Encoding Social Interactions: The Neural Correlates of True and False Memories

Benjamin Straube1,2,3, Antonia Green3, Anjan Chatterjee2, and Tilo Kircher1

Abstract

In social situations, we encounter information transferred in firsthand (egocentric) and secondhand (allocentric) communication contexts. However, the mechanism by which an individual distinguishes whether a past interaction occurred in an egocentric versus allocentric situation is poorly understood. This study examined the neural bases for encoding memories of social interactions through experimentally manipulating the communication context. During fMRI data acquisition, participants watched video clips of an actor speaking and gesturing directly toward them (egocentric context) or toward an unseen third person (allocentric context). After scanning, a recognition task gauged participants’ ability to recognize the sentences they had just seen and to recall the context in which the sentences had been spoken. We found no differences between the recognition of sentences spoken in egocentric and allocentric contexts. However, when asked about the communication context (“Had the actor directly spoken to you?”), participants tended to believe falsely that the actor had directly spoken to them during allocentric conditions. Greater activity in the hippocampus was related to correct context memory, whereas the ventral ACC was activated for subsequent inaccurate context memory. For the interaction between encoding context and context memory, we observed increased activation for egocentric remembered items in the bilateral and medial frontal cortex, the BG, and the left parietal and temporal lobe. Our data indicate that memories of social interactions are biased to be remembered egocentrically. Self-referential encoding processes reflected in increased frontal activation and decreased hippocampal activation might be the basis of correct item but false context memory of social interactions.

INTRODUCTION

Memories of social interactions are crucial components of human relationships. Nonverbal cues (such as gesture, body orientation, and eye gaze) are essential in social situations: They allow an individual to recognize that he or she is being directly addressed (e.g., Özyürek, 2002) and consequently define the egocentric or allocentric context in which communication occurs. Although the ability to recall if a past conversation occurred in an egocentric or allocentric context is undoubtedly important for maintaining interpersonal relationships, we know very little about the neural processes responsible for encoding the context of a social communication. In this study, we investigate the neural encoding of the social context of spoken and gestural communication.

Gestures made with the hands and arms often have a communicative function and frequently accompany speech (e.g., Kendon, 2004; Goldin-Meadow, 1999; McNeill, 1992). The neural basis of the processing such coverbal gestures has been investigated by an increasing number of fMRI studies (Dick, Goldin-Meadow, Hasson, Skipper, & Small, 2009; Green et al., 2009; Kircher, Straube, et al., 2009; Straube, Green, Weis, Chatterjee, & Kircher, 2009; Holle, Gunter, Rüschemeyer, Hennenlotter, & Iacoboni, 2008; Willems, Özyurek, & Hagoort, 2007). The processing of coverbal gestures involves the left inferior frontal gyrus (IFG), inferior parietal cortex, posterior temporal regions, and precentral gyrus. Little is known about the neural processes responsible for creating memories of speech and gesture communication, but past research indicates that left inferior frontal, posterior temporal, premotor, and hippocampal brain regions are involved (Straube et al., 2009). Until now, there has been no evidence about how egocentric versus allocentric contexts influence an individual’s memories of speech and gesture utterances.

People sometimes believe they recognize things that they have never actually encountered, for example, confusing a stranger with an old acquaintance. This phenomenon, known as false recognition, has been investigated in both neuropsychological and neuroimaging research (for a review, see Schacter & Slotnick, 2004). False recognition often occurs in everyday social situations. Although several studies have compared the neural activity that accompanies genuine recognition of studied items (e.g., Kircher et al., 2008) and false recognition of novel items (e.g., Slotnick & Schacter, 2004; Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Schacter, Reiman, et al., 1996), there has been little research conducted on the true and false recognition of social interactions. Past neuroimaging studies have shown increased neural activity in regions of the medial and lateral frontal cortex during false recognition.
of social interactions, attention processes that are elicited by Johnson & Raye, 1981). With regard to the memory encoding during retrieval (Johnson, Hashtroudi, & Lindsay, 1993; similarities between the event features that are reactivated these errors may arise as a consequence of the similarities lead to subsequent inaccurate memories. For example, assumed that cognitive processes engaged during encoding With regard to false memory encoding, it is generally as- information of false context memories are less well known. K. Kensinger & Schacter, 2005). Beside the medial-temporal structures, frontal (e.g., Kirchhoff, 2001; Kirchhoff, Wagner, Maril, & Stern, 2000). However, even during tasks that predominantly depend on item memory, hippocampal activation may help individuals associate newly learned information with items already stored in memory (Kircher et al., 2007). Despite controversial findings about the specific memory-related functions of the hippocampus and surrounding brain regions, there is general agreement that medial-temporal structures are involved in the recognition of source and item information. However, it is not known if encoding related activity in the medial-temporal lobe predicts subsequent memories of egocentric in comparison with allocentric communication situations.

Beside the medial-temporal structures, frontal (e.g., Kirchhoff et al., 2000) and parietal brain regions (e.g., Kensinger & Schacter, 2006) are active during encoding of items and their context. The neural correlates for the formation of false context memories are less well known. With regard to false memory encoding, it is generally assumed that cognitive processes engaged during encoding lead to subsequent inaccurate memories. For example, these errors may arise as a consequence of the similarities between how imagined and perceived events are encoded (Gonsalves et al., 2004; Gonsalves & Paller, 2000) as well as similarities between the event features that are reactivated during retrieval (Johnson, Hashtroudi, & Lindsay, 1993; Johnson & Raye, 1981). With regard to the memory encoding of social interactions, attention processes that are elicited by social cues (such as body orientation, e.g., Hietanen, 2002, and eye gaze, e.g., Hietanen, Nummenmaa, Nyman, Parkkola, & Hamalainen, 2006) may also play an important role in successful encoding and later remembering of contextual information of the communication situations. Their role may be particularly important, as direct human-to-human interaction is an essential mode of communication yet commonly results in false memories or misunderstandings. From a social psychologist’s perspective, an egocentric bias and related self-referential encoding effects (the effect that information relating to the self is preferentially encoded and organized above other types of information; Ross & Sicoly, 1979; Rogers, Kuiper, & Kirker, 1977) might be a source of biased memory encoding of social situations (for a review, see Schacter, Chiao, & Mitchell, 2003). Various medial cortical regions (including the medial orbital PFC, the ventromedial PFC, the sub- or pregenual ACC (PACC) and supragenual ACC [e.g., Kircher et al., 2001], the dorsomedial PFC, the medial parietal cortex, the posterior cingulate cortex, the retrosplenial cortex, and the precuneus [e.g., Kircher et al., 2000]; for a review, see Gillihan & Farah, 2005) have been found to be active during self-referential processing (Northoff et al., 2006). These regions have been subsumed under the term “cortical midline structures” and speculatively characterized as an anatomical and functional unit (Northoff & Bermpohl, 2004). Furthermore, one theory suggests the existence of a self-memory system that is functionally dissociable from general semantic processing and evokes distinct cognitive operations (Macrae, Moran, Heatherton, Banfield, & Kelley, 2001). For example, in a study by Macrae et al. (2004), participants evaluated the extent to which a series of personality characteristics were self-descriptive. They found that activity in the medial PFC during encoding of the characteristics predicted both subsequent memory performance and judgments of self-relevance. This result suggests that the advantage afforded to self-knowledge memory appears to depend on the additional recruitment of the medial frontal cortex (Macrae et al., 2004). However, besides this support for the theory that there is a specific self-memory system, the neural process underlying the formation of true and false memories of social interactions is not well known.

This study aimed to determine the neural correlates of encoding processes for item memory (spoken sentences accompanied by gesture) and source memory (egocentric and allocentric contexts) of social interactions. During fMRI data acquisition, participants were presented with video clips of an actor speaking and gesturing directly toward them (egocentric, E) or toward an unseen third person (allocentric, A; see Figure 1). After scanning, recognition performance for sentences (items) and communication context (source) was gathered. Behaviorally, we expected more accurate memory of egocentric scenes (E) compared with allocentric scenes (A). We also anticipated that individuals would more often misremember allocentric scenes than they would egocentric scenes, as egocentric communication situations may inherently be better remembered because of their heightened personal relevance (Schacter et al., 2003). In accordance with the relational memory theory (e.g., Eichenbaum & Cohen, 2001), we predicted that hippocampal areas (specifically the cornu ammonis [CA] re-
gion) would be active during the encoding of both sentences and communication contexts that are later correctly remembered. In addition, we predicted that only the encoding of correctly remembered sentences would correlate with activity in adjacent regions of the hippocampus (e.g., Kensinger & Schacter, 2006; Ranganath et al., 2004; Davachi et al., 2003). We predicted that the encoding of subsequently incorrectly remembered communication contexts would activate additional frontal (e.g., Kubota et al., 2006; Okado & Stark, 2005; Gonsalves et al., 2004) and parietal structures (e.g., Gonsalves et al., 2004; Gonsalves & Paller, 2000).

**METHODS**

**Participants**

Eighteen right-handed healthy male (Oldfield, 1971) volunteers, all native speakers of German (mean age = 24.1 years, SD = 2.8 years, range = 20 to 30 years) and without vision or auditory impairments, participated in the study. None of the participants had ever experienced any serious medical, neurological, or psychiatric illness. All participants gave written informed consent and were paid €20 for participation. The study was approved by the local ethics committee.

**Stimulus Construction**

Spoken sentences accompanied by expressive gestures were chosen to emphasize both the auditory and the visual aspects of a natural communication situation. The visual component is of special importance because the communication context was manipulated through the actor’s body orientation. The actor directly faced the participant in the egocentric context, whereas the actor addressed an unseen third person in the allocentric context. Two cameras simultaneously filmed the actor to control for variability between the two conditions (see Figure 1).

We used sentences and gestures with both object-related and person-related content. We initially created a set of 372 (186 egocentric [E] and 186 allocentric [A]) short video clips, consisting of 178 sentences with object-related content accompanied by iconic gestures (89 × 2) and 194 sentences with person-related content accompanied by emblematic gestures (97 × 2). A comparison of emblematic and iconic gestures independent of the memory data will be...
published elsewhere (Straube, Green, Jansen, Chatterjee, & Kircher, 2010) and is here not of interest. All spoken sentences were 5 to 10 words in length with an average duration of 2.32 sec (SD = 0.36) and a similar grammatical form (subject–predicate–object). The same male actor performed all the speech and gestures in a natural, spontaneous way. The procedure was supervised by two of the authors (B.S. and A.G.) and timed digitally. All video clips were 5 sec in length with at least 0.5 sec before and after the sentence onset and offset, during which the actor neither spoke nor moved.

For stimulus selection, validation, and the construction of two similar counterbalanced stimulus sets, 17 subjects rated each video on a scale from 1 to 7 on “addressing” (“To what degree does the actor address you?”) on the sentences’ social and descriptive content and familiarity (1 = very low to 7 = very high). In total, 120 items were selected, half with iconic gestures and half with emblematic gestures. Two experimental sets were created so that the same 60 information. For example, in the sentence “The pilot indicated that everything is all right,” the point of co-occurrence was when the end of the word (“right”) co-occurred with the emblematic gesture (thumb-and-index-finger ring gesture). These time points of co-occurrence occurred on average 2090 msec (SD = 505 msec) after the video started (1590 msec after speech onset).

Experimental Design and Procedure

During the fMRI scanning procedure, videos were presented via MR-compatible video goggles (VisuaStim©; Resonance Technology, Inc., Northridge, CA) and nonmagnetic headphones (audio presenting systems for stereophonic stimuli: Commander; Resonance Technology, Inc.), which also dampened scanner noise.

Sixty items of each of the two conditions were presented in a rapid event-related design, in a pseudorandomized order and counterbalanced across subjects. Each video was followed by a baseline condition (gray background with a fixation cross) with a variable duration of 3750 to 6750 msec (average = 5000 msec). This rapid event-related design was used to present the videos in a randomized sequence, but without extensive pauses, which would have reduced participants’ attention. The fast presentation of stimuli may have resulted in reduced effects of baseline contrasts for the conditions. However, the power of condition comparisons should be comparable with regular event-related designs because of the effect of randomization. The latter are of special interest in this study.

Subjects were instructed to watch the videos attentively, regardless of the actor’s orientation (egocentric or allocentric communication context). No instructions with regard to memory were given to the participants. During the overview scans, additional clips were presented with their volume adjusted to ensure that the sentences were well understood. Each participant performed two runs with 60 video clips and a total duration of 10.5 min each.

Behavioral Data Acquisition

Approximately 10 min after scanning, without prior notice, participants completed a paper and pencil test to gauge recognition of the sentences seen in the experiment. All sentences were presented in written form. An equal number of modified sentences for each condition was intermixed with actual sentences presented in the experiment. The sentences were modified only in the word that accompanied the gesture. For example, the sentence “The girl asks her friend to call” (spreading the little finger and the thumb next to the head) was modified to “The girl asks her friend for advice” (for another example, see Figure 1). Participants had to report if they had seen a video in which that sentence was spoken (indicate “old”) or not (indicate “new”) and whether the actor was oriented toward them (E) or toward another person (A). Participants rated their confidence...
in their responses on a scale from 1 (low confidence) to 7 (high confidence; see Figure 1). Altogether, 240 sentences were presented in random order on a piece of paper.

**fMRI Data Acquisition**

MRT was performed on a 3-T Siemens scanner (Siemens MRT Trio series). Functional data were acquired with echo-planar images in 38 transversal slices (repetition time = 2000 msec, echo time = 30 msec, flip angle = 90°, slice thickness = 3 mm, interslice gap = 0.50 mm, field of view = 220 × 199 mm, voxel resolution = 3.44 × 3.44 mm, matrix dimensions = 64 × 58 mm). Slices were positioned to achieve whole-brain coverage. Three hundred fifteen volumes were acquired during each of two functional runs.

**Data Analysis**

MR images were analyzed using Statistical Parametric Mapping (SPM; www.fil.ion.ucl.ac.uk) implemented in MATLAB 6.5 (Mathworks Inc., Sherborn, MA). For practical reasons, minimal error-prone script-based preprocessing and first-level analyses were performed with SPM2. The resulting outputs are comparable with and compatible with the newer version of SPM (SPM5), which was used for the second-level analyses. The first five volumes of every functional run were discarded to minimize T1 saturation effects. To correct for different acquisition times, we shifted the signal measured in each slice relative to the acquisition time of the middle slice using a slice interpolation in time. All images of one session were realigned to the first image of a run to correct for head movement and normalized into standard stereotaxic anatomical Montreal Neurological Institute (MNI) space by using the transformation matrix calculated from the first EPI-scan of each subject and the EPI template. Afterward, the normalized data with a resliced voxel size of 3.5 × 3.5 × 3.5 mm were smoothed with a 6-mm FWHM isotropic Gaussian kernel to accommodate intersubject variation in brain anatomy. A high-pass filter (128-sec cutoff period) was applied to remove low frequency fluctuations in the BOLD signal.

The anticipated hemodynamic response at the defined points of speech and gesture co-occurrence for each event-type was modeled by two response functions, a canonical hemodynamic response function (Friston et al., 1998) and its temporal derivative. The temporal derivative was included in the model to account for the residual variance resulting from small temporal differences in the onset of the hemodynamic response, which is not explained by the canonical hemodynamic response function alone. The functions were convolved with the event sequence on the basis of the individual subsequent memory performance of the subjects (memories of correct communication context: CC; incorrect communication context: IC; and not remembered items: M) in a general linear model. In a post hoc analysis (see below), the factor communication context (Egocentric: E and Allocentric: A) was also included resulting in the following six conditions: E-CC, E-IC, E-M, A-CC, A-IC, and A-M. A fixed event duration of one second was chosen to get a broader range of data around the speech–gesture segments and has also been applied successfully in past studies of co-verbal gesture processing (Straube et al., 2009, 2010). On the basis of the experience of prior investigations (Kircher, Blumel, et al., 2009; Kircher, Straube, et al., 2009; Straube et al., 2009), modeling the one second window (time logged to the keyword of each sentence) gives a better signal-to-noise ratio than modeling the whole video duration of 5 sec within our stimulus material.

A group analysis was performed by entering contrast images into a flexible factorial analysis as implemented in SPM5, in which subjects are treated as random variables. Voxels with a significance level of p < .001 uncorrected belonging to clusters with at least 10 voxels are reported. A Monte Carlo simulation of the brain volume of the current study was conducted to establish an appropriate voxel contiguity threshold (Slotnick, Moo, Segal, & Hart, 2003). Assuming an individual voxel type I error of p < .001, a cluster extent of 10 contiguous resampled voxels was indicated as sufficient to correct for multiple voxel comparisons at p < .05. Activation peaks of most of the activation clusters also held a false discovery rate (FDR). Corresponding corrected p values for each activation peak were included in Tables 1 and 2 and the Results section.

The reported voxel coordinates of activation peaks are located in MNI space. For anatomical localization, the functional data were referenced to probabilistic cytoarchitectonic maps (Eickhoff et al., 2005, 2007). For the comparison and presentation of distinct hippocampal activation within the CA subregion of the hippocampus (which is thought to be involved in memory binding processes and episodic memory; e.g., Eichenbaum, 2004), a small volume correction was applied to the contrast CC versus IC (see Results section) using an ROI, defined by the CA probability maps from Amunts et al. (2005). For the small volume correction, a more liberal whole-brain threshold was applied (p < .005 uncorrected), and the VOI was then restricted to the CA region of the hippocampus. The corresponding statistics of this procedure are reported in the Results section. All contrast estimates provided in Figures 3–5 present activation change within the whole activation clusters of the corresponding contrast. For this purpose, we calculated the average beta value for each subject and condition for the corresponding activation cluster of the group analysis. Thus, contrast bars present the average beta value of the subjects’ cluster averages. Error bars represent as the SEM (between-subject variability). Parameter estimates of Figure 6 present activation change within the entire subregions (CA and entorhinal...
cortex (EC]) of the hippocampus created with the same averaging procedure.

Statistical analyses of data other than fMRI were performed using SPSS version 14.0 for Windows (SPSS Inc., Chicago, IL). t Tests and ANOVAs were used for the analyses. Greenhouse–Geisser correction was applied whenever necessary. Discrimination performance ($d_0 = z(\text{hits}) - z(\text{FA})$; $c = -1/2 \cdot [z(\text{hits}) + z(\text{FA})]$; e.g., Macmillan & Creelman, 1991). Statistical analyses are two-tailed with $\alpha$ levels of significance of $p < .05$.

Contrasts of Interest

The fMRI analyses are structured in the following manner: First, comparisons between subsequently remembered sentences in the correct context (CC) and in the incorrect context (IC) in contrast to nonremembered sentences (misses: M) were performed to give an overview of the structures involved in memory processes with and without correct contextual information.

Second, subsequently remembered sentences in the correct context (CC) were contrasted with subsequently remembered sentences in the incorrect context (IC) to test the hypothesis that predominantly medial frontal brain regions are related to inaccurate context memory and hippocampal regions to correct context memory. Third, a post hoc analysis was performed to explore if the analyses reported above were influenced by the communication context (ego- or allocentric). Finally, an interaction analysis between communication context (ego- or allocentric) and memory quality (correct/incorrect context) was performed to explore brain regions related to egocentric encoding (sentences subsequently remembered as egocentric).

Thus, there was no separation of egocentric and allocentric items in the first two analyses to obtain more events and more reliable results for CC, IC, and M (given that CC are predominantly egocentric, IC are mainly allocentric, and M contains equal proportions of egocentric and allocentric stimuli; see Behavioral results). Because 10 of 18 subjects in the egocentric incorrect-context condition (E-IC) and 4 of 18 subjects in the allocentric correct-context condition (A-CC) had fewer than three trials per condition,

### Table 1. Activation for Correct (CC) and Incorrect Context Information (IC) versus Misses (M)

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Anatomical Region</th>
<th>Lat.</th>
<th>BA</th>
<th>$x$</th>
<th>$y$</th>
<th>$z$</th>
<th>$t$</th>
<th>*FDR</th>
<th>No. Voxels</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC &gt; M</td>
<td>Supramarginal gyrus</td>
<td>R</td>
<td>40</td>
<td>56</td>
<td>-28</td>
<td>46</td>
<td>5.38</td>
<td>0.018</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Postcentral/supramarginal gyrus</td>
<td>R</td>
<td>2</td>
<td>35</td>
<td>-39</td>
<td>49</td>
<td>5.35</td>
<td>0.018</td>
<td>101</td>
</tr>
<tr>
<td></td>
<td>Inferior/middle temporal gyrus</td>
<td>L</td>
<td>37</td>
<td>-53</td>
<td>-56</td>
<td>-4</td>
<td>5.06</td>
<td>0.030</td>
<td>81</td>
</tr>
<tr>
<td></td>
<td>Postcentral gyrus</td>
<td>L</td>
<td>2</td>
<td>-39</td>
<td>-42</td>
<td>60</td>
<td>4.89</td>
<td>0.033</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>Inferior frontal gyrus</td>
<td>L</td>
<td>45</td>
<td>-49</td>
<td>28</td>
<td>7</td>
<td>4.71</td>
<td>0.033</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Parahippocampal gyrus (CA)</td>
<td>L</td>
<td>-28</td>
<td>-28</td>
<td>-14</td>
<td>4.63</td>
<td>0.033</td>
<td>21</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Supramarginal gyrus</td>
<td>L</td>
<td>40</td>
<td>-46</td>
<td>-39</td>
<td>28</td>
<td>4.45</td>
<td>0.041</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Inferior frontal gyrus</td>
<td>L</td>
<td>44/45</td>
<td>-53</td>
<td>11</td>
<td>7</td>
<td>4.35</td>
<td>0.041</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Calcarine gyrus</td>
<td>R</td>
<td>17</td>
<td>14</td>
<td>-98</td>
<td>7</td>
<td>4.30</td>
<td>0.041</td>
<td>10</td>
</tr>
<tr>
<td>IC &gt; M</td>
<td>Premotor cortex</td>
<td>L</td>
<td>6</td>
<td>-4</td>
<td>-25</td>
<td>56</td>
<td>5.19</td>
<td>0.043</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Postcentral gyrus</td>
<td>L</td>
<td>2/3</td>
<td>-35</td>
<td>-42</td>
<td>60</td>
<td>5.08</td>
<td>0.043</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Premotor cortex</td>
<td>R</td>
<td>6</td>
<td>11</td>
<td>-7</td>
<td>56</td>
<td>4.90</td>
<td>0.043</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>Parahippocampal gyrus (CA)</td>
<td>L</td>
<td>-28</td>
<td>-28</td>
<td>-14</td>
<td>4.68</td>
<td>0.046</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Parahippocampal gyrus (EC)</td>
<td>R</td>
<td>25</td>
<td>-4</td>
<td>-25</td>
<td>4.65</td>
<td>0.046</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Postcentral gyrus</td>
<td>R</td>
<td>2/3</td>
<td>32</td>
<td>-35</td>
<td>42</td>
<td>4.65</td>
<td>0.046</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>Fusiform/hippocampus (SUB/CA)</td>
<td>L</td>
<td>-32</td>
<td>-18</td>
<td>-25</td>
<td>4.49</td>
<td>0.051</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Middle temporal gyrus</td>
<td>R</td>
<td>37</td>
<td>56</td>
<td>-46</td>
<td>11</td>
<td>3.63</td>
<td>0.087</td>
<td>10</td>
</tr>
</tbody>
</table>

Significance level ($t$ value), size of the respective activation cluster (No. voxels $\geq 10$) at $p < .001$ uncorrected ($p < .05$ corrected, see Methods), and possible false discovery rate correction (*FDR). Coordinates are listed in MNI space. BA is the Brodmann’s area nearest to the coordinate and should be considered approximate. Contrasts were named as follows: CC = correct context; IC = incorrect context; M = misses.
the post hoc analysis was performed in an unbalanced design (E-CC: n = 18, E-IC: n = 8; E-M: n = 18; A-CC: n = 14; A-IC = 18; A-M: n = 18). For the remaining sample the average number of trials were for E-CC = 29, E-IC = 12, E-M = 26, A-CC = 19, A-IC = 22 and A-M = 27. Contrast estimates were provided for the analyses that contrasted CC, IC, and M to explore the effect of the confounded variable (stimulus material; see Figures 3D and 4B and D).

RESULTS

Behavioral Results

Memory of Sentences

The percentage of study items correctly reported as old (hits) was 56.49% (SD = 19.54%) for the egocentric (E) and 54.82% (SD = 17.51%) for the allocentric condition (A). The corresponding false alarm rate (FA; the percentage of new modified sentences that were judged as old) was 12.04% (SD = 13.51%) for the E condition and 11.58% (SD = 12.56%) for the A condition. A 2 × 2 within-subjects ANOVA, with communication context (E vs. A) and memory performance (hits vs. FA), revealed a significant main effect of memory performance (hits > FA; F(1, 17) = 91.130, p < .001, η² = .843), no significant effect of the communication context, F(1, 17) = 1.405, p = .252, η² = .076, and no significant interaction between factors, F(1, 17) = 0.508, p = .486, η² = .094.

To assess differences in signal detection parameters across conditions, we calculated the discrimination index d. We obtained an average discrimination performance of d = .586 (SD = 0.274) for the E condition and d = .570 (SD = 0.240) for the A condition. The corresponding response criteria (c) were 0.209 (SD = 0.170) for the E condition and 0.223 (SD = 0.159) for the A condition. Both memory parameters did not differ between the E and the A conditions: d, t(17) = 0.718, p = .483; c, t(17) = −1.111, p = .282.

Memory of Communication Context

The percentage of study items correctly reported as previously seen in an egocentric context (E hits) was 49.81% (SD = 17.28%) of all egocentric encoded items (thus 88.5% of correct remembered items of the egocentric condition; SD = 30.7%) with a corresponding failure rate (E failure) of 6.47% (SD = 8.82%) of all egocentric encoded items (thus 11.5% of correct remembered items of the egocentric condition; SD = 15.7%). In contrast, the proportion of study items correctly reported as previously seen in an allocentric context (A hits) was 15.11% (SD = 9.93%) of all allocentric encoded items (thus 27.91% of correct remembered items of the allocentric condition; SD = 18.3%) with a corresponding failure rate (A failure) of 39.03% (SD = 15.42%) of all allocentric encoded items (thus 72.09% of correct remembered items of the allocentric condition; SD = 28.48%). A 2 × 2 within-subject ANOVA between communication context (E vs. A) and memory performance

Table 2. Interaction between Communication Context and Memory (E-CC > E-IC) > (A-CC > A-IC)

<table>
<thead>
<tr>
<th>Anatomical Region</th>
<th>Lat.</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>t</th>
<th>*FDR</th>
<th>No. Voxels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior medial</td>
<td>R</td>
<td>6/8</td>
<td>7</td>
<td>25</td>
<td>60</td>
<td>5.63</td>
<td>0.004</td>
<td>59</td>
</tr>
<tr>
<td>frontol gyrus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inferior parietal</td>
<td>L</td>
<td>40/7</td>
<td>−49</td>
<td>−60</td>
<td>42</td>
<td>5.39</td>
<td>0.004</td>
<td>113</td>
</tr>
<tr>
<td>lobule</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal ganglia</td>
<td>R</td>
<td>21</td>
<td>4</td>
<td>−11</td>
<td>11</td>
<td>4.84</td>
<td>0.007</td>
<td>69</td>
</tr>
<tr>
<td>(putamen)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle temporal</td>
<td>L</td>
<td>37</td>
<td>−56</td>
<td>−42</td>
<td>0</td>
<td>4.64</td>
<td>0.012</td>
<td>16</td>
</tr>
<tr>
<td>gyrus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle frontal/orbital gyrus</td>
<td>L</td>
<td>46</td>
<td>−39</td>
<td>46</td>
<td>14</td>
<td>4.42</td>
<td>0.017</td>
<td>30</td>
</tr>
<tr>
<td>Middle cingulate</td>
<td>R</td>
<td>23/31</td>
<td>7</td>
<td>−25</td>
<td>35</td>
<td>4.14</td>
<td>0.021</td>
<td>10</td>
</tr>
<tr>
<td>cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal ganglia</td>
<td>L</td>
<td>−28</td>
<td>7</td>
<td>−4</td>
<td>4.14</td>
<td>0.021</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>(putamen)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Superior frontal</td>
<td>R</td>
<td>46/10</td>
<td>18</td>
<td>46</td>
<td>35</td>
<td>4.13</td>
<td>0.021</td>
<td>17</td>
</tr>
<tr>
<td>gyrus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cerebellum</td>
<td>R</td>
<td>25</td>
<td>−81</td>
<td>−28</td>
<td>4.10</td>
<td>0.021</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Inferior frontal</td>
<td>L</td>
<td>47/10</td>
<td>−35</td>
<td>42</td>
<td>−11</td>
<td>3.87</td>
<td>0.029</td>
<td>12</td>
</tr>
<tr>
<td>gyrus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal ganglia</td>
<td>L</td>
<td>−21</td>
<td>0</td>
<td>11</td>
<td>3.86</td>
<td>0.030</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>(putamen)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significance level (t value), size of the respective activation cluster (No. voxels > 10) at p < .001 uncorrected (p < .05 corrected, see Methods), and possible false discovery rate correction (*FDR). Coordinates are listed in MNI space. BA is the Brodmann’s area nearest to the coordinate and should be considered approximate.
(hits vs. failures) indicated a significant main effect of memory performance, hits > failures, $F(1, 17) = 37.991$, $p < .001$, $\eta^2 = .691$, no significant effect of the communication context, $F(1, 17) = 2.166$, $p = .159$, $\eta^2 = .113$, and a significant interaction between factors, $F(1, 17) = 66.198$, $p < .001$, $\eta^2 = .796$ (see Figure 2A).

To assess differences in signal detection parameters across conditions, we further defined the discrimination index $d'$ for each orientation. We obtained an average discrimination performance of $d' = .577 (SD = 0.252)$ for the E condition and $d' = −.315 (SD = 0.238)$ for the A condition. The corresponding response criteria ($c$) were $0.291 (SD = 0.126)$ for the E condition and $0.300 (SD = 0.123)$ for the A condition. The ability to recall the communication context during the recognition task was significantly enhanced for the E condition in contrast to the A condition, $d', t(17) = 8.295, p < .001$.

Our data reveal an interaction between egocentric context and subsequent recollection of communication context. Egocentric videos were predominantly correctly remembered as egocentric (8 of 18 participants did not make a single error). However, allocentric videos tended to be falsely remembered as egocentric (3 of 18 participants did not make a single correct response). This effect is independent of the participants’ memory of the sentences, which did not differ between conditions.

Figure 2. Memory performance and confidence ratings for item and context memory. (A) The hit (left) and false alarms rate (right) for items (white) and communication contexts (gray) of ego- and allocentric video clips. (B) Corresponding discrimination performance ($d'$; left) and response criteria ($c$; right) for items (white) and context (gray) of ego- and allocentric video clips. (C) Results of the confidence ratings for correct (left) and incorrect responses (right). For conditions in which not all subjects provided responses, the number of remaining subjects is noted in the bar graph. The error bars indicate the SEM.
Analyses of false alarms (responses to new items during recognition) with regard to communication context were performed to investigate possible response biases unaffected by the actual encoding episode (these sentences were not actually encountered). We found more egocentric than allocentric responses for new sentences presented during the recognition task (E-CCnew: M = 9.44%, SD = 9.24%; E-ICold: M = 2.26%, SD = 4.49%; E-CCnew > E-ICold, t(17) = 4.867, p < .001; and A-CCnew: M = 3.24%, SD = 5.84%; A-ICold: M = 7.72%, SD = 7.63%; A-ICold > A-CCnew, t(17) = 3.767, p < .005). However, this effect is still smaller than the amount of egocentric responses in the egocentric condition as well as allococentric condition (E-CCold: M = 49.81%, SD = 17.34%; E-ICold: M = 6.48%, SD = 8.72%; [E-CCnew - E-ICold] < [E-CCold > E-ICold], t(17) = 7.591, p < .001; A-CCnew: M = 15.09%, SD = 9.99%; A-ICold: M = 38.98%, SD = 15.37%; [A-ICold - A-CCnew] < [A-ICold - A-CCold], t(17) = 4.869, p < .001). This is also reflected in the significant interaction effect in a three-factorial ANOVA, with the factors stimulus material (Ego-/Allocentric), responses to old and new items (Old/New), and memory about the context (CC/IC); main effect: Ego-/Allocentric, F(1, 17) = 2.582, p = .127, = .132; main effect: Old/New, F(1, 17) = 88.059, p < .001, = .838; main effect: Communication Context, F(1, 17) = 46.313, p < .001, = .751; interaction: Ego-/Allocentric × Old/New, F(1, 17) = .858, p = .367, = .048; interaction: Ego-/Allocentric × Communication Context, F(1, 17) = 74.518, p < .001, = .814; interaction: Old/New × Communication Context, F(1, 17) = 21.236, p < .001, = .555; interaction: Ego-/Allocentric × Old/New × Communication Context, F(1, 17) = 48.287, p < .001, = .740. Correspondingly, the “correct minus false” (old – new) proportion for egocentric responses (M = 0.4028, SD = 0.1968) is higher than for allococentric responses (M = 0.1178, SD = 0.0897), t(17) = 6.479, p < .001, suggesting that egocentric encoding leads to better memory.

Confidence Rating
Participants’ confidence ratings are presented in Figure 2C. For memories of sentences (white bars), we found higher confidence ratings for hits compared with false alarms, F(1, 17) = 37.539, p < .001, = .688, independent of communication context; egocentric vs. allocentric: main effect, F(1, 17) = 0.010, p = .922, = .001; interaction, F(1, 17) = 0.007, p = .934, = .001. We found that eight participants made no mistakes in the egocentric condition and three participants had no correct responses in the allocentric condition. Furthermore, the descriptive data indicate an interaction effect between confidence and condition, as the participants gave the highest confidence ratings for both correctly recognized E conditions and incorrectly recognized A conditions (see Figure 2). A comparison after participants with missing values were excluded confirms the interaction effect, F(1, 7) = 0.007, p < .001, = .863, demonstrating a trend for a main effect of communication context, E > A, F(1, 7) = 4.804, p = .064, = .407, and revealing no significant main effect of correct versus false responses, F(1, 7) = 0.370, p = .562, = .050.

There did not appear to be any differences in confidence ratings about item memory between egocentric and allocentric conditions. However, participants appeared to be more confident in their responses when they falsely believed that they were presented with an egocentric video as compared with when they falsely believed that they saw an allocentric video.

fMRI Results
Neural Encoding Processes Predicting Correct (CC) and Incorrect (IC) Recognition of the Communication Context versus Misses (M)
To identify the brain regions that are more active during the encoding of sentences that are subsequently remembered (in either the correct context [CC] or incorrect context [IC]) in contrast to nonremembered sentences (misses [M]), we included the corresponding contrast images of the individual first-level analyses in the flexible factorial analyses of SPM5. Further separation of egocentric and allocentric items was not performed to obtain more events and more reliable results for CC, IC, and M. However, contrast estimates resulting from the post hoc analyses presented in Figure 3D illustrate the activations of the hippocampal regions for CC, IC, and M separated into egocentric (E-CC, E-IC, E-M) and allocentric conditions (A-CC, A-IC, A-M).

For CC > M, the data revealed activity in the bilateral parietal and left lateral inferior frontal, posterior temporal, and hippocampal brain regions (see Table 1 and Figure 3; red). For IC > M, we observed bilateral parietal and precentral activation as well as activity in the bilateral medial-temporal lobe, predominantly in the EC and subiculum (see Table 1 and Figure 3; green). To identify the common activity between CC and IC conditions, we used a conjunction analysis and demonstrated bilateral superior parietal/postcentral activation for both conditions (CC > M) ∩ [IC > M]; MNIx, y, z: 32, −35, 42, r = 4.65, 28 voxels; MNIx, y, z: −39, −42, 60, r = 4.89, 14 voxels; see Figure 3; yellow).

Probabilistic cytoarchitectonic maps (Eickhoff et al., 2007) were applied to determine the specific anatomical location of the medial-temporal activation. For CC > M, the activation peak was most likely located in the CA region of the left hippocampus (MNIx, y, z: −28, −28, −14; assigned to CA; probability = 70% [40–90%]; FD: probability = 70% [0–80%]). However, for IC > M, additional regions of the bilateral EC and subiculum (SUB) were activated (right: MNIx, y, z: −25, −4, −25, assigned to amygdala: probability = 60% [10–100%]; EC: probability = 60% [10–100]; left: MNIx, y, z: −32, −18, −25, assigned to SUB; probability = 50% [30–70%]; CA: probability = 40% [20–80]; see Figure 3).
These data provide insight into the common and distinct neural encoding mechanisms that yield both accurate and inaccurate memories of the context in which a sentence was observed. Parietal and medial-temporal brain areas appear to be more active during the encoding of later correctly remembered sentences (hits) than during the encoding of nonremembered sentences (misses) independent of the communication context. The parameter estimates of the post hoc analyses (Figure 3D) indicate that activation of the CA region in the CC condition is predominantly due to the activation increase of the E-CC and not the A-CC condition. By contrast, activation of the EC and subiculum in the IC condition appears to result from the activation of both the E-IC and the A-IC conditions. This suggests that memory processes related to the binding of sentence and context within the CA region of the hippocampus are less involved in the encoding of allocentric conditions.

Figure 3. Activation for sentence memory with correct (CC) and incorrect memory for the communication context (IC) versus misses (M).
(A) The cortical activations for sentence memory with correct (CC, red) and incorrect recollection about the communication context (IC, green) in contrast to sentences that were not remembered (misses, M). (B) The medial-temporal activation pattern (from the same analyses as panel A) in sagittal (right) slices of the probability maps (Eickhoff et al., 2005, 2007; see Results section). Contrast estimates in panel C (middle) illustrate the differences for the clusters of medial-temporal activations for CC, IC, and M. Contrast estimates in panel D (right) illustrate the differences for the same regions in the post hoc analysis including the factor actor orientation (Ego- vs. Allocentric). CC: correct context; IC = incorrect context; M = misses; E-CC = egocentric correct context; E-IC = egocentric incorrect context; E-M = egocentric misses; A-CC = allocentric correct context; A-IC = allocentric incorrect context; A-M = allocentric misses; CA = cornu amonis; EC = entorhinal cortex; SUB = subiculum cortex.
Comparison of Neural Encoding Processes Predicting Subsequent Correct and Incorrect Recognition of the Communication Context (CC vs. IC)

We identified brain regions related to the encoding of accurate and inaccurate memories of the communication context through direct comparisons of CC and IC. As the CA subregion of the hippocampus is thought to have a specific role in episodic and associative memory processes (e.g., Eichenbaum, 2004), a small volume correction (SVC) for this region was also applied (see Methods section) to both contrasts (CC > IC and IC > CC).

Whole-brain analysis revealed an activation of the right calcarine gyrus for CC > IC (Brodmann’s area [BA] 17; MNI x, y, z: 14, −98, 7, t = 7.14, 211 voxels, FDR < 0.001). The analysis using SVC revealed a significant activation of the right CA region of the hippocampus (MNI x, y, z: 32, −32, −7, t = 3.98, 8 voxels, FDR = 0.034; see Figure 4A).

For IC > CC, whole-brain analysis revealed activation of the PAC (BA24, 25, 32; MNI x, y, z: 0, 32, −4, t = 4.70, 15 voxels, FDR = 0.173; see Figure 4A), the superior frontal cortex (BA9/6; MNI x, y, z: −21, −7, 67, t = 4.86, 16 voxels, FDR = 0.175), and the occipital lobe (BA18; MNI x, y, z: −11, −91, −7, t = 4.40, 19 voxels, FDR = 0.207). The SVC analysis revealed no additional significant activation of the CA region of the hippocampus.

Our results suggest that there are particular encoding processes that lead to accurate and inaccurate memories in the left CA region to be related to context memory, whereas the PAC and superior frontal cortex may be involved in the encoding of inaccurate memories.

The bar graphs of the post hoc analyses (Figure 4B) indicate that activation of the CA region in the CC condition is predominantly related to increased activation of the E-CC and not the A-CC condition. This suggests that memory processes related to the binding of sentence and context within the CA region of the hippocampus are less involved in the encoding of allocentric conditions. By contrast, increased activation within the PAC for IC > CC is predominantly due to differences in the allocentric condition (A-IC > A-CC) and not the egocentric condition (E-IC = E-CC). This suggests that increased activation in the PAC is not generally related to incorrect context memory but is unique to the encoding of incorrect context for allocentric situations. Contrast estimates for the superior frontal and occipital activations indicate that activity in these regions is predominantly related to the stimulus condition (Ego-Allocentric) and less to the subsequent memory performance.

Interaction Between Communication Context and Memory (E-CC > E-IC) > (A-CC > A-IC)

Previous analyses focused on the neural substrates of correct and incorrect memory of social interactions. However, the post hoc analyses that differentiated between egocentric and allocentric encoding episodes have indicated that the encoding context has an effect on these memory processes. We calculated an interaction between encoding context and context memory (E-CC > E-IC) > (A-CC > A-IC) to provide insight into the influence of encoding context on these memory processes. We found increased activation in bilateral and medial frontal and left temporal and parietal brain regions as well as the bilateral BG in this analysis (see Figure 4 and Table 2 for coordinates and statistics). Bar graphs in Figure 5 illustrate that these regions are more activated for sentences subsequently remembered as egocentric (E-CC and A-IC) than sentences remembered as allocentric (A-EC and A-CC). Thus, encoding processes that predict subsequent egocentric memories (regardless of if the episode was actually encountered in an egocentric condition) are related to bilateral and medial frontal and left temporal and parietal brain regions as well as the bilateral BG.

We extracted the average brain activation for each participant within ROIs of the left and right CA and the EC to explore the influence of encoding context on activation within medial-temporal structures. As illustrated by Figure 6, we found significant modulation of memory-related activation (CC > M) within all ROIs for the egocentric condition (E-CC > E-M), all ROIs together, t(17) = 2.686, p < .05, but not for the allocentric condition (A-CC > A-M), all ROIs together, t(13) = −.080, p = .937. Directed comparisons support the finding that the effect observed in the egocentric condition is present in all ROIs: left CA, t(17) = 3.249, p < .005; right CA, t(17) = 2.145, p < .05; left EC, t(17) = 2.552, p < .05; right EC, t(17) = 1.766, p < .05 (see Figure 6). The differences between subregions of the hippocampus did not reach the significant threshold.

These results indicate that hippocampal activations are modulated in relation to memory performance only in the egocentric condition. This suggests that processes that bind communication context and spoken sentence occur only for sentences remembered as egocentric that were actually encountered in an egocentric context.

DISCUSSION

Memories of interpersonal interactions comprise more than just the words spoken; they include additional important information about the context in which the communication occurs. Our study aimed to determine the neural encoding processes underlying successful recognition of earlier communications, with and without recollection of the context in which they were observed.

Our results indicate that memories of social interactions are egocentrically biased. Participants tended to report inaccurately that they had been directly addressed when the original event was presented in an allocentric context. At the neural level, we observed that activation of specific cortical and hippocampal brain regions during encoding predicted subsequent accurate and inaccurate recollection of contextual information. Activity in the right hippocampus was associated with successful encoding of speech,
gesture, and their social context. In contrast, the anterior cingulate, superior frontal, and bilateral EC/subiculum was associated with the inaccurate encoding of the social context of the original communications. These results agree with previous research on the memory processes involved in speech and gesture binding (Straube et al., 2009) and memory theories that suggest the hippocampal CA region plays a role in episodic or relational memory processes (e.g., Kensinger & Schacter, 2006; Eichenbaum, 2004; Ranganath et al., 2004; Davachi et al., 2003). Furthermore, our data suggest the frontal lobe is involved in processes that result in inaccurate memories, which agrees with past research on memory encoding (e.g., Kubota et al., 2006; Okado & Stark, 2005; Gonsalves et al., 2004) and recognition (Slotnick & Schacter, 2004; Cabeza et al., 2001; Swick & Knight, 1999; Schacter et al., 1997; Schacter, Curran, et al., 1996; Schacter, Reiman, et al., 1996; for a review, see Schacter & Slotnick, 2004).

 Straube et al. 317

Figure 4. Neural correlates of correct versus incorrect memory for the encoding context. (A) Results from the ROI analyses of the CA region of the hippocampus. The right hippocampus is activated for the direct comparison of correct versus incorrect memory for the communication context. Contrast estimates of the post hoc analyses (B; right) illustrate that this difference is mainly due to the difference in the egocentric condition. (C) Result of the reverse contrast (IC > CC). Contrast estimates on the right of panels A and C illustrate the differences between conditions from the original analyses. Contrast estimates in panels B and D illustrate the differences between conditions within the same regions from the post hoc analysis, including the factor actor orientation (Ego- vs. Allocentric). CC = correct context; IC = incorrect context; M = misses; E-CC = egocentric correct context; E-IC = egocentric incorrect context; E-M = egocentric misses; A-CC = allocentric correct context; A-IC = allocentric incorrect context; A-M = allocentric misses; CA = cornu amonis; OL = occipital lobe; SFG = superior frontal gyrus; L = left; R = right.
We found that the left inferior frontal gyrus and the posterior temporal lobe were more active during the encoding of items whose contexts were later correctly remembered (CC) than they were for misses (M). Past studies have shown that inferior frontal and posterior temporal brain regions are involved in speech–gesture integration (Kircher, Straube, et al., 2009) and are also related to memory binding processes (Straube et al., 2009). These memory and integration processes are most likely engaged during the encoding of memories with accurate contextual information as opposed to the encoding of memories with inaccurate contextual information. Straube et al. (2009) demonstrated that the individual subsequent memory performance for related abstract speech and gesture information is correlated with activity in the left inferior frontal and the posterior middle temporal gyrus during encoding. Although we presented written sentences without gestures during the recognition phase of this experiment, it is most

Figure 5. Interaction of communication context and context memory. Results from the post hoc analyses, showing activations for the interaction between encoding context (Ego- vs. Allocentric) and context memory [(E-CC > E-IC) > (A-CC > AIC)]. Results are presented on a single subject’s rendered brain (top and middle) and an axial slice of the anatomical toolbox (bottom). Contrast estimates represent the averaged beta value (arbitrary units [a.u.]) across all voxels of each activation cluster. Error bars represent the SEM. Contrast estimates show that all presented regions are more activated for trials subsequently remembered as egocentric (E-CC and A-IC) in contrast to those remembered as allocentric (E-IC and A-CC). CC = correct context; IC = incorrect context; M = misses; E-CC = egocentric correct context; E-IC = egocentric incorrect context; E-M = egocentric misses; A-CC = allocentric correct context; A-IC = allocentric incorrect context; A-M = allocentric misses; IPL = inferior parietal lobe; MTG = middle temporal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; L = left; R = right.
likely that gesture information is better incorporated in the neural representation of the communication episode when contextual information (such as the speakers’ body orientation) is also remembered. Therefore, the left lateralized fronto-temporal activation pattern for CC versus M possibly indicates that memory-binding processes of speech and gesture information are occurring.

In both CC and IC conditions (in contrast to M conditions), we observed bilateral postcentral/parietal brain activation during encoding. This observed activity might be due to heightened gesture processing in the dorsal visuospatial stream, eventually yielding more accurate memories (e.g., Cunnington, Windischberger, Robinson, & Moser, 2006; Weiss et al., 2006; Mülhau et al., 2005; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004). However, there is also evidence that the parietal lobe plays a role in episodic memory retrieval (e.g., Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Vilberg & Rugg, 2008; Naghavi & Nyberg, 2005; Wagner et al., 2005; Cabeza & Nyberg, 2000), working memory, and verbal storage processes (e.g., Herwig et al., 2003). Kahn, Davachi, and Wagner (2004) and Wheeler and Buckner (2003) observed activation in the left inferior parietal cortex during false alarms. In the study by Kahn et al., participants were presented with words while in a scanner and then were asked to identify the words they had seen in a recognition test. During the recognition phase, activity was observed in the left inferior parietal cortex during false alarms, which suggests that activation of this region is involved in perceived recognition. In addition, parietal regions appeared to interact with the hippocampal formation during successful recognition (Vincent et al., 2006). Past observations of parietal/postcentral activity during correct and incorrect recognition are consistent with our current finding that the parietal lobe is involved in encoding processes that lead to accurate and inaccurate memories of context information. Processes of imagining that occur during encoding, which might be related to parietal activations, are perhaps the basis of the formation

Figure 6. Medial-temporal lobe activation. Results from the ROI analyses of the CA and the EC of the left and right hippocampus. The sagittal (left) and coronal slices of a template brain illustrate the location of the subregions of the hippocampus (EC: black; CA: white). Contrast estimates represent the averaged beta value (arbitrary units [a.u.]) across voxels of each ROI. Error bars represent the SEM. Contrast estimates illustrate a modulation of activation with regard to memory quality within the CA region for the egocentric condition (CC > IC > M). The EC seems to be involved if item, but not context, is correctly remembered (E-IC and A-IC). For the allocentric context, the A-IC condition led to highest activation within CA and EC. L = left; R = right.
of false memories (Gonsalves et al., 2004; Gonsalves & Paller, 2000).

We found that PACC and superior frontal cortex were more active during encoding when communication context was later incorrectly remembered. This result is consistent with the view that the frontal cortex plays a role in false recognition (Slotnick & Schacter, 2004; Cabeza et al., 2001; Schacter et al., 1997; Schacter, Reiman, et al., 1996) and agrees with evidence that the ACC is involved in false recognition (Slotnick & Schacter, 2004). Interestingly, Kim and Cabeza (2007) found that the ACC (among other regions) is active during trials that participants are confident they have previously seen, regardless if they have actually encountered them before. The confidence ratings obtained in our study indicate that participants’ confidence in their memories of the communication context did not differ between true and false recognition. However, we observed activation of the ACC only during the encoding of trials in which the context was inaccurately remembered. Our post hoc analysis indicate that this effect is mainly due to differences in the allocentric condition (A-IC > A-CC), suggesting that the PACC has a specific role in trials subsequently falsely remembered as egocentric (self-referencing). By contrast, activation of the occipital and superior frontal cortex seems to be especially affected by the stimulus condition (ego-/allocentric), and results of the collapsed conditions may predominantly represent differences in the amount of egocentric and allocentric trials between CC, IC, and M (see Figure 4C and D).

Although most past research on the neural basis of true and false memories investigated retrieval processes, we looked at neural activity during encoding and compared these data to subsequent recognition performance. Participants remembered all sentences equally well, regardless of the communication context. However, memory of just the communication context was not only worse in allocentric conditions, participants tended to recall allocentric stimuli as having been encountered egocentrically. One interpretation of this finding is that the contextual information in the allocentric condition was less personally relevant for participants and therefore was less accurately remembered (e.g., Symons & Johnson, 1997). However, this interpretation accounts for poorer performance in the allocentric condition but does not explain why memories of social context are biased toward the egocentric condition. Furthermore, the fact that participants remembered sentences in both conditions equally well contradicts the theory that individuals were less attentive in allocentric situations. An alternative explanation is that participants may have imagined themselves as the unseen addressed person to get a better understanding of the communication and performed a mental rotation of the observed event during encoding. Processes responsible for such shifts in mental perspective are often referred to as “theory of mind” or “mentalizing” mechanisms (e.g., Frith & Frith, 1999). The occurrence of such processes during encoding may change the participant’s perception of the situation, leading to correct item memory (comparable with the egocentric condition), but a false memory about the encoding context of allocentric communications. According to this theory, the observed activation of the ACC could also reflect shifts in imagined perspective, which have been reported in other studies that investigated mentalizing or theory of mind processes (e.g., Kircher, Blumel, et al., 2009; Krach et al., 2008, 2009; Kedea, Berthoz, Wessa, Hilton, & Martinot, 2008; Cheng et al., 2007; Schulte-Ruther, Markowitsch, Fink, & Piefke, 2007; Amodio & Frith, 2006; Baird et al., 2006; David et al., 2006; Lawrence et al., 2006; Vogele et al., 2004) and other social processing mechanisms (for a review, see Lieberman, 2007). With regard to memory processes, an egocentric bias reflects the strong role played by the self in the encoding and retrieval of episodic memories (for a review, see Schacter et al., 2005). It has been shown that when information is encoded in relation to ourselves, it is usually better remembered than other types of semantic information (Rogers et al., 1977; for a review, see Symons & Johnson, 1997). Kelley et al. (2002) have used fMRI to reveal brain regions that play a role in the “self-reference effect.” Participants were scanned while they either decided whether a series of trait adjectives (e.g., honest, friendly) described themselves or decided whether they described a familiar other person (in this case, George Bush). The first condition has been used extensively to engage processing in relation to the self, whereas the latter condition is assumed to involve semantic, but not self-referential, encoding. Semantic but non-self-referential encoding was associated with activation in the left inferior PFC, whereas self-referential encoding was associated with activation in an inferior portion of the medial PFC (including inferior parts of the ACC). Consistent with our data, these findings suggest a specific role of the inferior medial frontal/ACC in self-referential encoding of information. Therefore, an egocentric bias and related self-referential encoding processes may be the basis of false context memory in the allocentric condition. To test this assumption in our fMRI data set, we performed an interaction analysis between communication context and context memory (E-CC > E-IC) > (ACC > A-IC). In this analysis, we found increased activation in bilateral and medial frontal and left temporal and parietal brain regions as well as the bilateral BG. These regions are more activated for sentences subsequently remembered as egocentric than sentences remembered as allocentric. Thus, encoding processes that predict subsequent egocentric memories (regardless of if the episode was actually encountered in an egocentric condition) are related to increased activation in a distributed network, including regions previously found to be involved self-referential encoding (e.g., Macrae et al., 2004; Kelley et al., 2002), mentalizing (e.g., Schulte-Ruther et al., 2007), and perspective taking (e.g., David et al., 2006; Vogele et al., 2004; for a meta-analysis about self-referential processes, see Northoff et al., 2006). However, some of these regions are also thought to be involved in false memory encoding (e.g., Gonsalves et al., 2004; PACC) and false recognition (e.g., Kim & Cabeza, 2007; left parietal and superior frontal cortex). Specifically, the
medial cortical regions appear to be involved in self-referential processing in the brain (Northoff et al., 2006; Northoff & Brembs, 2004; Kircher et al., 2000). Although the observation that the frontal lobe is related to correct and false memory processes is a consistent finding, there is a high heterogeneity in the specific location of frontal activation between the studies, which suggests functional differentiation within this brain region. In our study, we found that the PACC was specifically activated for incorrectly egocentric remembered sentences (A-IC > A-CC), whereas dorsal medial frontal and superior frontal regions appear to be related to general egocentric encoding (subsequent egocentric remembering: E-CC > E-IC and A-IC > A-CC). This suggests at least a functional differentiation between the PACC and the dorsomedial frontal cortex with regard to the creation of false memories about the communication situation. Findings from studies by Kim and Cabeza (2007), Gonsalves et al. (2004), and Slotnick and Schacter (2004) actually refer to regions located quite close to the activated location of the PACC found in our study. The corresponding cluster extent allows us to assume that there is at least an overlap of the reported regions. This indicates that the PACC is involved not only in false recognition (Kim & Cabeza, 2007; Slotnick & Schacter, 2004) but also in the creation of false memories (e.g., Gonsalves et al., 2004), which might be related to self-referential encoding (e.g., Kelley et al., 2002) and mentalizing processes (e.g., Schulte-Ruther et al., 2007) triggered by the communication situation (see Northoff et al., 2006). This is in line with the theory that neural activity in the ventral medial cortical structures (including the PACC) is involved in encoding the self-relatedness of stimuli and therefore representing them as self-referential (see Northoff et al., 2006). Our data suggest that general egocentric encoding processes exist within the medial and left lateral frontal cortex, whereas the PACC seems to be uniquely involved in additional processes related to the creation of a self-referential episode in an allocentric context. Self-referential processing (Northoff et al., 2006) and vivid imagining during stimulus processing (e.g., Gonsalves et al., 2004) might be the basis of processes that lead to correct item memory but incorrect context memory. As indicated by the association between bilateral activation of the BG and egocentric encoding (subsequent egocentric vs. allocentric remembering), this effect might be mediated by the reward system activated through self-referential processes (De Greck et al., 2008).

We also found that activity in the hippocampus was related to sentence and context memory. The left hippocampus (CA) appears to be related to memory of the sentence itself, independent of if the context in which it was observed is subsequently remembered. Activation of the bilateral EC and subiculum was observed for correctly remembered sentences with inaccurate memories of the communication context. In contrast, the right CA region of the hippocampus is more active in trials in which the context is later correctly recalled. These findings are consistent with evidence that the hippocampus (predominantly the CA region) plays a specific role in episodic or relational memory (e.g., Straube et al., 2009; Kircher et al., 2008; Kensinger & Schacter, 2006; Achim & Lepage, 2005; Eichenbaum, 2004; Ranganath et al., 2004; Davachi et al., 2005), but conflict with previous evidence that suggests that item and source memory both depend on the same medial-temporal lobe structures (e.g., Gold, Hopkins, & Squire, 2006). We found unique patterns of activation in the medial-temporal lobe structures for the encoding of accurate versus inaccurate episodic contextual information. The lateralization of hippocampal activity suggests that spatial encoding processes are involved when the communication context is correctly remembered (e.g., Bird, Shallice, & Cipolotti, 2007; Crane & Milner, 2005; Parslow et al., 2005; Treyer, Buck, & Schneider, 2005; Feigenbaum & Morris, 2004; Kessels, Hendriks, Schouten, van Asseleem, & Postma, 2004). This finding reflects the direct manipulation of a spatial variable (communication context/actor’s orientation) of the communication episode. This result may suggest that accurate memories of a communication context rely more on visuospatial processes than on abstract-social processes. However, alternative explanations for the right hippocampal activation (like the encoding of interesting emotional stimuli) are also plausible (see Hamann, Ely, Grafton, & Kilts, 1999).

The post hoc analyses of activation of the subregions of the hippocampus (CA and EC) indicate that the hippocampal activations are modulated in relation to memory performance only in the egocentric condition. This suggests that processes that bind communication context and spoken sentence occur only for sentences remembered as egocentric that were actually encountered in an egocentric context. For items in the allocentric condition, the reduced modulation of activation within the hippocampal subregions seems to be related to false memories of the encoding situation.

Further investigations into the unique encoding processes of multimodal communication (as well as the general processes responsible for item and source memory) are necessary to disentangle the underlying neural mechanisms. It is also important to note that the influence of gestures on self-referential encoding processes cannot be disentangled in this study. Gestures were included primarily to emphasize the visual component of the communication. However, they may have a fundamental influence on related memory processes. This should be clearly addressed in future studies because gestures themselves play an important role in memory encoding (Straube et al., 2009) and may be sufficient to elicit specific self-referential encoding processes. Furthermore, it might be interesting in future studies to investigate the effect of communication context with an implicit recognition task and then compare the neural encoding and retrieval processes in relation to self-relevant stimuli.

Here we investigated implicit encoding without any self or memory-related instruction. The previous rating (performed by an independent subject group) indicates no differences in familiarity and understanding of de-
scriptive or social contents of utterances in an egocentric or allocentric context. However, a participant’s perception of being addressed was significantly enhanced in the egocentric in contrast to the allocentric condition. Egocentric encoding processes might support item memory because egocentric and allocentric presented sentences were equally well remembered, although both were more likely to be remembered as having been encountered in an egocentric context than items not seen during fMRI measurement. With regard to the idea of self-referential encoding, increased activation in the PACC might reflect the increased processing effort for self-referential encoding in allocentric situations. The corresponding decreased activation in the CA region of the hippocampus is possibly related to reduced attention or even inhibition of spatial information in allocentric contexts. This suggests that an egocentric bias and related self-referent encoding processes are the basis of correct item memory but false memory about the encoding context of allocentric conditions.

In conclusion, our study demonstrated that distinct patterns of activation in cortical and hippocampal areas during encoding are associated with accurate and inaccurate memories of past communications. In addition to supporting theories that the hippocampus is involved in relational-associative memory, our results provide new insight into processes that lead to false memories of social interactions. One such process may involve an egocentric bias that leads participants to believe incorrectly they were directly addressed in past allocentric social situations. Self-referential encoding processes reflected in predominantly frontal activation increase and hippocampal activation decrease might be the basis of successful item memory but false memory of the social encoding context.

Acknowledgments

This research project was supported by a grant from the Interdisciplinary Center for Clinical Research “BIOMAT” (IZKF VV N68) within the Faculty of Medicine at the RWTH Aachen University, Germany. The authors thank Katharina Augustin, Bettina Freese, and Simone Schröder for help with the preparation and evaluation of the stimulus material, Thilo Kellermann for assistance with the fMRI analyses, and Bianca Bromberger for help with the editing of the manuscript.

Reprint requests should be sent to Dr. Benjamin Straube, Department of Psychiatry and Psychotherapy, Philipps-University Marburg, Rudolf-Bultmann Str. 8, 35039 Marburg, Germany, or via e-mail: straubeb@med.uni-marburg.de.

REFERENCES


