 s, one of two alternative response mapping screens appeared for 0.3 s, indicating the participant to convey her response by a response button in her left or right hand, respectively. This way, the participant's decision and subsequent motor response were decoupled. Each trial terminated with a variable inter-trial interval from 8.7 to 13.2 s (varying in steps of 1.5 s).

Neurobiology, University College London, London, UK; www.vislab.ucl.ac.uk/cogent_2000.php) in a Matlab environment (The Mathworks, Natick, MA, USA). Only data from odd runs (i.e. colour-coded runs) were used in the current study. After imaging, participants completed a German version of the Measure of Adolescents' Friendship Closeness questionnaire (Table 1, Beadnell et al., 2007) and an in-house questionnaire inquiring about their belief in the cover story. Finally, participants were debriefed.

MRI data acquisition

MRI data were acquired on a 3 Tesla scanner (Achieva, Philips Medical Systems). A T1 weighted anatomical image (MPRAGE, 160 sagital slices, resolution 1x1x1 mm^3, FOV 240×240 mm^2, flip angle 8°, TI 1010.73 ms) used for spatial normalization of individual data sets was obtained from each participant before functional imaging. Forty-seven T2*weighted echoplanar images (EPI) covering the whole brain were acquired during each run (42 axial slices per volume, tilt angle −30°, slice thickness 3 mm, no gap, interleaved order, in plane resolution 3x3 mm^2, FOV 240×240 mm^2, flip angle 90°, TE 35 ms, TR 3000 ms, no parallel imaging). Each functional run was preceded by two functional images not included in the analysis to allow for T1 saturation. Data of one functional run of each participant had to be discarded due to technical problems, leaving seven runs per participant for analysis.

Analysis of fMRI data

Image preprocessing and parameter estimation

Image preprocessing and BOLD (blood oxygen level dependent) activity estimation were conducted with SPM5 (Wellcome Department of Imaging Neuroscience, University College London, London, UK). Functional images were temporally and spatially preprocessed using standard procedures (slice acquisition time correction, concurrent spatial realignment and correction of image distortions, normalization into standard MNI space [Collins et al., 1994] based on the T1-weighted image of each participant and a T1-weighted template, and resampling at a spatial resolution of 3×3×3 mm^3). Then, individual maps of parameter estimates were obtained for each participant and sender-content combination based on a standard GLM that accounted for first-order autocorrelations and low-frequency drifts (high pass cut off period 128 s). The expected time course of BOLD activity during processing of text messages of each sender-content combination was modelled separately

for each run with a stick function, convolved with a standard hemodynamic response function as implemented in SPM5. Two additional regressors of no interest per run were used to model left and right button presses. This way, we obtained seven individual activity maps for each sender-content combination (*friend-happy*, *friend-sad*, *computer-happy*, *computer-sad*) and participant.

Univariate analysis

In the initial step of our analysis, we used standard univariate analysis to identify brain regions where voxel-wise levels of activity differed during the processing of text messages perceived as being sent by the participant's friend and text messages perceived as being sent by the computer. This was done, first, to confirm that our task activated the "mentalizing network" and, second, to identify potential target regions for the MVCA (see below). Three linear within-subject contrasts were computed: (i) text messages perceived as being sent by the participant's friend minus text messages perceived as being sent by the computer (main effect of sender), (ii) "*happy*" messages minus "*sad*" messages (main effect of content) and (iii) "*happy*" messages perceived as being sent by participant's friend minus "*sad*" messages perceived as being sent by the participant's friend minus "*happy*" messages perceived as being sent by the computer minus "*sad*" messages perceived as being sent by the computer (sender-by-content interaction). For random effects group analysis, individual contrast maps were spatially smoothed (8 mm isotropic Gaussian kernel) and entered into a one-sample T-test.

Searchlight-based multivoxel pattern analysis (MVPA)

In the second step of our analysis, we used searchlight-based multivoxel pattern analysis (MVPA) (Haynes and Rees, 2006; Kriegeskorte et al., 2006) to search for brain regions where the *sensory content* of text messages ("*happy*" and "*sad*") was encoded in local patterns of neural activity, independent of the perceived source.

In this approach, a spherical local neighbourhood (the "searchlight") is created around each voxel of the brain. A classifier is then trained to distinguish between the spatial patterns of neural activity within this sphere elicited by stimuli of two different classes (e.g. "*happy*" and "*sad*" messages). Finally, the same classifier is tested on a new set of patterns of neural activity elicited by stimuli of the same two classes, but during different runs, and the test accuracy is written to centre voxel of the sphere. This way, the complete brain volume is tested,

Table 1
Friendship questionnaire (Beadnell et al., 2007) and German translation.

	Question	German translation
Item 1	Are you and this person friends?	Seid Ihr Freunde?
Item2	How often do you share your thoughts and feelings with this person?	Wie häufig teilst Du Deine Gedanken und Gefühle mit dieser Person?
Item 3	How often do you and this person do fun things together outside of school?	Wie häufig verbringt Ihr die Freizeit miteinander?
Item 4	How often do you and this person talk on the phone or via computer together?	Wie häufig telefoniert oder emailt Ihr?
Item 5	How often do you tell this person things you don't tell others?	Wie häufig erzählst Du dieser Person Dinge, die Du keinem anderen erzählst?
Item 6	How close do you feel to this person?	Wie nah fühlst Du Dich dieser Person?

and an individual accuracy map is obtained for each participant for a given classification problem.

In the current study, the searchlight radius was set to 9 mm (corresponding to 123 voxels) and a support vector machine (SVM) with a linear kernel and a hard margin as implemented in LIBSVM (http://www.csie.ntu.edu.tw/~cjlin/libsvm) was used for classification. To ensure that classification was based on multivoxel patterns of neural activity and not on the average level of activity within a sphere, the spatial mean of each pattern was set to zero.

Because the aim of this step of our analysis was to identify brain regions that encode content-specific sensory information independent of the perceived source, we used a *cross-sender classification scheme* that allowed us to identify brain regions where content-specific sensory information is encoded in patterns of neural activity that are invariant across senders. Specifically, we trained a classifier either on all patterns of neural activity elicited by text messages ascribed to the participant's friend (7 training samples/class) and then tested the classifier on all patterns of neural activity elicited by text messages ascribed to the computer (7 test samples/class), or vice versa (i.e. two cross-validation runs). For random effects group analysis, accuracy maps obtained with the searchlight-based MVPA were spatially smoothed (6 mm isotropic Gaussian kernel) and entered into a one-sample t-test

Please note that the cross-sender classification scheme described above is a very strict test of the hypothesis that sensory information is encoded in spatial patterns of neural activity that are invariant across senders. However, even if in a given brain region sensory content is encoded in patterns of neural activity that are highly similar across senders, encoding can still be more accurate for text messages ascribed to one sender than for text messages ascribed to another sender. To test for this possibility, a ROI (region of interest) - based MVPA was performed in all brain regions identified with the whole-brain searchlight-based MVPA (i.e. on all voxels within a sphere with a radius of 9 mm [i.e. 123 voxels] centred at the peak voxel of any significant cluster identified with the searchlight-based MVPA). For this analysis, we used a *within-sender classification scheme* that allowed us to compare classification accuracies for text messages ascribed to the participant's friend and for text messages ascribed to the computer. The classifier was first trained and tested only on patterns of neural activity elicited by text messages ascribed to the participant's friend, and then trained and tested only on patterns of neural activity elicited by text messages ascribed to the computer (7 leave-one out cross validation runs, 6 training samples/class and 1 test sample/class in each cross-validation run). Classification accuracies obtained for text messages ascribed to the participant's friend were then subtracted with classification accuracies obtained for text messages ascribed to the computer.

Searchlight-based multivoxel connectivity analysis (MVCA)

In the final and most important step of our analysis we aimed to identify brain regions that changed the strength of their functional coupling with ensembles of sensory-content encoding voxels, depending on the perceived sender. For this, we used a novel analysis of interregional coupling that combines the searchlight-based approach described above with the logic of a psychophysiological interaction analysis (PPI, Friston et al., 1997), i.e. it searches for context-dependent changes in functional connectivity between *ensembles of voxels*. We refer to this analysis as searchlight-based multivoxel connectivity analysis (MVCA).

In this approach, a seed region is determined whose functional connectivity with other regions in the brain is to be examined. Next, in analogy to the searchlight-based MVPA described above, a spherical local neighbourhood (the "searchlight") is created around each voxel of the brain. Finally, an $n_{voxel\ seed} \times n_{voxel\ target}$ matrix is computed for each searchlight that contains, in a given cell$_{ij}$, the difference of the strength of connectivity between two voxels $v_{seed\ i}$ and $v_{target\ j}$ between two conditions A and B (Fig. 2). The average of this matrix represents the change in the strength of multivoxel functional connectivity between the seed

region and the target region between the two conditions, Δ *strength of multivoxel connectivity*, and is written to the centre voxel of the searchlight. This way, the complete brain volume is tested, and an individual multivoxel connectivity map is obtained for each participant.

Please note that while this approach allows to quantify changes of the strength of functional coupling between ensembles of voxels, it is insensitive to the sign of single voxel-wise functional connectivities. In this regard, the MVCA resembles other multivoxel approaches: multivoxel approaches, in contrast to most univariate approaches, do not ask whether the level of overall neural activity is higher in one condition or the other (or, in the case of MVCA, whether functional coupling between two brain regions is positive or negative), but whether a brain region carries stimulus-specific information (or, in the case of MVCA, whether the *strength of coupling* between ensembles of voxels changes from one condition to another).

As for the searchlight-based MVPA, the searchlight radius for the MVCA was set to 9 mm (corresponding to 123 voxels). To separate multivoxel connectivities from any correlated fluctuations of the average level of activity in the seed and the target region, the spatial mean of all voxels within a searchlight was set to zero. Voxel-by-voxel correlations were computed as Pearson's correlation coefficient over the 7 "*happy*" and the 7 "*sad*" activity maps for each sender (i.e. n = 14 data points for each correlation). All correlation coefficients were Fisher-transformed ($\log[[1 + r]/[1-r]]/2$) before subtraction. Note that although voxel-wise differences were computed between the absolute values of Fisher-transformed correlation coefficients (i.e. between two approximately half-normal distributions) the resulting Δ *strength of multivoxel connectivity* can be assumed to be approximately normally distributed, because each Δ *strength of multivoxel connectivity* represents the mean of $> 100 \times 100$ voxel-wise differences per matrix (Fig. 2). For random effects group analysis, connectivity maps were spatially smoothed (6 mm isotropic Gaussian kernel) and entered into a one-sample T-test. Overlaps between significant changes in the strength of functional connectivity (detected with the searchlight-based MVCA) and the "mentalizing network" (identified with the univariate analysis) were computed as percentage of voxels of any cluster identified with the searchlight-based MVCA that were also significantly activated in the univariate analysis.

To further characterize changes of the strength of functional coupling between brain regions detected with the searchlight-based MVCA we performed three additional analyses.

First, to test whether the searchlight-based MVCA indeed detected changes in functional coupling between ensembles of voxels that would have remained undetected with a conventional univariate approach, we performed a univariate functional connectivity analysis, using the same seed region as in the searchlight-based MVCA. For this analysis, parameter estimates for each "*sad*" and each "*happy*" message were averaged across all voxels in the seed region and across all voxels in the searchlight. As above, Pearson's correlation coefficients were computed over the 7 "*happy*" and the 7 "*sad*" activity maps for each sender (i.e. n = 14 data points for each correlation). In this analysis, the difference of the Fisher-transformed correlation coefficient for condition A (i.e. text messages perceived as being sent by the participant's friend) and B (i.e. text messages perceived as being sent by the computer) simply represents the change of the strength of *univariate* connectivity between the seed region and the target region between the two conditions.

Second, to confirm that neural activity in any region detected with the searchlight-based MVCA was indeed more accurately explained by neural activity in the seed region than by the text message itself, we performed a second MVCA with two artificial seed data sets (one for condition *friend*, the other for condition *computer*) in which the voxel-wise level of activity in all trials with "*happy*" messages was dummy-coded with {1}, and the voxel-wise level of activity in all trials with "*sad*" messages was dummy-coded with {−1}. In other words, we generated seed data that precisely reflected the stimulus type and were not filtered by any neural activity. A finding that a given target
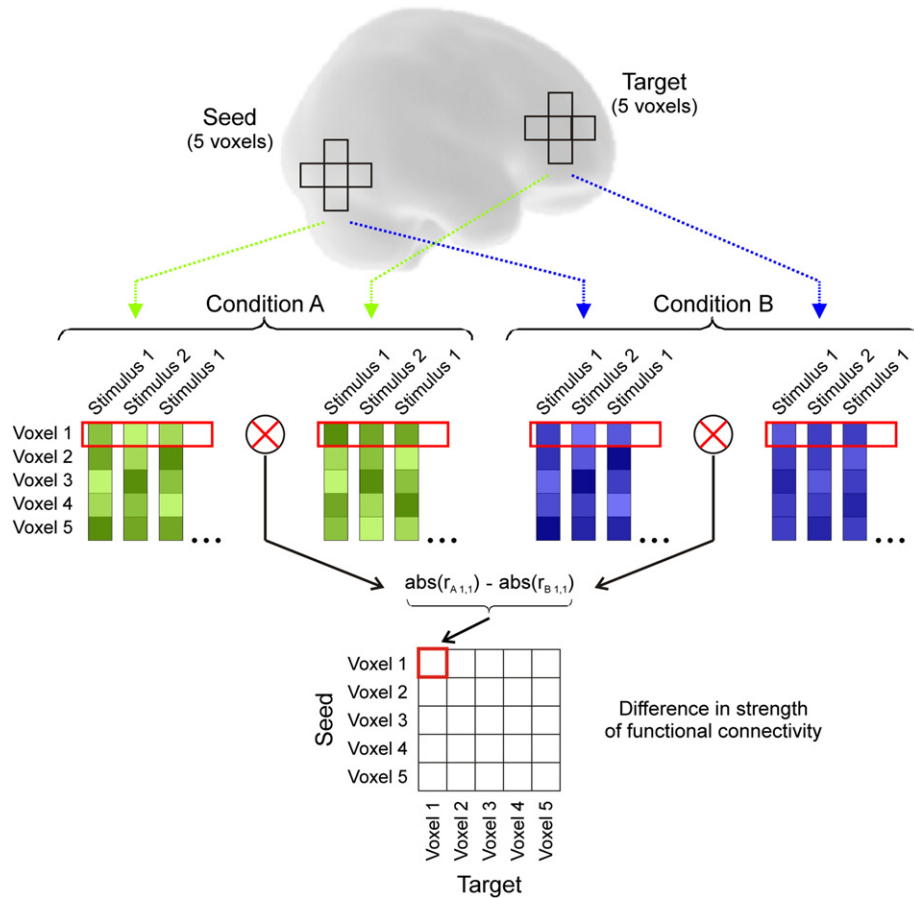
Fig. 2. Multivoxel connectivity analysis (MVCA). The idea of MVCA is to assess context-dependent changes of the strength of functional coupling between *ensembles of voxels* in a seed region and a target region. For this, an $n_{voxel\ seed} \times n_{voxel\ target}$ matrix is computed that contains, in a given cell$_{ij}$, the difference of the strength of connectivity between two voxels $v_{seed\ i}$ and $v_{target\ j}$ between two conditions A (e.g. text messages ascribed to participant's friend, green) and B (e.g. text messages ascribed to the computer, blue). Voxel-by-voxel connectivities are computed across all trials of a given condition (e.g. all "*happy*" and "*sad*" text messages ascribed to participant's friend and all "*happy*" and "*sad*" text messages ascribed to the computer). The average of this matrix represents the change in the strength of multivoxel functional connectivity between the seed region and the target region between the two conditions, *Δstrength of multivoxel connectivity*.

region would show a significant *Δ strength of multivoxel connectivity* for the real data but not for the dummy-coded data would indicate that neural activity in the target region is more accurately explained by neural activity in the seed region than by the type of the text message ("*happy*" or "*sad*") alone.

Third, a significant increase of the strength of functional coupling between ensembles of voxels does not necessarily mean that more content-specific information is conveyed from the seed region to the target region in one condition than in the other. To test this, we performed a ROI-based MVPA using a within-sender classification scheme as described above in all brain regions identified with the whole-brain searchlight-based MVCA (i.e. on all voxels within a sphere with a radius of 9 mm [i.e. 123 voxels] centred at the peak voxel of any significant cluster identified with the searchlight-based MVCA).

Correlation between real-life social ties and neural encoding

Finally, we asked whether any sender-dependent encoding of content-specific information of text messages would not only depend on whether the perceived sender was a human or a computer, but was further modulated by the receiver's social closeness to the sender. To test this, we used the within-sender classification accuracies obtained with the ROI-based MVCA described above, subtracted them (*friend* minus *computer*), and correlated the difference with the participants' self-reported intensity of friendship with their friend.

Statistical inference and anatomical labelling

All group statistical parametric maps (univariate, searchlight-based MVPA, searchlight-based MVCA) were thresholded at a voxel-wise threshold of T = 3.4 (corresponding to a probability of false positives of p = .002 for single voxels) and group statistical inference was based on the spatial extent of clusters of suprathreshold voxels, using a probability of false positives of $p_{cluster} = .05$, corrected for multiple comparisons according to non-stationary Random Field Theory (Hayasaka et al., 2004). Significant clusters were labelled with the AAL atlas (Tzourio-Mazoyer et al., 2002).

For all ROI analyses, a probability of false positives of p = .05 was adopted, and one-tailed statistics were used if we had an a-priori one-sided hypothesis (i.e. stronger within-sender classification accuracies for text messages perceived as being sent by the participant's friend than for text messages perceived as being sent by the computer in any cluster detected with the searchlight-based MVCA, and a positive correlation between this difference and intensity of friendship).

Results

Behavioural data

When explicitly asked after the imaging procedure, all but two participants (who were excluded from further analysis, see Methods) reported that they had believed that they had received text messages from
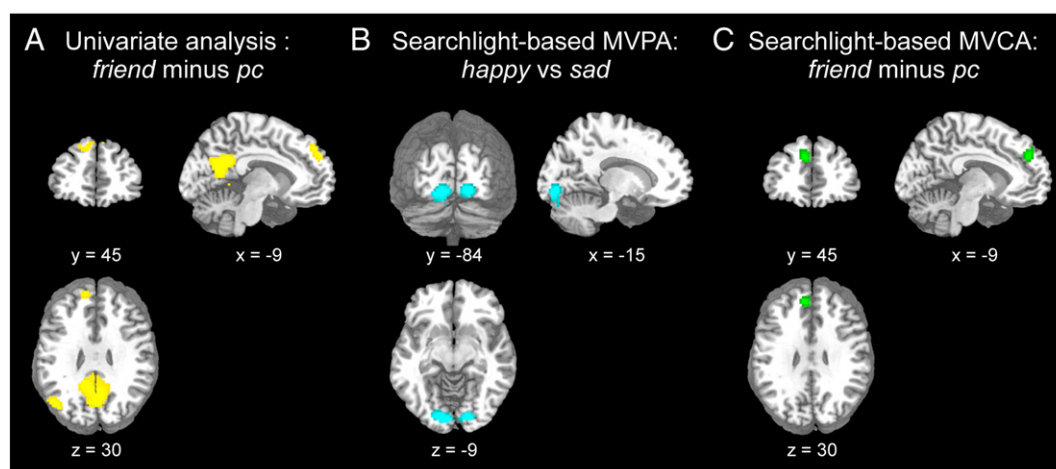
Fig. 3. Neural encoding of content-specific sensory information and sender-dependent functional coupling between ensembles of voxels. A, Statistical parametric map (SPM) showing clusters where the *overall level of neural activity* increased during processing of text messages perceived as being sent by the participant's friend, relative to the processing of text messages perceived as being sent by the computer. B, SPM showing the two clusters in the left and right ventral occipitotemporal cortex (VOT), identified with searchlight-based MVPA, where *content-specific sensory information* was encoded in patterns of neural activity that were invariant across senders. C, SPM showing the cluster in the dorsal medial prefrontal cortex (dmPFC), identified with searchlight-based MVCA, that showed significantly stronger *multivoxel functional coupling* with the sensory-content encoding clusters in the VOT when the text message was perceived as being sent by the participant's friend than when it was perceived as being sent by the computer. All SPMs are thresholded at a voxel-wise threshold of T = 3.4 (p = .002, uncorrected) and only clusters that survive correction for multiple comparisons are shown ($p_{cluster}$ = .050, corrected), except the cluster in the right VOT in B, which was just below statistical significance ($p_{cluster}$ = .054, corrected). All SPMs are projected onto a T1-weighted map of a standard brain (MNI).

their friend. These participants identified the alleged sender correctly in 98.9 +/− 0.3 % (mean +/− SEM) of all trials, indicating reliable performance, and responded equally fast to all messages (*friend-happy*, 529 +/− 21 ms; *friend-sad*, 540 +/− 29 ms, *computer-happy*, 547 +/− 23 ms, *computer-sad*, 538 +/− 23 ms; main effect of sender, F(1,17) = 1.7, p = .21; main effect of content, F(1,17) = 0.8; p = .38; sender-by-content interaction F(1,17) = 2.9, p = .11), indicating similar performance across conditions. Given the very small number of incorrect responses, trials with incorrect responses were treated as trials with correct responses in the analysis of the fMRI data.

Univariate analysis

In the initial step of our analysis we contrasted neural activity during processing of text messages perceived as being sent by the participant's friend with neural activity during processing of text messages perceived as being sent by the computer in a standard univariate approach. As expected, we found a significant increase of activity during processing of text messages perceived as being sent by the participant's friend in a distributed set of brain regions, including the dorsal medial prefrontal cortex (dmPFC), the precuneus, the left temporoparietal junction (TPJ) and the left and right temporal pole (TP) (Fig. 3A and Table 2). This pattern of activity is consistent with activity in the "mentalizing

network" reported in previous studies (Frith and Frith, 2003; Gallagher and Frith, 2003; Mitchell, 2009) and supports the assumption that participants were not just responding to the colour of the text message, but made a decision on who had sent a text message. As expected, standard univariate analysis did not reveal any overall or sender-dependent differences in neural activity between "*happy*" and "*sad*" messages.

Searchlight-based multi-voxel pattern analysis (MVPA)

In the second step of our analysis, we searched for brain regions that encoded the sensory content of text messages independent of the social context. Searchlight-based cross-sender MVPA detected a cluster in the left ventral occipitotemporal cortex (VOT), where the classifier could accurately discriminate between "*happy*" and "*sad*" messages (accuracy = .62 + / - .02 [mean +/- SEM]), and a second cluster in the right VOT were the performance of the classifier was just below statistical significance (accuracy = .61 + / - .02, Fig. 3B and Table 2). In other words, in these regions content-specific sensory information of text messages was encoded in spatial patterns of neural activity that were invariant across senders.

ROI-based within-sender MVPA within the left and right cluster showed that "*happy*" and "*sad*" messages ascribed to the participant's

Table 2
Significantly activated clusters in the whole brain analyses.

Brain region	Location of peak	Coordinates of peak	T-value at peak	Cluster size	corrected $p_{cluster}$
A. Univariate analysis: *friend* minus *pc*					
Precuneus	Precuneus R	[6–54 15]	6.8	785	.001
Temporoparietal junction (TPJ)	Medial temporal gyrus L	[−42 −63 18]	5.3	182	.013
Dorsomedial prefrontal cortex (dmPFC)	Superior medial frontal gyrus R	[9 39 51]	4.8	171	.014
Temporal pole (TP)	Inferior temporal gyrus L	[−48 3–36]	4.8	51	.047
Temporal pole (TP)	Inferior temporal gyrus R	[45 6–36]	5.0	24	.040
B. Searchlight-based MVPA: *happy* versus *sad*					
Ventral occipitotemporal cortex (VOT)	Lingual gyrus L	[−15 -84 -9]	6.1	138	.022
Ventral occipitotemporal cortex (VOT)	Lingual gyrus R	[18–84 -6]	7.2	78	.054
C. Searchlight-based MVCA: *friend* minus *pc*					
Dorsomedial prefrontal cortex (dmPFC)	Superior medial frontal gyrus L	[−9 45 30]	5.4	64	.033

Ordering of clusters is by cluster size. Locations of peaks are labelled with the AAL atlas (Tzourio-Mazoyer et al., 2002). Coordinates are in MNI space. L, left hemisphere; R, right hemisphere

friend could not be better discriminated than "*happy*" and "*sad*" messages ascribed to the computer (left VOT, T(17) = 1.1, p > .200, two-tailed; right VOT, T(17) = 0.4, p > .500, two-tailed). This provides additional evidence that neural encoding of text messages in the VOT is not modulated by the perceived sender.

Searchlight-based multi-voxel connectivity analysis (MVCA)

In the third and most important step of our analysis we asked how content-specific sensory information of text messages is relayed to higher stages of processing. Particularly, we were interested to see whether any region of the "mentalizing network" would change the strength of its functional coupling with the sensory-content encoding clusters in the VOT, depending on the perceived sender of the message. For this, we used searchlight-based MVCA with a combined seed region, i.e. all voxels within two spherical seed regions with a radius of 9 mm, one centred at the peak voxels in the left VOT and the other centred at the peak voxel of the right VOT (246 voxels in total). This analysis detected a cluster in the dorsal medial prefrontal cortex (dmPFC) that showed significantly stronger functional coupling with the sensory-content encoding clusters in the VOT when the text message was perceived as being sent by the participant's friend than when it was perceived as being sent by the computer (Fig. 3C and Table 2). Notably, this cluster partly overlapped (34 percent) with the cluster in the dmPFC that showed an increased level of overall activity in response to text messages sent by the participant's friend in the standard univariate analysis (see Fig. 3A and C).

To test for possible laterality effects in functional connectivity between the dmPFC and the left and right VOT, we performed two separate searchlight-based MVCAs, one using only data from the spherical seed region in the left VOT, the other only using data from the spherical seed region in the right VOT (i.e. 123 voxels in each seed region). These analyses detected a large cluster in the dmPFC that showed significantly stronger functional coupling with the sensory-content encoding cluster in the left VOT ([−9 48 36], T(17) = 5.2, k = 122 voxels, $p_{cluster}$ = .040, corrected) and a second cluster in the superior frontal gyrus that showed the same behaviour ([−21 15 60], T(17) = 6.0, k = 70 voxels, $p_{cluster}$ = .045, corrected). Searchlight-based MVCA with the right VOT seed region alone revealed no significant cluster. At a lower height threshold (T = 2.9, p = .005, uncorrected) we detected a cluster in the dmPFC in the vicinity of the cluster detected with the searchlight-based MVCA with the left VOT seed region that did not survive correction for multiple comparisons ([−6 48 30], T(17) = 3.3, k = 10 voxels). A direct comparison of the searchlight-based MVCA with the left and right VOT did not reveal any significant differences; therefore, laterality effects will not be discussed further.

In contrast to the searchlight-based MVCA with real data, the dummy-coded MVCA did not detect any significant clusters. This indicates that neural activity in the dmPFC was indeed more accurately explained by neural activity in content-encoding clusters in the VOT than by the text message itself.

Furthermore, ROI-based within-sender MVPA within the significant cluster in the dmPFC confirmed that relevant information was transmitted from the sensory-content encoding visual region to the dmPFC, again depending on the perceived sender: Within-sender classification accuracies were significantly higher for text messages perceived as being sent by the participant's friend than for those perceived as being sent by the computer (T(17) = 2.0, p = .031, one-tailed), while cross-sender classification accuracies were at chance level (T(17) = −0.4, p > 0.50, one-tailed).

Finally, as expected, univariate functional connectivity analysis, averaging the level of neural activity across all voxels in the seed region and across all voxels in the searchlight, did not detect any significant sender-dependent differences in functional coupling between the sensory-content encoding regions in the VOT and any other brain region.

Correlation between real-life social ties and neural encoding

In our final analysis, we asked whether encoding of content-specific information of text messages in the dmPFC might not only depend on whether the perceived sender is a human or a computer, but is further modulated by the receiver's social closeness to the sender. In other words, we asked whether participants who reported a higher intensity of friendship with their friend would show a more accurate neural encoding of text messages ascribed to their friend. This was indeed the case. An initial analysis indicated that self-reported intensity of friendship (average of items 2–6 in Table 1) explained 17 percent of the variance of individual differences in within-sender classification accuracies in the dmPFC (r = .41, T(16) = 1.8, p = .045, one-tailed). However, this correlation disappeared after one participant, whose difference in within-sender classification accuracy was more than two SDs lower than the group average, was excluded. Correlation analysis using single items of the friendship questionnaire as predictors indicated that individual differences in within-sender classification accuracies were best predicted (34 percent explained variance) by the amount of time participants reported to spend with their friend outside university / work (r = .56, T(16) = 2.7, p = .008, one-tailed). This correlation remained significant after the outlier was removed (r = .52, T(15) = 2.4, p = .015, one-tailed, Fig. 4).

Interestingly, the positive relation between intensity of friendship and selective encoding of text messages perceived as being sent by the participant's friend did not seem to be mediated by the overall level of activity in the dmPFC: although there was a considerable overlap between the cluster in the dmPFC that showed a significant sender-dependent change of overall neural activity and the cluster that showed a significant sender-dependent change of functional coupling with the sensory-content encoding region (see Fig. 3A and C and above), the level of neural activity in the dmPFC ([−9 45 30]) did not predict individual differences in within-sender classification accuracies in the dmPFC, neither when all participants were included in the analysis (r = −.20, T(16) = −0.8, p > .500, one-tailed) nor when the outlier was removed (r = −.24, T(15) = −1.0, p > .500, one-tailed).
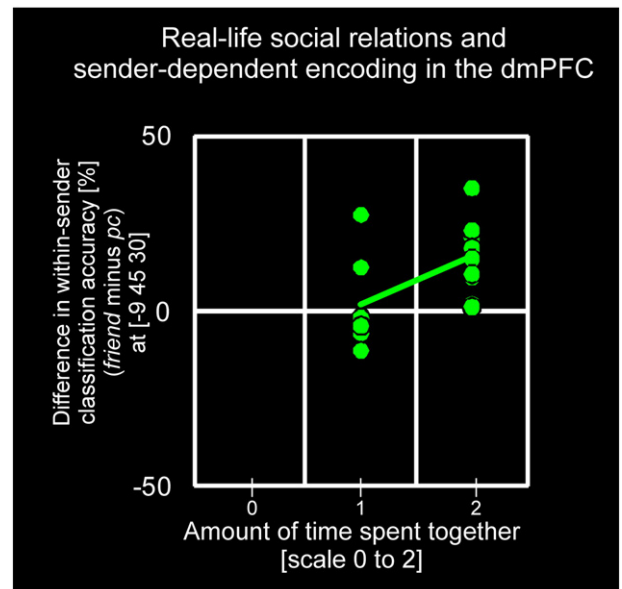

Fig. 4. Real-life social relations and neural encoding of content-specific information of text messages in the dmPFC. The plot shows the correlation between the amount of time participants reported to spend with their friend outside university/work and individual differences of within-sender classification accuracies in the dorsal medial prefrontal cortex (dmPFC). Each dot denotes one participant. Data of one participant are removed (see text). Numbers on the x-axis indicate how much of her spare time a participant spent with her friend (item 3 in Table 1; 0, never; 1 sometimes; 2 often). No participant in the current study responded with "0".

Discussion

In the current study we aimed to investigate the selective gating of the flow of neural information during ongoing communication between human communication partners. Specifically, we asked whether content-specific information of short text messages is selectively relayed from sensory cortex to higher stages of processing, depending on the perceived sender of the message.

Neural encoding of short text messages in the visual occipital cortex

To keep the current experiment simple, and to permit classification analysis with a reasonable number of trials, we limited the set of text messages in the current study to two alternative single-word messages ("*happy*" and "*sad*") whose low-level visual features and semantic content were closely tied. Furthermore, the colour of the text messages indicated who had sent a text messages, such that colour and source were tied within participants. Although this approach did not allow us to map the entire processing stream of text messages (which presumably comprises many distributed neural nodes and pathways, see e.g. Jobard et al., 2003), our analysis revealed two clusters in the posterior ventral occipitotemporal cortex (VOT) where content-specific sensory information of short text messages was encoded in a sender-independent manner. This is in line with previous studies that have shown that the VOT contains multiple word-processing areas that are organized in a hierarchic way, whereby full words are processed most anterior and low-level word-related visual features are processed most posterior (e.g. Vinckier et al., 2007).

Although the precise functional organization of the VOT is still unclear, the sensory content-encoding clusters found in the current study most likely belong to visual area VO-1 (Brewer et al., 2005; Wandell et al., 2007), which is located just posterior-medial to the visual word form area (VWFA) (e.g. Dehaene and Cohen, 2011; Yeatman et al., 2013). This region has been shown to be sensitive to complex shape patterns (e.g. Altmann et al., 2003), and, more recently, to visual-spatial features of letters (Rothlein and Rapp, 2014), which might constitute a processing stage prior to word abstraction.

Our finding of sender-independent encoding of short text messages in this region is particularly interesting as a recent study in the somatosensory domain suggests that neural responses to tactile communication signals such as a caring touch can be modulated by the perceived source at very early stages of sensory processing (Gazzola et al., 2012). These seemingly discrepant findings might point to differences in the functional organisation of the processing stream of physical communication signals (like a touch) and more abstract verbal communication signals.

Relay of sensory information to the "mentalizing network"

The most important finding of the current study is the observation that a region in the dorsal medial prefrontal cortex (dmPFC) changed the strength of its multivoxel functional coupling with the two sensory-content encoding clusters in the visual cortex, depending on whether a text message was perceived as being sent by the participant's friend or by the computer. Importantly, neural activity in this region was more accurately predicted by neural activity in the sensory-content encoding clusters in the VOT than by the text message itself. These findings add to previous evidence that language-related brain areas are functionally connected to the medial prefrontal cortex (mPFC) (Spotorno et al., 2012), and that the VOT is structurally connected to the mPFC via fibre bundles of the inferior fronto-occipito fasciculus (Yeatman et al., 2013).

Furthermore, these findings support and extend current accounts of mPFC function. The mPFC has been shown to be activated not only when individuals believe they are interacting online with a human partner (Gallagher et al., 2002; Rilling et al., 2004; Fukui et al., 2006; Gilbert et al., 2007; Krach et al., 2009), but also when they make off-line inferences about another person's mental state (Fletcher et al., 1995; Brunet et al., 2000; Gallagher et al., 2000; Ochsner et al., 2004; Ruby and Decety, 2004; Perner et al., 2006; Saxe and Powell, 2006; Gobbini et al., 2007; Mitchell, 2008; Aichhorn et al., 2009; Atique et al., 2011). This has led to the suggestion that the mPFC might serve some specific cognitive functions that are critical for making inferences about another person's mental state, such as directing attention towards one's own or another person's mental state (Gallagher and Frith, 2003; Kampe et al., 2003) or projecting oneself into a world that differs from one's one current physical or mental state (Mitchell, 2009). A study by Peelen et al. (2006) provided first evidence to challenge this process-centred view. Using multivoxel spatial correlation analysis, that study showed that the mPFC carries content-specific information about another person's mental state at a supra-modal level. The authors proposed that the overall level of neural activity in the mPFC might covary with particular cognitive processes or computations, while the specific content of these computations might be represented at a finer-grained level of cortical organization in these regions. The findings of the current study supplement this model by providing evidence that content-specific sensory information of communication signals is differently gated to the dmPFC, depending on the perceived source of the communication signal.

Importantly, neural encoding of content-specific information in the dmPFC does not only seem to be a function of whether the perceived sender is a human or a computer, but seems to be further modulated by the receiver's social closeness to the sender. The more time a participant reported to spend with her friend outside university / work, the stronger was the selective increase of encoding accuracy of communication signals believed to be sent by the participant's friend. Two partly independent interindividual factors might contribute to this modulation of encoding accuracy. First, the level of neural activity in the dmPFC has been shown to increase not only when people think about or interact with other humans, but to be further modulated by perceived social proximity (Mitchell et al., 2006; Rilling et al., 2008; Leiberg et al., 2012). Thus, one might hypothesise that the more accurate neural encoding of text messages believed to be sent by a close friend might be driven by a stronger increase of the overall level activity in the dmPFC when participants believed they were communicating with a friend they saw very often. However, post-hoc analysis of our data did not lend support to this hypothesis: The level of dmPFC activity did not predict individual differences in within-sender classification accuracy. Second, re-enactment of stored sender-related information during the processing of communication signals could enrich the sparse content of short text messages and thereby lead to a more distinct neural representation of the communication signal itself. This would be in line with our finding that differences in within-sender classification accuracies in the dmPFC were better explained by the amount of spare time friends spent together than by any other item of the friendship questionnaire, which might be indicative of the amount of sender-related information the perceiver could re-enact when receiving a text message.

Potential limitations

Addressing potential limitations of the current study it is, first of all, important to note that the findings of the current study cannot easily be explained by increased visual attention to text messages ascribed to the participant's friend. First, participants did not respond faster to text messages ascribed to their friend as one would expect had they processed these signals more attentively. Second, neither the overall level of activity nor the neural encoding of sensory information in the visual cortex was modulated by social context, which would be at odds with the common finding that visual attention modulates neural activity in visual cortex (e.g. Datta and DeYoe, 2009). Third, selective visual attention has repeatedly been reported to be associated with an increase of activity in a distinct set of lateral prefrontal and parietal brain regions (Corbetta and Shulman, 2002), which were not activated in the current

study. Instead, we found robust activity in the "mentalizing network", a set of brain regions that has consistently be associated with neural processes underlying social cognition. These findings speak against the assumption that the selective gating of content-specific sensory information observed in the current study can be explained by visual attention.

A second point important to address is the fact that communication in the current study was limited to a binary electronically transmitted signal ("*happy*" or "*sad*") and strictly unidirectional from the sender to the perceiver. While this experimental approach certainly did not permit to examine all neural processes that occur during natural communication, it allowed us to quite unequivocally link the observed modulation of neural information flow to the perceived source of the messages. Sender-dependent modulation of neural information flow was observed despite the fact that the semantic content of the text messages was very sparse and uniform across senders and despite the fact that information flow was unidirectional and did not require (or even permit) the participant to respond. Thus, the observed modulation of neural information flow cannot easily be explained by different message contents or response requirements. This suggests that the sender-dependent selective modulation of neural information flow ("social gating") observed in the current study is an effect that occurs during processing of communication signals from different sources even if there is no need to respond.

Finally, it should be mentioned that the current study investigated only female – female communication. This was done because investigating all possible 2×2 sex-by-sex interaction pairs would have increased the sample size by factor four. Although we have no strong reason to believe that the effects observed in the current study are limited to communication between females, future studies should aim to include larger samples, including all same-sex and opposite-sex female and male dyads.

Conclusions

In sum, the current study shows that even in a very simple experimental communication setting as used in the current study the human brain shows a remarkable sensitivity to social context: "social gating" mechanisms, possibly akin to the sensory gating mechanisms that filter sensory signals from the physical world, channel information from socially relevant sources to higher stages of processing that enable social cognition.

Emerging new analysis techniques that assess functional connectivities across ensembles of voxels like the searchlight-based MVCA used here will permit to investigate the flow of neural information during ongoing communication in the human brain more detail. Intriguing questions for future studies are how the "social gating" of neural information is modulated by the degree of mutual interaction between communication partners, and how the human brain recombines message-related and sender-related information when receiving communication signals from multiple human partners.

Acknowledgments

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