Language in context: MEG evidence for modality general and specific responses to reference resolution

Language in context

Christian Brodbeck¹,², Laura Gwilliams¹,³ and Liina Pykkänen¹,²,³

¹Department of Psychology, New York University, 6 Washington Place, New York, NY 10003, USA
²Department of Linguistics, New York University, 10 Washington Place, New York, NY 10003, USA
³NYU Abu Dhabi Institute, New York University Abu Dhabi, PO Box 129188, Abu Dhabi, United Arab Emirates

DOI: 10.1523/ENEURO.0145-16.2016

Received: 12 December 2016

Revised: 5 December 2016

Accepted: 7 December 2016

Published: 15 December 2016

Author Contributions: CB and LP designed research, CB and LG performed research, CB and LG analyzed data, CB wrote the paper.

Funding: National Science Foundation (NSF)
100000001
BCS-1221723

Funding: NYUAD Institute
G1001

Conflict of Interest: Authors report no conflict of interest

Correspondence should be addressed to CB (christianbrodbeck@nyu.edu)

Cite as: eNeuro 2016; 10.1523/ENEURO.0145-16.2016

Alerts: Sign up at eneuro.org/alerts to receive customized email alerts when the fully formatted version of this article is published.
1. Manuscript Title: Language in context: MEG evidence for modality general and specific responses to reference resolution
2. Abbreviated Title: Language in context
3. List all Author Names and Affiliations in order as they would appear in the published article:
   i. Christian Brodbeck\textsuperscript{1,3}
   ii. Laura Gwilliams\textsuperscript{1,3}
   iii. Liina Pylkkänen\textsuperscript{1,2,3}
   iv. \textsuperscript{1}Department of Psychology, New York University, 6 Washington Place, New York, NY 10003, USA
   v. \textsuperscript{2}Department of Linguistics, New York University, 10 Washington Place, New York, NY 10003, USA
   vi. \textsuperscript{3}NYU Abu Dhabi Institute, New York University Abu Dhabi, PO Box 129 188, Abu Dhabi, United Arab Emirates
4. Author Contributions: CB and LP designed research, CB and LG performed research, CB and LG analyzed data, CB wrote the paper.
5. Correspondence should be addressed to CB (christianbrodbeck@nyu.edu)
6. Number of Figures: 6
7. Number of Tables: 0
8. Number of Multimedia: 0
9. Acknowledgements: This research was supported by the National Science Foundation Grant BCS-1221723 (LP) and grant G1001 from the NYUAD Institute, New York University Abu Dhabi (LP). Two creative commons licensed icons were used: The “Sound” icon in Figures, and by Freepik from http://www.flaticon.com and the “Click” icon in Figures and by Creative Stall from http://thenounproject.com.
10. Conflict of Interest: Authors report no conflict of interest
11. Funding sources: National Science Foundation Grant BCS-1221723 (LP) and grant G1001 from the NYUAD Institute, New York University Abu Dhabi (LP).
12. Number of words for Abstract: 213
13. Number of words for Significance Statement: 109
14. Number of words for Introduction: 747
15. Number of words for Discussion: 3000
Language in context: MEG evidence for modality general and specific responses to reference resolution

Christian Brodbeck\textsuperscript{1,3}
Laura Gwilliams\textsuperscript{1,3}
Liina Pylkkänen\textsuperscript{1,2,3}

\textsuperscript{1}Department of Psychology, New York University, 6 Washington Place, New York, NY 10003, USA
\textsuperscript{2}Department of Linguistics, New York University, 10 Washington Place, New York, NY 10003, USA
\textsuperscript{3}NYU Abu Dhabi Institute, New York University Abu Dhabi, PO Box 129188, Abu Dhabi, United Arab Emirates

Acknowledgements:
This research was supported by the National Science Foundation Grant BCS-1221723 (LP) and grant G1001 from the NYUAD Institute, New York University Abu Dhabi (LP). Two creative commons licensed icons were used: The “Sound” icon in Figures 2, 5 and 6 by Freepik from http://www.flaticon.com and the “Click” icon in Figures 2 and 3 by Creative Stall from http://thenounproject.com.

Abstract
Successful language comprehension critically depends on our ability to link linguistic expressions to the entities they refer to. Without reference resolution, newly encountered language cannot be related to previously acquired knowledge. The human experience includes many different types of referents, some visual, some auditory, some very abstract. Does the neural basis of reference resolution depend on the nature of the referents or do our brains utilize a modality general mechanism for linking meanings to referents? Here we report evidence for both. Using MEG, we varied both the modality of referents, which consisted either of visual or auditory objects, and the point at which reference resolution was possible within sentences. Source localized MEG responses revealed brain activity associated with reference resolution that was independent of the modality of the referents, localized to the medial parietal lobe and starting around 415 ms after onset of reference resolving words. A modality-specific response to reference resolution in auditory domains was also found in the vicinity of auditory cortex. Our results suggest that referential language processing cannot be reduced to processing in classical language regions and representations of the referential domain in modality-specific neural systems. Instead, our results suggest that reference resolution engages medial parietal cortex which supports a mechanism for referential processing regardless of the content modality.
Significance statement

Reference resolution is an elementary mechanism for language comprehension, connecting language meaning to pre-existing knowledge. It is unknown whether reference resolution depends on brain mechanisms specific to the modality of the referents, for example whether they are visual or auditory objects, or whether our brains utilize a modality general mechanism for linking meanings to referents. Here we show using source localized MEG that reference resolution is associated with a response in the medial parietal lobe, independent of referent modality, supporting a modality-general mechanism for reference resolution. An additional response associated with resolving reference to auditory objects in auditory cortex suggests that modality-specific representations of the referents are also involved.

Introduction

A crucial precondition for understanding a sentence in context is identifying the entities that the sentence is about. This was demonstrated in a classic study, which showed how a text passage that appears incomprehensible when presented in isolation becomes perfectly natural when presented after a picture that provides meaningful referents for the text (Bransford & Johnson, 1972). However, much of the research on the neural basis of language comprehension ignores this referential dimension, studying generic sentences presented without a specific context. Here we report a study in which we deliberately manipulated the relationship between background knowledge and linguistic expressions to uncover the neural basis of successful reference resolution.

Unlike in most laboratory experiments, language comprehension in the real world takes place in a rich context. Language comprehenders must not only decode the literal meaning of a message, but also connect it to mental models representing what the message is about (Graesser, Millis, & Zwaan, 1997). A body of evidence suggests that such models are connected to modality-specific cognitive systems. For example, even when participants are looking at a blank screen while listening to stories, their eye movement patterns reflect spatial configurations described in the language input (Spivey & Geng, 2001; Altmann, 2004; Altmann & Kamide, 2009). Furthermore, EEG data suggests that readers resolving reference to an item on a previously seen visual display access a retinotopic representation (Brodbbeck, Gwilliams, & Pylkkänen, 2015).

These observations resonate with theories of embodied meaning, according to which meaning is represented in the same cognitive systems that also process sensory information (Barsalou, 1999; Hauk, Davis, Kherif, & Pulvermüller, 2008). Theories of strong embodiment go as far as proposing that lexical meanings are represented in sensory regions (Pulvermüller, 2013), implying that the task of mapping meanings to referents could be performed by modality-specific systems exclusively (red path in Figure 1). But even if lexical semantics involves amodal regions, it is still possible that situation models, in which specific referents are represented, are constrained to sensory-specific cortices (blue path in Figure 1). In such a model, amodal regions should be sensitive to lexical, but not referential properties of language input.
Alternatively, reference resolution could involve an amodal or modality-general mecha-
nism that mediates between lexical and referential meanings. Such a mechanism could be
related to amodal discourse representations (Graesser et al., 1997), but it might also be re-
quired by embodied theories of meaning, for example to coordinate referents of different
modalities.

A number of fMRI and PET studies have investigated linguistic contrasts that involved ref-
ferential properties. Coherent language, which involves repeated reference to the same enti-
ties, consistently activates medial frontal and medial parietal regions in addition to classic
perisylvian language areas (Ferstl, Neumann, Bogler, & von Cramon, 2008). More specifical-
ly, medial as well as lateral parietal areas were more active in response to sentence pairs
introducing a conjoined subject (e.g., *Jeremy and Roger*) compared to a individually intro-
duced referents, suggesting that these regions might be involved in creating and tracking
discourse referents (Boiteau, Bowers, Nair, & Almor, 2014). Medial and lateral parietal, as
certain as frontal areas were also activated by sentences containing unresolved referential
ambiguities (Nieuwland, Petersson, & Van Berkum, 2007). While these results point to a
number of brain regions that could be involved in referential processing, the low temporal
resolution of fMRI and PET makes it difficult to link brain activation to specific linguistic
processes, which follow each incoming word in a rapidly cascading fashion. Finally, none of
these studies explicitly manipulated the modality of the referents, so their results could be
related to imagery associated with language comprehension.

Reference resolution itself is inherently difficult to separate from other cognitive processes
associated with managing referents, such as retrieving referents from memory and locating
them in the environment (see Discussion). Here we tried to create an experimental situa-
tion which minimizes memory retrieval and scanning of the environment by presenting
simple referential contexts immediately preceding linguistic stimuli that contained referen-
tial expressions. We used MEG to directly contrast reference resolving words with non-
resolving controls. In order to locate a response involved in reference resolution independ-
ent of the modality of the referential domain, we constructed parallel conditions with audi-
tory and visual referential domains (see Figures 2 and Figure 3). We predicted two
possible response patterns: regions that track the set of possible referents should exhibit
more activation for the ambiguous condition, in which the expression is compatible with
two referents, while regions that become active when reference is resolved should exhibit
more activity in the resolving condition.

**Materials and methods**

**Participants**

We collected data from 26 right-handed native English speakers recruited from the com-
munity on the New York University, Abu Dhabi campus. Two participants were excluded
because of excessive artifacts leading to less than 70% good trials, leaving 24 participants
for the final analysis (18 female, mean age 24, range 19-50). New York University Abu Dha-
bi is an English speaking university located just outside the city of Abu Dhabi. Our partici-
pants were thus immersed in an English speaking environment that involves little contact with local languages unless students and staff actively seek it out. Out of the 24 participants in the final analysis, 16 had grown up speaking only English, whereas 8 had grown up bilingually. The second native language varied between participants (Hindi, Japanese (2), Malayalam, Mandarin, Spanish, Urdu, Vietnamese). The protocol was approved by the Institutional Review Board of New York University Abu Dhabi, and all participants provided written consent before beginning the experiment.

**Materials**

Each trial consisted of presentation of a referential domain, followed by a question about the domain, presented word for word (see Figure 2 and Figure 3). Participants’ task was to answer questions such as *Was the grunt in the end?* by pressing one of two response buttons. Target stimuli were referential expressions which were identical in their linguistic surface properties but differed in whether they resolved reference, for example, *the grunt* in a context that contained one or two grunts.

**Auditory referential domains**

For auditory referential domains, we selected 10 sounds with monosyllabic names that were easily identifiable and for which short (~100-300 ms) and long (~500-600 ms) variants were clearly distinguishable. Nine sounds (bark, buzz, caw, chirp, cluck, croak, honk, mew, splash) were extracted from sounds available under a creative commons license ([http://freesound.org](http://freesound.org)) and one (beep) was created from a 1000 Hz sine wave.

Figure 2 shows a sample trial for the auditory referential domains. Each referential domain consisted of 3 sounds, played sequentially. All domains were constructed such that 2 sounds shared the name, and 2 other sounds had the same length. Presentation of the domain started with a fixation cross for 600 ms, followed by the 3 sounds. For long sounds, the stimulus onset asynchrony was 1000 ms, for short sounds it was 700 ms. The domain was followed by the question in serial visual presentation, with function words presented for 400 ms and content words presented for 600 ms. The last word of the question was ended with a question mark and stayed on the screen until the participant made a yes/no response via button press.

The target for analysis was the first noun in the question, marked with an arrow in Figure 2. In trials of the reference resolving condition, the noun named a unique sound, i.e., the sound that did not share its name with another sound in the domain. In control trials, the noun did not resolve reference because it was compatible with two sounds in the domain that shared the same name. In this case, the noun was followed by a prepositional phrase that used the referent’s location for disambiguation, for example *the grunt in the middle.*

When the noun resolved reference, the question continued asking for the temporal location of the sound, for example *Was the grunt in the middle?*. In control trials the question asked for the length of the sound, as in *Was the grunt in the middle long?*. The correct answer to the question was “yes” on exactly half of the trials, counterbalanced between conditions.

This design assured that conditions were indistinguishable up to the critical noun.
When hearing one of the sounds by itself, it might have been difficult to judge its length, i.e., whether it was the long or the short token. However, because the question only asked for the length of the sound in the control condition, this question always followed domains that included both the long and the short version of the same sound, allowing for a direct comparison of the two versions.

A list of all possible referents was generated by permuting referent name (10 nouns), referent length (long or short) and referent location (first, second or third sound). One such list was assigned to the resolving noun condition, another one to the ambiguous noun condition, and a third was split between the two condition to produce 30 trials in each cell of the Reference × Location design. The remaining elements of each trial were filled in using a balanced randomization procedure. The same trials were presented to each participant, but the order was randomized for each session.

**Visual referential domains**

For the visual referential domains, we selected ten objects with monosyllabic names that could be used to generate easily identifiable outline images (truck, star, house, car, fish, pig, tree, bird, boat, cat). Outlines were created based on photos using the Inkscape vector drawing application (http://www.inkscape.org). To match visual referential domains in complexity to the auditory domains, where sounds were either long or short, we chose just two colors, black and white.

Trials were constructed analogously to the trials with auditory referential domains. Figure 3 shows a sample trial for each condition. Each referential domain consisted of 3 objects arranged vertically. All domains were constructed such that 2 objects shared the shape, and 2 other objects shared the color. Each trial started with presentation of a fixation cross for 600 ms, followed by the referential domain presented for 300 ms, and the question after an interstimulus interval of 300 ms. Presentation of the questions followed the same protocol as for auditory referential domains.

In visual domain trials, the form of the referential expression was varied as an additional factor. In half of the trials referential expressions were constructed in parallel to the auditory domain condition, with resolving noun contrasted with ambiguous nouns followed by a prepositional phrase specifying the location (e.g., the bird vs the bird in the middle). In the other half of the trials, the referential expression was an adjective-noun phrase, such as the black bird. In those expressions, the adjective was the target. In a domain with only one black item, the adjective resolved reference, while in trials with two black items the noun did. Because the location was never included in the referential expression these questions always asked for the location of the referent. Referential expressions with adjective targets were not included with auditory referential domains because sounds would have been harder to distinguish based on length alone.

Including reference resolving adjectives gave us an additional distinction between reference resolution at complete and incomplete linguistic phrases. There is evidence that the status of an expression as a complete linguistic phrase interacts with referential processing. Eye tracking studies suggest that listeners predict whether a potentially complete
noun phrase will be followed by a prepositional phrase or not, based on whether they could
resolve reference, i.e., if a noun phrase is compatible with several potential referents they
expect additional information to disambiguate between competing referents (Spivey,
Tanenhaus, Eberhard, & Sedivy, 2002; Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy,
1995). A response to reference resolving nouns (the bird) could thus also indicate the com-
pletion of a linguistic phrase, since the comprehender would expect the phrase to be elabo-
rated in the control condition (the bird in the middle). Adjectives did not entail this contrast
since they were always followed by a noun (the black bird). In contrast, referential pro-
cessing should happen at incomplete phrases too. Eye tracking as well as EEG evidence
suggest that language comprehenders use the information in reference resolving adjec-
tives. For example, when participants are instructed to Touch the starred yellow square in a
context with only one starred item, they look at the target item shortly after the word
starred (Eberhard, Spivey-Knowlton, Sedivy, & Tanenhaus, 1995; Sedivy, K. Tanenhaus,
Chambers, & Carlson, 1999). Similarly, readers presented with a referential expression in
which the adjectives allows resolving reference to an object on the left or the right side of a
visual display exhibit an event-related potential that is sensitive to the location of the refer-
ent starting around 333 ms after adjective onset (Brodbbeck et al., 2015). Including advec-
tives as targets thus allowed us to distinguish between phrasal and referential processing.

The same procedure as for auditory domains was employed to create 30 trials per condi-
tion in the Reference (target resolving or ambiguous) by location (top, middle, bottom) by
Target (noun, adjective) design (cf. Figure 3).

**Lexical variables**

The present study was specifically designed to assess reference resolution in different con-
texts: in auditory and visual referential domains, and with information conveyed by a noun
or an adjective. Stimuli were developed with a focus on creating natural referential situa-
tions. Within each context, target words were identical between the resolving and ambigu-
ous target conditions, and since our hypotheses did not pertain to main effects of context,
matching target words between different contexts was not a priority. Between contexts,
target items differed both in variability (two adjective tokens were used whereas 10 noun
tokens were used per modality) and in word frequency. Lexical frequency was assessed us-
ing the contextual diversity variable in the SUBTL corpus (Brysbaert & New, 2009), a sim-
ple count variable that reflects in how many out of 8388 films and television episodes this
word occurred at least once. Nouns describing auditory objects were less frequent than
nouns describing visual objects (range 6-383 for auditory nouns and 1056-6040 for visual
nouns); visual adjectives fell in the range of the visual nouns (white: 3355; black: 3190).

**Procedure**

Before the recording session, participants’ head shape was digitized using an optical Fast-
SCAN scanner (Polhemus, VT, USA, [http://www.polhemus.com]. The scan included the po-
positions of five marker coils that were later attached to the participant’s head. At the begin-
ing and end of each experimental session, the position of those marker coils was recorded
relative to the MEG sensors, and this record was later used to coregister the head shape
relative to the MEG sensor positions for the source localization procedure.
Participants were familiarized with the task and introduced to the MEG recording procedure. MEG acquisition took place in a magnetically shielded chamber, in which participants were lying in a supine position with their head resting in the helmet-shaped dewar containing the SQUIDs. Stimuli were presented with PsychoPy (http://www.psychopy.org, RRID:SCR_006571), projected onto a screen above the participants’ head. Participants were allowed to complete as many practice trials as they needed to feel comfortable with the task with both visual and auditory referential domains. They were asked to move as little as possible and to try not to blink while reading the questions. They were given the option to pause the experiment after every trial by pressing the response button twice when giving their answer.

Stimuli were presented in blocks of 45 trials. Auditory and visual referential domains were presented in separate interleaved blocks, and the beginning of each block announced the modality of the domains, so that participants knew which modality to attend to. Within auditory and visual domain trials, the order of trials was randomized. Since there were twice as many visual as auditory trials, blocks were presented in V-A-V-A-V-... sequence. After each block, participants had the opportunity to take a brief self-terminated break.

For 3 participants the MEG session was interrupted. One session was interrupted by a fire alarm, one due to excessive tiredness and one for a bathroom break. All affected participants finished the experiment on the same (two participants) or a different day (one participant). Marker positions from the first session were used online to match the head position in the second session closely to the first session.

Data acquisition and analysis

Continuous MEG was recorded with a 208 channel axial gradiometer system (Kanazawa Institute of Technology, Kanazawa, Japan) at a sampling rate of 1000 Hz. Data were band pass filtered between 0.1 and 200 Hz online.

Preprocessing

Nonperiodic environment noise was removed from the raw data by regressing the signal against 16 orthogonal reference sensors using the continuously adjusted least squares method (Adachi, Shimogawara, Higuchi, Haruta, & Ochiai, 2001). Data were then converted to the FIFF format and processed with mne-python (V 0.11, http://martinos.org/mne, RRID:SCR_005972) (Gramfort et al., 2013, 2014) and additional tools available in Eelbrain (V 0.22.1, http://pythonhosted.org/eelbrain, RRID:SCR_014661)

Bad channels were excluded from analysis based on visual inspection. Data were low-pass filtered at 40 Hz. Epochs from -100 to 600 ms relative to onset of the target words were extracted and screened for artifacts. Epochs exceeding a +/- 2000 femto-tesla absolute threshold were removed automatically. In addition, sub-threshold epochs were manually removed if channels close to the eyes significantly diverged for longer than 300 ms, indicating presence of an ocular artifact. If an individual channel within an epoch significantly deviated from the group average, it was interpolated just for that epoch. Good epochs were
downsampled to 200 Hz, averaged per condition and baseline corrected with the 100 ms pre-stimulus interval.

Source estimation

Because structural MRI datasets were not available for our participants, we used the “fsaverage” average brain model included with FreeSurfer (http://surfer.nmr.mgh.harvard.edu, RRID:SCR_001847) for source localization. To provide better localization accuracy, the fsaverage model was scaled to match each individual’s head shape, acquired before the experiment (see Procedure). The complete co-registration procedure proceeded as follows:

First, the fsaverage head model was aligned with the participant’s head shape by matching the nasion position. The fsaverage head model was then modified using rotation and uniform scaling, with the nasion as center, to minimize the distance of the pre-auricular points on the two head models using an iterative least squares procedure. Finally, minor adjustments to the translation were made as necessary, in order to fit the head scan to the fsaverage head shape while taking skull-external properties (e.g., amount of hair) into consideration.

The source space was defined on the white matter surface with the topology of a recursively subdivided icosahedron (“ico-4” option). Sources lying in the corpus callosum and subcortical structures were excluded based on the PALS-B12 atlas (Van Essen, 2005). Anatomical areas were labelled based on the Desikan-Killiany Atlas (Desikan et al., 2006). Pre- and post-rolandic gyri and the insula, where we did not expect any meaningful effects, were excluded from the analysis, resulting in approximately 1950 source locations in each hemisphere.

For each subject a separate inverse solution was computed based on the covariance matrix from the 100 ms baseline period (good trials only). Brain activity was estimated across space and time using distributed noise normalized minimum norm current source estimates (Dale et al., 2000). Noise-normalization provides advantageous localization accuracy over raw minimum norm estimates for non-superficial sources (Hauk, Wakeman, & Henson, 2011), which was relevant because of the midline regions which were of interest (see Introduction). For each source location, current was estimated at 3 orthogonal dipoles to form a 3-dimensional current vector, of which only the length was retained to provide a non-directional measure of activation. These orientation-free source estimates take into account that the fsaverage brain, while providing approximate locations of anatomical features, might not accurately reflect precise individual cortical folding patterns.

Because source activity was estimated on the same brain model, though scaled to different sizes, estimates for different subjects were directly comparable without morphing data from one brain model to another.

Statistical analysis

The primary statistical analysis was based on a mass-univariate analysis with spatio-temporal permutation cluster tests (Holmes, Blair, Watson, & Ford, 1996; Maris & Oostenveld, 2007). Source estimates of condition averages for each subject entered the analysis. A repeated measures ANOVA F-value was computed for each source at each time
point in a pre-specified anatomical area and time window. This F-map was thresholded at
an F-value corresponding to an uncorrected p-value of .05. Clusters were formed based on
direct adjacency in space and time. For each cluster, the exceedance mass was calculated
(the sum of all F-values in the cluster). The same procedure was repeated in 10000 random
permutations of the original data, shuffling condition labels within subject to take into ac-
count the within-subject nature of the design. For each permutation, the largest cluster
mass value was retained to form a non-parametric estimate of the distribution of the larg-
est cluster mass value under the null hypothesis that condition labels are exchangeable. Fi-
ally, a p-value was computed for each cluster in the original F-map as the proportion of
permutations that yielded a cluster with a larger mass than the cluster under question. We
report all clusters that reached a p-value of .05 or smaller.

To describe the pattern of activation in each significant cluster we then extracted and plot-
ted the time course of activation, as well as the average activation in the cluster. For the
time course, we created a region of interest (ROI) encompassing all sources that were part
of the cluster at any point in time. For the average activation we used the cluster as a spa-
tio-temporal mask to extract a single average activation value for each subject and condi-
tion. All plots indicate within-subject standard errors as a measure of variability (Loftus &
Masson, 1994).

Analysis design and parameters

The goal of the primary analysis was to test whether reference resolution was associated
with a certain brain response across different contexts, or whether there was a response to
reference resolution that depended on the context, i.e., the modality of the referential do-
main or the target word type. We thus performed an initial 2 × 3 × 3 ANOVA with factors
reference (reference resolving vs ambiguous target), condition (auditory domain with noun
targets, visual domain with noun targets, visual domain with adjective targets) and location
of the referent in the domain (first/top, middle, last/bottom).

Prior fMRI work on referential language processing (Boiteau et al., 2014; Nieuwland et al.,
2007; Almor, Smith, Bonilha, Fridriksson, & Rorden, 2007) and coherent language (Fersl et
al., 2008) suggest a large number of brain regions with possible involvement in reference
resolution. To account for this, our initial analysis included the cortex of both hemispheres
except for the pre- and postrolandic gyri and insula as defined in the Desikan-Killiany Atlas
(Desikan et al., 2006). This region is illustrated at the top right of Figure 4.

We used a time window of 200-600 ms relative to target word onset for this analysis. Tra-
tional models from electrophysiology have suggested that lexical access occurs shortly
after 300 ms relative to a written word presentation (Grainger & Holcomb, 2009; Py-
lkkänen & Marantz, 2003). Since a word has to be recognized before it can be related to the
referential domain, this estimate would provide a lower bound for expected effects of ref-
erral processes. However, more recent evidence suggests that access to lexical and se-
matic information can happen by around 200 ms (Hauk, Coutout, Holden, & Chen, 2012),
and shortly after that effects of semantic composition can be detected (Bemis & Pylkkänen,
2011). We thus used a large time window to include potential early effects.
Based on the result of a main effect of reference resolution in the initial analysis, we then
performed a conjunction analysis to confirm the presence of a response regardless of the
modality of the referential domain (Nichols, Brett, Andersson, Wager, & Poline, 2005). First,
two t-maps were created, one comparing reference resolving to ambiguous targets in audi-
tory domains and another one in visual domains. The conjunction map was defined as the
element-wise minimum of those two maps (t_conjunction = min(t_reference auditory, t_reference visual)).
Clusters were formed using a threshold equivalent to the one-tailed p-value of .05. The sig-
nificance of clusters was assessed with a permutation test, as described above, by repeating
the analysis in 10000 permutations with shuffled condition labels.

After the result of a main effect of reference resolution in the medial posterior region of the
left hemisphere, we performed a post-hoc test in a more constrained region to ascertain the
absence of an interaction effects which would qualify the result for the main effect. For this
purpose we defined a spatial region, slightly larger than the main effect cluster, using labels
from the Desikan-Killiany Atlas (Desikan et al., 2006). The labels included were: the para-
central lobule, precuneus, cuneus, pericalcarine cortex, the lingual gyrus and the posterior
and isthmus divisions of the cingulate gyrus. These roughly correspond to Brodman areas
23, 26, 29-31, the medial aspects of 1-5 and 7 and the medial superior parts of 18 and 19.

Finally, we also assessed modality-specific effects of reference resolution for auditory and
visual domains in more targeted tests. Targeted anatomical search regions were defined
based on labels in the Desikan-Killiany Atlas (Desikan et al., 2006). For auditory domains,
we defined a search region broadly construed to auditory cortex. This region included the
transverse temporal, superior temporal and supramarginal gyri of both hemispheres
(roughly, Brodman areas 22 and 40-42). Several lines of research suggest that auditory
objects are represented in the superior temporal gyrus adjacent to primary auditory areas
(Bizley & Cohen, 2013; Ding & Simon, 2012; Giordano, McAdams, Zatorre, Kriegeskorte, &
Belin, 2013). We included supramarginal gyrus because activation associated with (non-
linguistic) auditory imagery tends to extend into this region (McNorgan, 2012). We also
performed an analogous analysis for visual referential domains in the occipital lobe as de-
dined by the PALS-B12 atlas (Brodman areas 17-19), although this last test was more ten-

tative, because brain activity related to concurrent visual presentation of the sentence
stimuli could interfere with our ability to record activity associated with visual referents.

With one exception we are not reporting any analyses of brain responses to events subse-
dquent to the targets, because our stimuli were not designed to analyze these. As illustrated
in Figures 2 and 3, after the target word there were systematic differences between stimuli
with reference resolving targets and stimuli with ambiguous targets. The possible excep-

tion is nouns in the visual, adjective-noun phrase condition (see Figure 3, bottom). Here,

nouns following ambiguous adjectives resolve reference, whereas nouns following refer-

ence resolving adjectives are in a referential sense redundant. However, this prediction is
somewhat weakened because EEG data suggest the possibility of a reference resolution-
like response to nouns in adjective-noun phrases even after adjectives resolve reference
(Brodbeck et al., 2015). This could, for example, reflect a process of double checking that

the noun fits with the referent. We analyzed the response to these nouns analogously to the
other analyses described above, except that we used -100 to 1200 ms epochs relative to
onset of the adjective and baseline corrected before onset of the adjective to avoid a base- 
line in a region that already differed between condition.

Analysis of behavioral data

Behavioral performance was evaluated using mixed effects logistic regression models with 
correctness of the response as binary outcome measure (see Fitzmaurice, Laird, & Ware, 
2011). Models were fitted with the glmer command of the lme4 package (Bates, Mächler, 
Bolker, & Walker, 2015, p. 4) in R (Core Team, 2016). All models included random inter-
cepts for participant as well as item, considering each unique trial to be a separate item. 
Significance was evaluated using type-II Wald $X^2$ tests implemented in the car package (Fox 
& Weisberg, 2011).

It should be noted that the post-target regions of the stimulus sentences differ markedly 
between sentences with reference-resolving and ambiguous targets. The analysis of behav-
ioral data thus does not directly speak to the difficulty of resolving reference early or late in 
the sentence, but rather reflects a compound measure of difficulty of the different condi-
tions. The one effect for which conditions were adequately matched concerns the location 
of the referent. Thus, a significant effect of referent location would indicate that the loca-
tion of the referent affected the difficulty of the task.

Finally, to test whether the results of the MEG analysis are related to behavioral perfor-
mane we computed the correlation between estimated brain activity and the proportion 
of correct responses. For each subject and each condition, we extracted the mean activation 
in the spatio-temporal region identified by the significant clusters from the MEG analysis. 
We then calculated the difference between the response to reference resolving and ambig-
uous targets. To test for a correlation across subjects, we correlated this measure with the 
total proportion of correct responses for each subject. To test for a correlation within sub-
ject, we computed for each subject the correlation between the difference values and pro-
portion correct responses in each condition (3 conditions x 3 referent locations) and sub-
mittted the resulting $r$ values to a one-sample $t$-test. For determining the proportion of cor-
rect responses we only considered those trials which also entered the MEG analysis.

Results

Behavioral performance

Among the participants included in the final analysis, behavioral performance ranged from 
71.1% to 98.7% correct answers. A mixed effects logistic regression model with fixed ef-
ects Reference (2 levels: reference resolved by the target or in the post-target region), Mo-
dality/target (3 levels: auditory domain with noun target, visual domain with noun target 
or visual domain with adjective target) and Location of the referent (3 levels) indicated that 
the effect of condition interacted significantly with reference ($X^2(2) = 6.54, p = .038$) as well 
as location ($X^2(4) = 9.58, p = .048$). To resolve these interactions we proceeded with a sepa-
rate analysis for auditory and visual domains.
In auditory domains, there were significant main effects of both reference ($X^2(1) = 9.78, p = .002$) and location ($X^2(2) = 13.82, p = .001$). The significant main effect of reference indicated that the percentage of correct response was higher when reference was resolved early by the noun ($M = 87.0\%$ correct) than when reference was resolved late, by the prepositional phrase ($M = 83.8\%$). This is not unexpected, since questions in the latter condition were slightly more complicated. The main effect of location indicated that responses were more accurate when the referent was the last of the three sounds ($M = 88.1\%$) than when it was to the second ($M = 83.5\%, t(23) = 3.37, p = .003$) or the first sound ($M = 84.7\%, t(23) = 3.02, p = .006$). Behavioral performance thus indicated a recency effect with improved performance on trials in which the referent was the most recently heard sound.

No effects were significant for the visual domains. Overall, responses were more accurate in blocks with visual domains ($M = 91.1\%$) than in blocks with auditory domains ($M = 85.4\%, t(23) = 6.46, p < .001$).

**Modality-general response**

Our primary analysis used a spatio-temporal cluster based permutation test to find effects associated with reference resolution in the neural response to target words (see Figure 2 and Figure 3). The test was based on a repeated measures ANOVA with a 2 (reference resolving or ambiguous target) × 3 (condition: auditory domain with noun target, visual domain with noun target or visual domain with adjective target) × 3 (location of the referent) design. The test was performed in the time window from 200-600 ms, and including all parts of the cerebral cortex except the pre- and postrolandic gyri and insula. Results indicated a significant cluster for the main effect of reference in the medial parietal lobe (415-600 ms, $p = .012$, see Figure 4). In this region, activation increased whenever the target word resolved reference. Time course plots for the cluster region suggested that this was the case in visual as well as auditory referential domains.

The same test also indicated a main effect of condition at two largely symmetric sites with peaks in the temporal lobes of the two hemispheres (left hemisphere 320-600 ms, $p < .001$; right hemisphere 350-600 ms, $p = .009$). Pairwise comparison of average activation in the cluster area suggests that after visual domains, the response was higher for nouns than for adjectives, with an even stronger response for nouns after auditory domains. The spatial distribution of the effect resembles previous reports of N400 effects localized with distributed minimum norm estimates of MEG data (Halgren et al., 2002; Lau, Gramfort, Hamalainen, & Kuperberg, 2013; Lau, Weber, Gramfort, Hamalainen, & Kuperberg, 2014).

However, this result is difficult to interpret, because a number of variables were not balanced between conditions, leading to differences in lexical frequency and predictability on various levels in addition to possible baseline differences caused by differences between auditory and visual referential domains. In particular, previous research suggests that lexical frequency and predictability interact in influencing N400 amplitudes (Dambacher, Kliegl, Hofmann, & Jacobs, 2006; Van Petten & Kutas, 1990, 1991). Because of these complications and because this effect of condition does not influence the interpretation of our primary result related to reference resolution we will not discuss it further here.

No other effect in the ANOVA revealed significant clusters.
Since our study was specifically directed at finding a response to reference resolution that
is present for auditory as well as visual domains, we followed up on this initial finding with
a test for conjunction of activity related to reference resolution after auditory and visual
domains. Results are shown in Figure 5. The conjunction analysis revealed a single cluster
in the medial posterior left hemisphere (500-600 ms, p = .002) with very similar localiza-
tion as the main effect in the ANOVA. Figure 5 also displays plots of the activation in the
ROI defined by the cluster depending on condition. These plots show that reference resolu-
tion was associated with an increase in medial parietal activation across the different con-
ditions.

The ANOVA and the conjunction test results both suggest a shared neural response for ref-
erece resolution in auditory and visual domains. A difference in localization and/or timing
in the responses should manifest itself in a significant Reference × Condition interaction,
but no such interaction was found. However, this null result could also be due to the fact
that the primary analysis was very conservative. The spatio-temporal cluster based test,
correcting for multiple comparison across a large spatio-temporal region, is maximally sen-
sitive to spatially and temporally extended effects. However, given a largely shared re-
ponse, an interaction effect reflecting a temporal or spatial difference might be temporally
short-lived or spatially constrained. The conservative primary test might thus have missed
subtle interaction effects. In order to test for this possibility, we repeated the ANOVA test,
but constrained it to a smaller spatio-temporal region. Spatially, the test was restricted to a
medial posterior region in the left hemisphere, only slightly larger than the significant clus-
ter associated with reference resolution. Temporally, the test was restricted to the time
window of the ANOVA cluster, i.e., 415-600 ms. No significant Reference × Condition (or
higher level) interaction was found (all p ≥ .230). The finding that the conjunction effect
starts at 500 ms, while the ANOVA main effect starts at 415 ms might specifically indicate
that the effect differs in onset latency between auditory and visual domains. For an even
more liberal test of this hypothesis we repeated the same ANOVA restricted temporally to
the window from 415-500 ms, but also this test revealed no significant Reference × Condi-
tion (or higher level) interaction (all p ≥ .170). The lack of a significant interaction effect
suggests that apparent differences in timing were not reliable. In sum, we found evidence
for a shared response to reference resolution in auditory and visual domains in the left me-
dial parietal lobe, and no evidence that this response differs in its spatial or temporal dis-
tribution depending on the modality of the referential domain.

MEG activation increase in the medial parietal lobe in association with reference resolution
was not significantly correlated with behavioral performance. This was the case for the
cluster found in the ANOVA (across subjects: r(22) = .30, p = .159, within subjects: mean r = 
-.09, t(23) = -1.25, p = .22) as well as the cluster from the intersection analysis (across sub-
jects: r(22) = .32, p = .129, within subjects: mean r = -.132, t(23) = -1.68, p = .106).

In the analysis of nouns in adjective-noun phrases (see Figure 3, bottom) no significant dif-
cference was found between reference resolving and redundant nouns.
Effects in modality-specific areas

We also performed directed tests for activation related to reference resolution in brain regions known to be involved in modality-specific representations. For auditory domains, this included Heschl’s gyrus and the superior temporal and supramarginal gyri of both hemispheres. The 2 (reference) × 3 (location) ANOVA resulted in a cluster with main effect of reference with a maximum in the vicinity of posterior auditory cortex (420-600 ms, p < .001, see Figure 1). Pairwise comparison suggests that this effect was due to an increase in activation when reference was resolved.

Visual inspection of the time course of activation in Figure 6 suggests that the time course differed depending on the position of the referent. While this difference did not result in a significant Reference × Location interaction at the cluster level, the divergence might simply be too short-lived for the spatio-temporal cluster method, which is maximally sensitive to effects that are extended in space and time. We thus performed a post-hoc analysis to test for an influence of referent position on the time course of activation. We extracted the average time course of activation for each of the reference resolving conditions (reference to first, second and last sound) in the spatial ROI identified by the cluster with main effect of reference. We then performed a temporal cluster-based permutation test with a one-way ANOVA (reference resolution to the first, second or last sound) in the time window around the onset of main effect of reference resolution, 350-450 ms. The test procedure was analogous to the spatio-temporal cluster test, except that the data was lacking a spatial dimension, and clusters were formed over contiguous time points only. This test revealed a significant effect of referent position (395-420 ms, p = .037). The average activation in this time window was higher for reference to the last sound compared to the first (t(23) = 2.49) as well as the second sound (t(23) = 2.42). The first time point at which the activation to reference resolving nouns differed from the average activation to non-referential nouns at an uncorrected p ≤ .05 was 380 ms for reference to the last sound, 490 ms for the second and 440 ms for the first. This analysis suggests a recency effect, with reference to the most recent sound leading to relatively earlier activation. While this finding is based on a post hoc test after a more conservative test did not result in a significant interaction effect, and thus requires empirical verification, the finding is consistent with the recency effect found in the behavioral performance data.

The corresponding analysis for activity associated with reference resolution in visual domains in the occipital lobe did not yield any significant clusters.

Discussion

Our results provide evidence for a brain system recruited during referential language processing that is independent of the modality of the referents and involves the medial parietal lobe. To our knowledge this is the first report of a brain response that is associated with successful reference resolution and not tied to the modality of the referential domain. Crucially, the high temporal resolution of MEG allowed us to attribute this response directly to the reference resolving words, starting approximately 415 ms after word onset. Our results thus go beyond prior hemodynamic studies that implicated the same region in coherent
language processing, but did not target reference resolution in particular and were unable
to attribute the response to a specific stage of sentence comprehension.

Reference resolution is inherently difficult to separate from other cognitive processes asso-
ciated with managing situation models. At its core, we consider reference resolution to in-
volve identifying an entity in a mental model based on a linguistic description. However, an
out-of-the-blue reference to an entity that is not immediately present also involves retriev-
ing the relevant entity from memory. For example, when captain Ahab asks a passing ship
"Have ye seen the White Whale?" (italics indicate critical expression) he brings to the atten-
tion of the addressee an entity that has not been present in the recent discourse or imme-
diate environment. In other situations, reference is made to entities that are not necessarily
remembered but are part of the immediate context, as when Ishmael says “Landlord! I’ve
changed my mind about that harpooneer. —I shan’t sleep with him. I’ll try the bench here.”

While interpreting such a referential expression does not require memory retrieval, it di-
 rects attention to the environment for a referent. In the present study we tried to create an
experimental situation which minimizes memory retrieval and scanning of the environ-
ment by presenting referential contexts immediately preceding linguistic stimuli that con-
tained referential expressions. The following passage constitutes a textual illustration of
such a situation: “The four whales slain that evening had died wide apart; one, far to wind-
ward; one, less distant, to leeward; one ahead; one astern. These last three were brought
alongside ere nightfall; but the windward one could not be reached till morning”. Here,
memory demands should be minimal because the referents are active immediately before
the referential expression, although there might still be additional cognitive processes trig-
gered by accessing the referent, for example processes related to situating it in the referen-
tial domain.

Modality-general response

Our main result is a response to reference resolution in the medial parietal lobe. We did not
find any evidence that this brain response was modulated by the modality of the referents;
however, this null result should be interpreted with care. It is possible that the follow-up
tests we performed, despite relaxed statistical criteria, were not sensitive enough to detect
a subtle effect. For example, it is possible that medial parietal cortex is characterized by a
subtle anatomical subdivision with spatially alternating areas that respond to different
modalities. Such an effect would be difficult to detect with MEG which has a source localiza-
tion accuracy in the order of tens of millimeters (cf. Hauk et al., 2011). Importantly, howev-
er, we showed a significant conjunction effect for visual and auditory referents, indicating
that even if there might be undetected differences between modalities, the medial parietal
lobe, broadly defined, responded to referents in both modalities.

Given the uncertainty inherent in MEG source localization, there are several regions that
could be involved in generating the reported reference-sensitive response, including
precentral, posterior cingulate cortex and retrosplenial cortex. Although anatomical and
functional connectivity patterns suggest a more fine grained division of these regions
(Margulies et al., 2009), they are frequently co-activated in fMRI studies (Ranganath &
Ritchey, 2012). With this in mind we will discuss possible connections to other work in-
volving these regions as a group.
A meta-analysis of hemodynamic studies found the left precuneus among the brain regions that were reliably more active for coherent language compared to incoherent language (Ferstl et al., 2008). Most of the included studies compared comprehension of coherent stories (Xu, Kemeny, Park, Frattali, & Braun, 2005) or sentence pairs (Ferstl & von Cramon, 2002) to unconnected counterparts. While this is a broad contrast, a crucial component of coherence is repeated reference to the same entities. Our results showing increased activity directly after presentation of a reference resolving word thus go beyond these previous results and suggest a more specific role for medial parietal cortex in invoking known entities as referents.

Interestingly, we observed the same response not only for complete noun phrases, like the bird, but also for incomplete phrases that provided enough information to resolve reference, like the black in a context with only one black item. This suggests that this response is associated with reference resolution as a cognitive process that uses information extracted from language, but is not tied by its formal properties, i.e., does not have to wait for a complete noun phrase to resolve reference. This result adds neurophysiological evidence for the hypothesis that reference resolution is quick and incremental (Tanenhaus et al., 1995).

An involvement of medial parietal cortex in reference resolution adds a new component to our understanding of medial parietal lobe function. The medial parietal lobe has been consistently implicated in episodic memory. Brain damage involving retrosplenial cortex is associated with episodic memory deficits (Maguire, 2001). In addition, functional imaging studies frequently associated the medial parietal lobe with episodic retrieval. This includes, for example, tasks like recalling the second word of a learned word pair given the first (Krause, 1999), or recalling some aspect of the context in which an item was previously seen as opposed to merely recognizing that it has been previously presented (e.g. Lundstrom, 2003; Lundstrom, Ingvar, & Petersson, 2005).

If the medial parietal lobe is associated with retrieving referents, then why were ambiguous expressions, which were compatible with two referents, not associated with more activation than resolving expressions? At least two answers can be conceived of. First, it is possible that our participants did not retrieve referential candidates when faced with temporary referential ambiguity. This would be in contrast to results from visual world studies, in which people listening to referentially ambiguous expressions tend to look at potential referents in a visual display (Tanenhaus et al., 1995). However, this difference could be due to differences between the two paradigms; for example, visual world studies tend to have more complex referential domains, and domains are still available for inspection at the time of comprehension. A second possibility is that multiple referential candidates were in fact retrieved, eliciting medial parietal lobe activation. If this was the case, our results would suggest that resolving reference elicits more activation than retrieving referential candidates.

Like episodic memory tasks, reference resolution entails access to a contextually situated cognitive representation, the referent. Unlike typical episodic memory studies, in our paradigm, presentation of the referential domain and reference resolution were mere seconds apart. Similarly, a temporally separated study phase is not a necessary precondition for medial parietal involvement in processes involving the construction of episodic scenes.
such as imagining future or fictitious events (Buckner & Carroll, 2007; Schacter & Addis, 2007). In a synthesis of the literature, Ranganath and Ritchey (2012) suggested a functional explanation for these observations. They argued that retrosplenial and parahippocampal cortex, which are functionally connected with precuneus and posterior cingulate cortex (Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008), are part of a memory system for context memory. In the domain of language processing, this system is thought to be responsible for constructing discourse or situation models (Zwaan, 2015). Since reference resolution involves locating referents in such context representations, our findings provide more specific support for this hypothesis, which has the potential to connect research on language and memory.

This interpretation is also consistent with the results from fMRI investigations of referential processing using text stimuli. One study found that stimuli containing conjoined referents (e.g., Jeremy and Roger) were associated with increased activity in the precuneus (Boiteau et al., 2014). A similar parietal response, also extending to more dorsal areas, was observed when a passage repeatedly referred to the same person by name instead of with a pronoun (Almor et al., 2007). The authors argued that, because of the strong expectation that repeated references to the same person should use pronouns, readers temporarily interpreted the repeated name as introducing a new referent, and that parietal regions were involved in handling the additional discourse referent and resolving its coreference with the first name.

Another study localized the response to sentences containing referentially ambiguous pronouns, as in Ronald told Frank that he ..., and found a strong peak in the medial parietal lobe (Nieuwland et al., 2007). Superficially, this is the opposite of our finding, which was more medial parietal activity for unambiguous reference. However, our stimuli only contained temporary ambiguities that were resolved after at most 3 additional words (the grunt at the beginning), while the fMRI study involved permanent ambiguities that were never resolved. The low temporal resolution of fMRI cannot distinguish between a direct response to the ambiguous pronouns and a later, possibly extended response to ambiguous sentences. Indeed, the BOLD signal was modeled as an extended response from the critical pronoun up to the onset of the sentence final word (p. 996). Rather than contradicting our results, this finding thus suggests that medial parietal lobe activation is not only involved when a referent is found, but can also be recruited in situations that require dealing with openly ambiguous referential expressions, which might reflect an extended search through a situation model for possible referents. Finally, a study that focused on explicit pronoun co-reference judgements implicated in particular the lateral frontal lobes for processing of ambiguities, which could thus be related to higher level decision making demands (McMillan, Clark, Gunawardena, Rantz, & Grossman, 2012). Together, these results suggest a more complex picture of the processing of referential ambiguities with functionally separable contributions from different brain regions.

Our design resembles short term memory tasks, in which a recognition task follows presentation of study items after only seconds. This analogy suggests the alternative possibility that the medial parietal lobe is involved merely in recalling the spatiotemporal properties of the referents. While our design by itself cannot exclude this possibility, it is rendered less plausible when considering other research: short term memory tasks for visual
features tend to engage lateral rather than medial parietal regions (e.g. Bettencourt & Xu, 2015; Kawasaki, Watanabe, Okuda, Sakagami, & Aihara, 2008; Todd & Marois, 2004), nor do auditory short term memory tasks tend to engage the medial parietal lobe (e.g. Kumar et al., 2016). On the other hand, medial parietal regions are recruited by tasks that involve judgements of complex spatial or temporal relations (Galati, Pelle, Berthoz, & Committeri, 2010; Kwok & Macaluso, 2015), which is more consistent with an involvement in relational models as argued above. Furthermore, an explanation based solely on short term memory access might have difficulty accounting for results from the hemodynamic studies discussed above, which implicated the medial parietal lobe in referential language processing while using linguistic stimuli.

More generally, it could be argued that the medial parietal lobe is involved in encoding perceptual as opposed to semantic relations. This explanation could account for fMRI studies of language processing, assuming that participants in those studies maintained perceptual models during language comprehension. This assumption is reasonable given evidence that even purely linguistic stimuli seem to be encoded involving modality-specific systems (see source cited in the Introduction). At least, the evidence presented here suggests that representations in the medial parietal lobe are not purely visual, but multisensory. This issue also highlights a larger question for future research concerning the extent to which sensory representations are essential to discourse models, or whether they are epiphenomenal.

A further possibility is that the medial parietal lobe response reflects a priming effect of the ambiguous targets, because ambiguous targets were applicable to two entities in the referential domain, whereas reference resolving words were applicable only to one. We considered this explanation unlikely because semantic priming effects tend to start earlier, even when sounds prime words (Vanpetten & Rheinfelder, 1995), and localize to temporal and sometimes frontal regions (Lau, Phillips, & Poeppel, 2008; Lau et al., 2013, 2014). Both characteristics apply to the N400-like responses we observed as main effects between target conditions, suggesting that we did have the power to detect such priming effects, had they been present.

In sum, our results, together with the literature on the medial parietal lobe, suggest that this region is involved in representing entities with contextual associations, and thus in maintaining situation models for language comprehension.

**Activity in modality-specific brain systems**

Our results suggest that resolving reference to a previously heard sound is associated with an increase in activation in the vicinity of auditory cortex. This response occurred in the absence of concurrent auditory stimulation, suggesting that it is associated with retrieval of sensory properties of the referent. More detailed analysis suggested that reference to the most recent sound was associated with faster activation, consistent with theories suggesting that the most recent in a sequence of items stored in short term memory is more accessible (McElree & Dosher, 1989).

The localization of this effect in the vicinity of auditory cortex is compatible with auditory imagery, which is associated with activation posterior to Heschl’s gyrus bilaterally.
(McNorgan, 2012), although the same regions might also encode more abstract information (Linke & Cusack, 2015). In our study the response was left-lateralized, paralleling neuroimaging (McNorgan, 2012) as well as behavioral (Prete, Marzoli, Brancucci, & Tommasi, 2016) evidence for a tendency towards functional left-lateralization of imagery.

Given that this response likely reflects activation of modality-specific representations, the direction of the effect is interesting. Ambiguous nouns were compatible with two auditory objects; activating two tokens as part of the referential search could lead to more activity than activating a single token. Instead, we found that auditory cortex becomes more active once a unique referent is found. This result suggests that auditory cortex becomes more involved not during the search for a referent but when the referent is found, consistent with the need to retrieve a more detailed representation of the referent to answer the question.

The parallel test for activity associated with reference resolution to visual referents did not reveal any significant clusters. While one possibility is that visual referential domains were processed differently from the auditory domains, there are other possible explanations for this null result. Processing the visually presented words could have interfered with, or overshadowed a response associated with the referential domain. Reference resolution in auditory domains was not associated with such a competing process, as words were presented visually. Furthermore, previous results suggest that reference resolution in visual domains is associated with a brain response that depends on the spatial position of the referent along the horizontal axis (Brodbbeck et al., 2015), consistent with results indicating that visual short-term memory access is associated with a brain response that depends on the horizontal position of the item that is accessed (Hopf et al., 2000; Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004). However, in the present study, referents were arranged vertically, and to our knowledge, location-dependent activity in the vertical dimension is not an established phenomenon.

While the behavioral results paralleled the recency-effect observed in the auditory domains, with better performance when the referent was the most recently presented sound, the location of the referent did not influence behavioral performance in visual domains. This could reflect the fact that in visual domains all referents were presented concurrently, contrasting with the serial presentation of the auditory referents.

**Models of language comprehension**

The response in auditory cortex started at practically the same time as the medial parietal, modality-general response; if considering reference to the most recent sound, it preceded it. This observation constrains the functional interpretation of the two responses. Specifically, the medial parietal response does not seem to be the earliest response reflecting reference resolution. On the other hand, we cannot exclude the possibility that reference resolution involves modality-specific systems, while the medial parietal response reflects a subsequent process such as integrating the referent in a situation model.

In the context of models of visual word perception (e.g. Pylkänen & Marantz, 2003; Grainger & Holcomb, 2009) the onset around 400 ms puts our effects in a post-lexical time win-
dow. This is in agreement with a sequential model in which reference resolution follows lexical processing. Consistent with this, we observed an N400-like response with an onset around 320 ms. Given that the N400 is thought to reflect access to lexical information (Lau et al., 2014) this suggests that activation of lexical information preceded reference resolution.

By describing a neural response to reference resolution, our results add a critical component to the sequence of computational steps in language comprehension that can be tracked with electrophysiology. Our results thus offer not only novel insights into the neural basis of reference resolution, but also new tools to study language processing.

Conclusions

Our results provide evidence against a model of referential language processing in which semantic language representations interact with representations of the referential domain exclusively in modality specific brain systems. Instead, our findings suggest that a brain system including a medial parietal region supports referential language processing with an increase in activity when the referent of an expression can be resolved. This finding provides a crucial bridge between language processing and the memory literature which attributes context representations based on situation models to medial parietal brain regions (Ranganath & Ritchey, 2012). In addition, our results provide a possible explanation for the consistent observation of medial parietal activity during tasks involving coherent language (Ferstl et al., 2008; Boiteau et al., 2014; Nieuwland et al., 2007). While our finding thus provides a considerable advance in region-function mapping, reference resolution is not a monolithic process, and it will be a task for future research to clarify the precise computational steps that engage medial parietal and modality-specific regions.

References

Adachi, Y., Shimogawara, M., Higuchi, M., Haruta, Y., & Ochiai, M. (2001). Reduction of non-periodic environmental magnetic noise in MEG measurement by continuously adjusted least squares method. *IEEE Transactions on Applied Superconductivity, 11*(1), 669–672. https://doi.org/10.1109/77.919433

Almor, A., Smith, D. V., Bonilha, L., Fridriksson, J., & Rorden, C. (2007). What is in a name? Spatial brain circuits are used to track discourse references. *Neuroreport, 18*(12), 1215–1219. https://doi.org/10.1097/WNR.0b013e32810f2e11
841 Altmann, G. T. M. (2004). Language-mediated eye movements in the absence of a visual world: the “blank screen paradigm.” *Cognition, 93*(2), B79–B87. https://doi.org/10.1016/j.cognition.2004.02.005

844 Altmann, G. T. M., & Kamide, Y. (2009). Discourse-mediation of the mapping between language and the visual world: eye movements and mental representation. *Cognition, 111*, 55–71. https://doi.org/10.1016/j.cognition.2008.12.005

847 Barsalou, L. W. (1999). Perceptions of perceptual symbols. *Behavioral and Brain Sciences*, 22(4), 637–660. https://doi.org/10.1017/S0140525X99532147

849 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

852 Bemis, D. K., & Pylkkänen, L. (2011). Simple Composition: A Magnetoencephalography Investigation into the Comprehension of Minimal Linguistic Phrases. *The Journal of Neuroscience, 31*(8), 2801–2814. https://doi.org/10.1523/JNEUROSCI.5003-10.2011

855 Bettencourt, K. C., & Xu, Y. (2015). Decoding the content of visual short-term memory under distraction in occipital and parietal areas. *Nature Neuroscience, 19*(1), 150–157. https://doi.org/10.1038/nn.4174

858 Bizley, J. K., & Cohen, Y. E. (2013). The what, where and how of auditory-object perception. *Nature Reviews Neuroscience, 14*(10), 693–707. https://doi.org/10.1038/nrn3565

860 Boiteau, T. W., Bowers, E., Nair, V. A., & Almor, A. (2014). The neural representation of plural discourse entities. *Brain and Language, 137*, 130–141. https://doi.org/10.1016/j.bandl.2014.08.003
Brodbeck, C., Gwilliams, L., & Pyllkänen, L. (2015). EEG can track the time course of successful reference resolution in small visual worlds. *Frontiers in Psychology, 6*, 1787. https://doi.org/10.3389/fpsyg.2015.01787

Brysbaert, M., & New, B. (2009). Moving beyond Kucera and Francis: a critical evaluation of current word frequency norms and the introduction of a new and improved word frequency measure for American English. *Behav Res Methods, 41*, 977–90. https://doi.org/10.3758/BRM.41.4.977

Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences, 11*(2), 49–57. https://doi.org/10.1016/j.tics.2006.11.004

Dale, A. M., Liu, A. K., Fischl, B. R., Buckner, R. L., Belliveau, J. W., Lewine, J. D., & Halgren, E. (2000). Dynamic statistical parametric mapping: combining fMRI and MEG for high-resolution imaging of cortical activity. *Neuron, 26*(1), 55–67. https://doi.org/10.1016/S0896-6273(00)81138-1

Dambacher, M., Kliegl, R., Hofmann, M., & Jacobs, A. M. (2006). Frequency and predictability effects on event-related potentials during reading. *Brain Research, 1084*(1), 89–103. https://doi.org/10.1016/j.brainres.2006.02.010

Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., … Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage, 31*(3), 968–980. https://doi.org/10.1016/j.neuroimage.2006.01.021
886 Ding, N., & Simon, J. Z. (2012). Emergence of neural encoding of auditory objects while listening to competing speakers. *Proc Natl Acad Sci U S A, 109*, 11854–9. https://doi.org/10.1073/pnas.1205381109

889 Eberhard, K. M., Spivey-Knowlton, M. J., Sedivy, J. C., & Tanenhaus, M. K. (1995). Eye movements as a window into real-time spoken language comprehension in natural contexts. *Journal of Psycholinguistic Research, 24*(6), 409–436. https://doi.org/10.1007/BF02143160

892 Ferstl, E. C., Neumann, J., Bogler, C., & von Cramon, D. Y. (2008). The extended language network: A meta-analysis of neuroimaging studies on text comprehension. *Human Brain Mapping, 29*(5), 581–593. https://doi.org/10.1002/hbm.20422

896 Ferstl, E. C., & von Cramon, D. Y. (2002). What Does the Frontomedian Cortex Contribute to Language Processing: Coherence or Theory of Mind? *NeuroImage, 17*(3), 1599–1612. https://doi.org/10.1006/ning.2002.1247

899 Fitzmaurice, G. M., Laird, N. M., & Ware, J. H. (2011). *Applied longitudinal analysis* (2nd ed). Hoboken, NJ: Wiley.

901 Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression* (Second). Thousand Oaks CA: Sage. Retrieved from http://soserv.socsci.mcmaster.ca/jfox/Books/Companion

904 Galati, G., Pelle, G., Berthoz, A., & Committeri, G. (2010). Multiple reference frames used by the human brain for spatial perception and memory. *Experimental Brain Research, 206*(2), 109–120. https://doi.org/10.1007/s00221-010-2168-8
Giordano, B. L., McAdams, S., Zatorre, R. J., Kriegeskorte, N., & Belin, P. (2013). Abstract Encoding of Auditory Objects in Cortical Activity Patterns. *Cerebral Cortex, 23*(9), 2025–2037. https://doi.org/10.1093/cercor/bhs162

Graesser, A. C., Millis, K. K., & Zwaan, R. A. (1997). Discourse comprehension. *Annual Review of Psychology, 48*(1), 163–189. https://doi.org/10.1146/annurev.psych.48.1.163

Grainger, J., & Holcomb, P. J. (2009). Watching the Word Go by: On the Time-course of Component Processes in Visual Word Recognition. *Language and Linguistics Compass, 3*(1), 128–156. https://doi.org/10.1111/j.1749-818X.2008.00121.x

Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., … Hämäläinen, M. S. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in Neuroscience, 7*, 267. https://doi.org/10.3389/fnins.2013.00267

Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., … Hämäläinen, M. S. (2014). MNE software for processing MEG and EEG data. *NeuroImage, 86*, 446–460. https://doi.org/10.1016/j.neuroimage.2013.10.027

Halgren, E., Dhond, R. P., Christensen, N., Van Petten, C., Marinkovic, K., Lewine, J. D., & Dale, A. M. (2002). N400-like Magnetoencephalography Responses Modulated by Semantic Context, Word Frequency, and Lexical Class in Sentences. *NeuroImage, 17*(3), 1101–1116. https://doi.org/10.1006/nimg.2002.1268

Hauk, O., Coutout, C., Holden, A., & Chen, Y. (2012). The time-course of single-word reading: Evidence from fast behavioral and brain responses. *NeuroImage, 60*(2), 1462–1477. https://doi.org/10.1016/j.neuroimage.2012.01.061

Hauk, O., Davis, M. H., Kherif, F., & Pulvermüller, F. (2008). Imagery or meaning? Evidence for a semantic origin of category-specific brain activity in metabolic imaging. *European
930 Journal of Neuroscience, 27(7), 1856–1866. https://doi.org/10.1111/j.1460-
931 9568.2008.06143.x
932 Hauk, O., Wakeman, D. G., & Henson, R. N. (2011). Comparison of noise-normalized minimum
933 norm estimates for MEG analysis using multiple resolution metrics. NeuroImage, 54(3),
934 1966–1974. https://doi.org/10.1016/j.neuroimage.2010.09.053
935 Holmes, A. P., Blair, R. C., Watson, G., & Ford, I. (1996). Nonparametric Analysis of Statistic
936 Images from Functional Mapping Experiments. Journal of Cerebral Blood Flow & Met-
937abolism, 16(1), 7–22. https://doi.org/10.1097/00004647-199601000-00002
938 Hopf, J. M., Boelmans, K., Schoenfeld, M. A., Luck, S. J., & Heinze, H. J. (2004). Attention to
939 features precedes attention to locations in visual search: Evidence from electromagnetic
940 brain responses in humans. J Neurosci, 24, 1822–1832.
941 https://doi.org/10.1523/Jneurosci.3564-03.2004
942 Hopf, J. M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., & Heinze, H. J.
943 (2000). Neural sources of focused attention in visual search. Cereb Cortex, 10, 1233–
944 1241. https://doi.org/10.1093/cercor/10.12.1233
945 Kahn, I., Andrews-Hanna, J. R., Vincent, J. L., Snyder, A. Z., & Buckner, R. L. (2008). Distinct
946 Cortical Anatomy Linked to Subregions of the Medial Temporal Lobe Revealed by In-
947 trinsic Functional Connectivity. Journal of Neurophysiology, 100(1), 129–139.
948 https://doi.org/10.1152/jn.00077.2008
949 Kawasaki, M., Watanabe, M., Okuda, J., Sakagami, M., & Aihara, K. (2008). Human posterior
950 parietal cortex maintains color, shape and motion in visual short-term memory. Brain Re-
951 search, 1213, 91–97. https://doi.org/10.1016/j.brainres.2008.03.037
Krause, B. J. (1999). Episodic retrieval activates the precuneus irrespective of the imagery content of word pair associates: A PET study. *Brain, 122*(2), 255–263. https://doi.org/10.1093/brain/122.2.255

Kumar, S., Joseph, S., Gander, P. E., Barascud, N., Halpern, A. R., & Griffiths, T. D. (2016). A Brain System for Auditory Working Memory. *Journal of Neuroscience, 36*(16), 4492–4505. https://doi.org/10.1523/JNEUROSCI.4341-14.2016

Kwok, S. C., & Macaluso, E. (2015). Immediate memory for “when, where and what”: Short-delay retrieval using dynamic naturalistic material: Neural Correlates of Immediate Episodic Retrieval. *Human Brain Mapping, 36*(7), 2495–2513. https://doi.org/10.1002/hbm.22787

Lau, E. F., Gramfort, A., Hamalainen, M. S., & Kuperberg, G. R. (2013). Automatic Semantic Facilitation in Anterior Temporal Cortex Revealed through Multimodal Neuroimaging. *Journal of Neuroscience, 33*(43), 17174–17181. https://doi.org/10.1523/JNEUROSCI.1018-13.2013

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience, 9*(12), 920–933. https://doi.org/10.1038/nrn2532

Lau, E. F., Weber, K. P., Gramfort, A., Hamalainen, M. S., & Kuperberg, G. R. (2014). Spatio-temporal Signatures of Lexical-Semantic Prediction. *Cereb Cortex.*

Linke, A. C., & Cusack, R. (2015). Flexible Information Coding in Human Auditory Cortex during Perception, Imagery, and STM of Complex Sounds. *Journal of Cognitive Neuroscience, 27*(7), 1322–1333. https://doi.org/10.1162/jocn_a_00780
Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review, 1*(4), 476–490. https://doi.org/10.3758/BF03210951

Lundstrom, B. N. (2003). Isolating the retrieval of imagined pictures during episodic memory: activation of the left precuneus and left prefrontal cortex. *NeuroImage, 20*(4), 1934–1943. https://doi.org/10.1016/j.neuroimage.2003.07.017

Lundstrom, B. N., Ingvar, M., & Petersson, K. M. (2005). The role of precuneus and left inferior frontal cortex during source memory episodic retrieval. *NeuroImage, 27*(4), 824–834. https://doi.org/10.1016/j.neuroimage.2005.05.008

Maguire, E. A. (2001). The retrosplenial contribution to human navigation: a review of lesion and neuroimaging findings. *Scandinavian Journal of Psychology, 42*(3), 225–238. https://doi.org/10.1111/1467-9450.00233

Margulies, D. S., Vincent, J. L., Kelly, C., Lohmann, G., Uddin, L. Q., Biswal, B. B., … Petrides, M. (2009). Precuneus shares intrinsic functional architecture in humans and monkeys. *Proceedings of the National Academy of Sciences, 106*(47), 20069–20074. https://doi.org/10.1073/pnas.0905314106

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods, 164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

McElree, B., & Dosher, B. A. (1989). Serial position and set size in short-term memory: The time course of recognition. *Journal of Experimental Psychology: General, 118*(4), 346–373. https://doi.org/10.1037/0096-3445.118.4.346
McMillan, C. T., Clark, R., Gunawardena, D., Ryan, N., & Grossman, M. (2012). fMRI evidence for strategic decision-making during resolution of pronoun reference. *Neuropsychologia, 50*(5), 674–687. https://doi.org/10.1016/j.neuropsychologia.2012.01.004

McNorgan, C. (2012). A meta-analytic review of multisensory imagery identifies the neural correlates of modality-specific and modality-general imagery. *Frontiers in Human Neuroscience, 6.* https://doi.org/10.3389/fnhum.2012.00285

Nichols, T. E., Brett, M., Andersson, J., Wager, T. D., & Poline, J. B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage, 25,* 653–60. https://doi.org/10.1016/j.neuroimage.2004.12.005

Nieuwland, M. S., Petersson, K. M., & Van Berkum, J. J. A. (2007). On sense and reference: examining the functional neuroanatomy of referential processing. *NeuroImage, 37*(3), 993–1004. https://doi.org/10.1016/j.neuroimage.2007.05.048

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci, 8,* 976–87. https://doi.org/10.1038/nrn2277

Prete, G., Marzoli, D., Brancucci, A., & Tommasi, L. (2016). Hearing it right: Evidence of hemispheric lateralization in auditory imagery. *Hearing Research, 332,* 80–86. https://doi.org/10.1016/j.heares.2015.12.011

Pulvermüller, F. (2013). How neurons make meaning: brain mechanisms for embodied and abstract-symbolic semantics. *Trends Cogn Sci, 17,* 458–70. https://doi.org/10.1016/j.tics.2013.06.004
1017 Pylkkänen, L., & Marantz, A. (2003). Tracking the time course of word recognition with MEG. *Trends in Cognitive Sciences, 7*(5), 187–189. https://doi.org/10.1016/S1364-
1019 6613(03)00092-5
1020 R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/
1022 Ranganath, C., & Ritchey, M. (2012). Two cortical systems for memory-guided behaviour. *Nature Reviews Neuroscience, 13*(10), 713–726. https://doi.org/10.1038/nrn3338
1024 Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*(1481), 773–786. https://doi.org/10.1098/rstb.2007.2087
1028 Sedivy, J. C., K. Tanenhaus, M., Chambers, C. G., & Carlson, G. N. (1999). Achieving incremental semantic interpretation through contextual representation. *Cognition, 71*(2), 109–
1030 147. https://doi.org/10.1016/S0010-0277(99)00025-6
1031 Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: eye movements to absent objects. *Psychological Research-Psychologische Forschung*, 1033 65, 235–241. https://doi.org/10.1007/s004260100059
1034 Spivey, M. J., Tanenhaus, M. K., Eberhard, K. M., & Sedivy, J. C. (2002). Eye movements and spoken language comprehension: Effects of visual context on syntactic ambiguity resolution. *Cognitive Psychology, 45*(4), 447–481. https://doi.org/10.1016/S0010-
1037 0285(02)00503-0
1038 Tanenhaus, M. K., Spivey-Knowlton, M. J., Eberhard, K. M., & Sedivy, J. C. (1995). Integration of visual and linguistic information in spoken language comprehension. *Science*, 268(5217), 1632–1634. https://doi.org/10.1126/science.7777863

1041 Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, 428(6984), 751–754. https://doi.org/10.1038/nature02466

1043 Van Essen, D. C. (2005). A Population-Average, Landmark- and Surface-based (PALS) atlas of human cerebral cortex. *NeuroImage*, 28(3), 635–662.

1045 https://doi.org/10.1016/j.neuroimage.2005.06.058

1046 Van Petten, C., & Kutas, M. (1990). Interactions between sentence context and word frequency in event-related brainpotentials. *Memory & Cognition*, 18(4), 380–393.

1048 https://doi.org/10.3758/BF03197127

1049 Van Petten, C., & Kutas, M. (1991). Influences of semantic and syntactic context on open- and closed-class words. *Memory & Cognition*, 19(1), 95–112.

1051 https://doi.org/10.3758/BF03198500

1052 Vanpetten, C., & Rheinfelder, H. (1995). Conceptual relationships between spoken words and environmental sounds: Event-related brain potential measures. *Neuropsychologia*, 33(4), 485–508. https://doi.org/10.1016/0028-3932(94)00133-A

1055 Xu, J., Kemeny, S., Park, G., Frattali, C., & Braun, A. (2005). Language in context: emergent features of word, sentence, and narrative comprehension. *NeuroImage*, 25(3), 1002–1015. https://doi.org/10.1016/j.neuroimage.2004.12.013

1058 Zwaan, R. A. (2015). Situation models, mental simulations, and abstract concepts in discourse comprehension. *Psychon Bull Rev*. https://doi.org/10.3758/s13423-015-0864-x
Figure legends

Figure 1: Modality-specific and -general representations: Possible flow of information between modality-general and modality-specific representations of both linguistic meaning and referents. Information originates at the top in linguistic form information, i.e., written or spoken words. This input triggers retrieval of meanings, which in turn are used to find referents. Some theories suggest the existence of a “semantic hub” that is involved in processing semantic representations regardless of the modality of their content (Patterson, Nestor, & Rogers, 2007), while others suggest that meaning is exclusively represented in modality-specific brain systems (Pulvermüller, 2013). Both of these theories are potentially compatible with a model in which referents are represented exclusively in modality-specific brain systems (blue and red arrows, respectively). This hypothesis would suggest that the “referents” box at the bottom left can be removed from the diagram, since referential processing is constrained to modality-specific representations.

Figure 2: Design for auditory referential domains. Time proceeds from left to right, with vertical offset indicating elements that differ between conditions. The arrow indicates the target word for analysis. The upper sequence illustrates a trial in which the target word grunt resolves reference, whereas the lower sequence illustrates a trial in which it does not, and reference is resolved by adding the prepositional phrase in the middle. Below the displays, presentation time of each frame is indicated in ms.

Figure 3: Design for visual referential domains. Time proceeds from left to right, with vertical offset indicating elements that differ between condition. The arrow indicates the target word for analysis. For both trials with noun targets and trials with adjective targets, the upper sequence illustrates a trial in which the target resolves reference, and the lower sequence illustrates a trial in which reference is resolved later in the sentence. Below the displays, presentation time of each frame is indicated in ms.

Figure 4: Full model ANOVA results. The ANOVA analysis revealed a significant spatiotemporal cluster for the main effect of reference resolution in the medial parietal lobe of the left hemisphere, indicating an activity increase associated with reference resolution starting at 415 ms after target word onset. **Top left:** Anatomical extent of the cluster, shown on a lateral and a medial view of the left hemisphere. Each source that was part of the cluster at any time point is color coded, indicating the sum of F-values over time, i.e., how much that particular source contributed to the cluster’s mass. **Top right:** The anatomical region included in the test is indicated in blue; the left hemisphere is shown for illustration, but the test also included the corresponding area of the right hemisphere. **Bottom:** The time course of activation in the ROI defined by the cluster in response to the target words, shown separately for auditory and visual referential domains for illustration purposes. Time 0 ms corresponds to the onset of the visual presentation of the target word. The time course plots indicate within-subject standard errors. The time region covered by the cluster is indicated with gray shading (415-600 ms).

Figure 5: Test for conjunction of reference resolution in auditory and visual referential domains. **Top:** Anatomical extent of the cluster, showing for each anatomical source the sum of the t-values over time, i.e., indicating how much each source contributes to the cluster mass statistic (details analogous to Figure 4). **Below:** activation in the ROI defined by the cluster in
the different conditions. **Left:** schematic depiction of the referential domains for each condition, and a corresponding example target word. Referents are color-coded for clarity of the results only – referents in the visual referential domains that were presented to subjects were always black and white. **Middle:** the time course of activation in response to the target word presentation in the region of interest defined by the spatial extent of the cluster. The time region covered by the cluster is indicated with gray shading. **Right:** bar-plots show the average activation for each condition in the spatio-temporal region covered by the cluster. In both time- and bar-plots, variability is indicated with the within-subject standard error.

**Figure 6:** Results in auditory cortex. A significant cluster indicated an activation increase when reference was resolved to auditory objects. The time course of activation in the ROI defined by the cluster is plotted separately according to the sequential position of the referent in the auditory domain. For each plot, the relevant position of the referent is indicated in the schematic of the referential domain. Other details are analogous to previous figures.
Noun target

Noun resolving

Was   the   bird   in   the

middle?

Noun ambiguous

+   600   300/300 ISI   400   400   600   400   400

Presentation times [ms]

Adjective target

Adjective resolving

Was   the   black   bird   in   the   middle?

Adjective ambiguous

+   600   300/300 ISI   400   400   600   600   400   400

Presentation times [ms]
Main effect of reference resolution

Time-course in cluster-based ROI:

Auditory Domains

Visual Domains

Activation [tSPM]

Reference resolving
Reference ambiguous

Region for spatio-temporal clusters:

Sum of F-values

[Graphs showing time-course of activation for auditory and visual domains with reference resolving and ambiguous conditions]
Reference resolution in visual domains and reference resolution in auditory domains

Auditory domains, noun targets:

... grunt

Visual domains, noun targets:

... cat

Visual domains, adjective targets:

... white
