The sound of concepts:
The link between auditory and conceptual brain systems

Markus Kiefer[1], Eun-Jin Sim[1,2], Bärbel Herrnberger[1], Jo Grothe[1] and Klaus Hoenig[1,2]

[1]*University of Ulm, Department of Psychiatry, Ulm, Germany*

[2]*Transfer Center for Neurosciences and Learning, Ulm, Germany*

Correspondence to:

Markus Kiefer
University of Ulm
Department of Psychiatry
Section for Cognitive Electrophysiology
Leimgrubenweg 12, 89075 Ulm, Germany

Phone: +49 731 500 21455   Fax: +49 731 500 41064
E-mail: Markus.Kiefer@uni-ulm.de
URL: http://www.uni-ulm.de/~mkiefer/

Concepts in long-term memory are important building blocks of human cognition and are the basis for object recognition, language and thought. While it is well accepted that concepts are comprised of features related to sensory object attributes, it is still unclear how these features are represented in the brain. Of central interest is whether concepts are essentially grounded in perception. This would imply a common neuroanatomical substrate for perceptual and conceptual processing. Here we show using functional magnetic resonance imaging and recordings of event-related potentials that acoustic conceptual features rapidly recruit auditory areas even when implicitly presented through visual words. Recognizing words denoting objects for which acoustic features are highly relevant (e.g.,”telephone”) suffices to ignite cell assemblies in the posterior superior and middle temporal gyrus (pSTG/MTG) that were also activated by listening to real sounds. Activity in pSTG/MTG had an onset of 150 ms and increased parametrically as a function of acoustic feature relevance. Both findings suggest a conceptual origin of this effect rather than post-conceptual strategies such as imagery. The presently demonstrated link between auditory and conceptual brain systems parallels observations in other memory systems suggesting that modality-specificity represents a general organizational principle in cortical memory representation. The understanding of concepts as a partial reinstatement of brain activity during perception stresses the necessity of rich sensory experiences for concept acquisition. The modality-specific nature of concepts could also explain the difficulties in achieving a consensus about overall definitions of abstract concepts such as freedom or justice unless embedded in a concrete, experienced situation.

The nature of concepts has been the long-standing focus of philosophical reflections and, more recently, of experimental empirical investigation. Imaging the human brain during conceptual processing in space and time now allows addressing these fundamental questions about human cognition objectively. Traditionally, starting with Immanuel Kant's philosophical considerations on categories, concepts are specified as abstract mental entities different from perceptual or motor brain systems [1,2]: Sensory or motor information about objects and events is transformed into a common abstract representation format, in which original modality-specific information is lost. Perceptual and motor representations play at best an epiphenomenal role for conceptual processing and are only evoked by imagery processes after the concept is fully accessed [3].

Challenging this classical view, recent modality-specific approaches propose close links between the perceptual and motor brain systems on the one hand and the conceptual system on the other hand. They assume that concepts are embodied [4] in the sense that they are essentially grounded in perception and action [5-9]: Conceptual features (e.g., visual, acoustic, action-related) are stored in modality-specific brain areas typically involved in processing the corresponding sensory and motor information, respectively. According to this view, conceptual representations are established by the learning-based formation of cortical cell assemblies in sensory and motor areas during concept acquisition [7,10]. For example, the repeated experience of picking up the receiver of a ringing telephone establishes cell assemblies in motor, auditory and visual cortex, which code action-related, acoustic and visual features, respectively. Ignition of these modality-specific cell assemblies either bottom-up by words and objects, or top-down by thought constitutes the concept (e.g., telephone).

Support for modality-specific approaches comes from behavioural [11], neuropsychological [8], electrophysiological [12] and neuroimaging studies [9]. Although some studies found activity in sensory brain areas during conceptual tasks convincing evidence for a link between perceptual and conceptual systems is missing so far: Conceptual categories with a strong emphasis on visual features (i.e., natural kinds) elicited enhanced activity in visual brain areas [13]. However, these findings were not consistently replicated [14], or could be alternatively explained by perceptual processing of the visual stimuli themselves [15,16] or by post-conceptual strategic processes such as visual imagery [3].

Bridging the gap between the perceptual and conceptual system, we investigated the neural representation of acoustic conceptual features during the recognition of visually presented object names. This procedure has two advantages: Firstly, perceptual processing of the stimulus can be easily distinguished from processing of the conceptual feature of interest at a functional and neural level. Secondly, the implicitness of the task discourages post-conceptual imagery strategies. Hence activity in auditory brain areas in response to a visual word must reflect conceptual processing of acoustic object features. In brief, the critical question arises whether recognizing the word “telephone”, for instance, suffices to rapidly ignite cell assemblies in auditory brain areas.

To address this question, we recorded brain responses during conceptual and perceptual processing of acoustic object features. Brain activity was measured with both high spatial (functional magnetic resonance imaging, fMRI) and high temporal resolution (event-related potentials, ERPs). In the conceptual task, participants performed lexical decisions on words that were visually presented among pseudowords. The lexical decision task induces an implicit access to conceptual word meaning [17], but does not afford explicit retrieval of specific conceptual information such as acoustic features. Words either named objects for which acoustic conceptual features were of high (“telephone”) or low relevance (“envelope”). Word sets (with vs. without acoustic features) differed only with respect to the relevance of acoustic conceptual features, but were matched for confounding conceptual and linguistic variables (see also Supplementary Methods). In the perceptual task, participants listened to real sounds (e.g., ringing, barking). This task served as functional localizer to identify brain areas involved in the auditory processing of real sounds in comparison to acoustic coloured noise and a resting condition.

In the first two of three experiments, we assessed with fMRI whether conceptual (experiment 1) and perceptual (experiment 2) processing of acoustic information activates overlapping areas in auditory cortex in the same participant sample. In the third experiment, we determined the temporal onset of brain activity to words with acoustic features using ERP recordings during the conceptual task of experiment 1 in a new participant group. An early temporal onset within the first 200 ms of visual word processing would confirm a conceptual origin and exclude late post-conceptual imagery.

Figure 1 about here

In the conceptual task of experiment 1, we identified brain areas with higher activity to words with acoustic conceptual features ($p < .05$, corrected for multiple comparisons across the entire brain). As shown in Fig. 1A, the largest cluster of voxels was found in left posterior superior gyrus (pSTG) and middle temporal gyrus (pMTG) corresponding to BA 21 and 22, respectively. Smaller clusters were obtained in left supramarginal and right fusiform gyri. Words without acoustic conceptual features, in contrast, did not elicit a significantly higher MR signal. Latencies and error rate of lexical decisions were comparable for both word types hence ruling out any explanations based on task difficulty. Most importantly, we observed a specific brainbehaviour relation between brain activity and relevance ratings of acoustic conceptual features in left pSTG/MTG: The MR signal in this area was parametrically modulated and increased linearly as a function of the relevance of acoustic features for a concept as measured by the word ratings (Fig. 2). In contrast, the relevance of visual and action features did not significantly modulate the MR signal in left pSTG/MTG. This convincingly shows that this area is essentially involved in representing acoustic conceptual features

Figure 2 about here

In the perceptual task of experiment 2, we determined brain areas involved in listening to real sounds ($p < .01$, corrected for multiple comparisons across the entire brain). When contrasted to the resting condition, both active conditions (real sounds, acoustic noise) recruited the superior temporal cortex including the temporal plane bilaterally (Fig. 1B). Based on the known neuroanatomy of the auditory system [18], the temporal plane comprises primary auditory cortex while the neighbouring areas in superior and middle temporal gyri encompass auditory association areas. The MR signal was generally higher to real sounds than to acoustic noise in the temporal plane and in superior temporal cortex. Most importantly, the large cluster that responded to real sounds encompassed a region in left pSTG/MTG which overlapped with the cluster activated by words with acoustic conceptual features (Fig. 1C). Hence, perceiving real sounds and processing of acoustic conceptual features share a common neural substrate in temporal cortex.

Figure 3 about here

ERP recordings of experiment 3 revealed that auditory areas are rapidly ignited at about 150 ms after word onset (Fig. 3). ERPs to words with and without conceptual features diverged significantly ($p < .05$) from each other within a time window of 150-200 ms at central electrodes where acoustically evoked potentials are recorded typically. Source analysis of scalp ERPs with minimum norm estimates identified generators in pSTG/MTG (BA 21, 22). Taking into account the limited spatial resolution of ERPs, this result is in good agreement with our fMRI findings. The time course of brain activity as derived from ERPs allows determining whether the present activation in temporal cortex is due to conceptual processing of acoustic features or auditory imagery. Previous studies estimated that visual word recognition is completed at about 150 ms [19]. In our study, activity in response to acoustic conceptual features starts immediately thereafter at 150 ms. This early onset suggests that the activity observed in auditory association areas reflects access to acoustic conceptual features rather than imagery processes. Such post-conceptual processes can only be evoked later in time after the concept has been fully accessed.

Figure 4 about here

The involvement of pSTG/MTG in higher level sound processing has been shown by previous imaging studies as summarised in Fig. 4. This region contributes to the processing of complex sounds including human voices [20,21] and is activated during sound recognition [22], episodic recall of sounds [23], and music imagery [24,25]. Activity in posterior superior temporal gyrus was also observed for decisions on acoustic object attributes [26] and during recognition of novel objects for which acoustic attributes were learned in a preceding training phase [27]. Patients with a lesion in this area exhibit sound recognition deficits [28]. The present study shows for the first time that pSTG/MTG is the neural substrate of acoustic conceptual features: This region responds to acoustic conceptual features even when probed implicitly with activity being specifically modulated by the differential relevance of acoustic conceptual features.

Unlike perceptual sound processing and sound imagery [24,25], conceptual processing of acoustic features is confined to higher-level auditory association cortex and does not encompass primary and secondary auditory cortex within the temporal plane. These differences in functional neuroanatomy might reflect differences in experiential quality. Conceptual processing of acoustic features lack the vivid sensory experience typically present in perception and imagery: Obviously, we do not experience a “ringing” sound when reading the word “telephone”. Left pSTG/MTG may therefore serve as an auditory convergence zone [29] that codes higher-level acoustic object information contributing to a concept. Although perceptual and conceptual processing of acoustic features considerably overlap in functional neuroanatomy as demonstrated here, both levels of representation are not identical.

In conclusion, our results provide strong evidence for a link between perceptual and conceptual acoustic processing, with the left pSTG/MTG as the shared neural substrate. Hence, conceptual processing of acoustic features involves a partial reinstatement of brain activity during perceptual experience. Our findings are important for several reasons: Firstly, they resolve the fierce debate about the nature of concepts, which meanwhile lasts for several hundred years. They clearly demonstrate that concepts are essentially grounded in the perceptual brain systems and refute the notion of concepts as abstract, amodal mental entities. Secondly, they draw a strong parallel with the functional neuroanatomy of episodic or working memory systems, in which retrieval of sensory properties of an event recruits corresponding modality-specific cortex [23]. This renders it likely that modality-specificity is a general organizational principle in cortical memory representation. Finally, they stress the necessity of sensory experiences in the relevant modalities in order to acquire a rich, fully developed concept of the environment. Conversely, a lack of multimodal sensory experience such as during extensive TV or video game exposure would result in an impoverished development of conceptual representations in children. The modality-specific nature of concepts could also explain why a consensus about the meaning of abstract concepts such as “freedom” or “justice” is notoriously difficult to achieve unless embedded in a concrete, experienced situation. Hence, appropriate knowledge of the nature of concepts is fundamental for interacting successfully with one’s physical and social world.

Methods

Sixteen healthy right-handed native German-speaking subjects participated in the fMRI experiments (experiments 1 and 2), and a new sample of twenty subjects participated in the ERP experiment (experiment 3).

For the conceptual task (experiments 1 and 3), participants were presented with visual words and legally spelled pseudowords. Participants decided as quickly and as accurately as possible whether or not the presented letter string formed a real word (lexical decision task). Half of the words referred to objects with high relevance, the other half to objects with low relevance of acoustic features. Both word sets included an equal amount of living and non-living objects. They differed only with regard to acoustic features, but not to visual and motor features as well as to emotional valence according to a prior rating study. Sets were also equated for word length and frequency.

For the perceptual task (experiment 2), eight blocks of real sounds from animals and objects as well as acoustic noise stimuli were presented binaurally via headphones. Each acoustic stimulation block was followed by a resting block, in which only the fixation cross was presented. Participants listened to the acoustic stimuli while maintaining fixation.

Functional MR images (experiments 1 and 2) were recorded with a 3 Tesla Allegra MRI system (Siemens, Erlangen, Germany) using a T2*-weighted EPI sequence. Data were preprocessed and analyzed statistically in a random effects model with SPM2 (http://www.fil.ion.ucl.ac.uk/spm/spm2.html). ERP scalp potentials (experiment 3) were collected using an equidistant montage of 64 electrodes. ERPs to words with and without acoustic conceptual features were statistically compared using repeated measures analyses of variance. In order to determine the neural sources, we calculated maps of estimated cortical currents from the grand mean ERPs according to the minimum-norm method [30].

References

1. Anderson, J. R. *The architecture of cognition* (Lawrence Erlbaum Associates, Inc, Hillsdayle, NJ, 1983).

2. Tyler, L. K. & Moss, H. E. Towards a distributed account of conceptual knowledge. *Trends Cognit. Sci.* **5**, 244-252 (2001).

3. Machery, E. Concept empiricism: A methodological critique. *Cognition* **104**, 19-46 (2007).

4. Gallese, V. & Lakoff, G. The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognit. Neuropsychol.* **22**, 455-479 (2005).

5. Barsalou, L. W., Simmons, W. K., Barbey, A. K. & Wilson, C. D. Grounding conceptual knowledge in modality-specific systems. *Trends Cognit. Sci.* **7**, 84-91 (2003).

6. Kiefer, M. & Spitzer, M. The limits of a distributed account of conceptual knowledge. *Trends Cognit. Sci.* **5**, 469-471 (2001).

7. Pulvermüller, F. Brain mechanisms linking language and action. *Nature Rev. Neurosci.* **6**, 576-582 (2005).

8. Warrington, E. K. & McCarthy, R. Categories of knowledge. *Brain* **110**, 1273-1296 (1987).

9. Martin, A. & Chao, L. L. Semantic memory and the brain: Structure and processes. *Curr. Op. Neurobiol.* **11**, 194-201 (2001).

10. Kiefer, M., Sim, E.-J., Liebich, S., Hauk, O. & Tanaka, J. W. Experience-dependent plasticity of conceptual representations in human sensory-motor areas. *J. Cognit. Neurosci.* **19**, 525-542 (2007).

11. Helbig, H. B., Graf, M. & Kiefer, M. The role of action representations in visual object recognition. *Exp. Brain. Res.* **174**, 221-228 (2006).

12. Kiefer, M. Repetition priming modulates category-related effects on event-related potentials: Further evidence for multiple cortical semantic systems. *J. Cognit. Neurosci.* **17**, 199-211 (2005).

13. Martin, A., Wiggs, C. L., Ungerleider, L. G. & Haxby, J. V. Neural correlates of category-specific knowledge. *Nature* **379**, 649-652 (1996).

14. Gerlach, C. A review of functional imaging studies on category specificity. *J. Cognit. Neurosci.* **19**, 296-314 (2007).

15. Gerlach, C., Law, I., Gade, A. & Paulson, O. B. Perceptual differentiation and category effects in normal object recognition: A PET study. *Brain* **122**, 2159-2170 (1999).

16. Kiefer, M. Perceptual and semantic sources of category-specific effects in object categorization: Event-related potentials during picture and word categorization. *Mem. Cognit.* **29**, 100-116 (2001).

17. Kiefer, M. The N400 is modulated by unconsciously perceived masked words: Further evidence for an automatic spreading activation account of N400 priming effects. *Cognit. Brain Res.* **13**, 27-39 (2002).

18. Howard, M. A. et al. Auditory cortex on the human posterior superior temporal gyrus. *J Comp Neurol* **416**, 79-92 (2000).

19. Pulvermüller, F., Shtyrov, Y. & Ilmoniemi, R. Brain signatures of meaning access in action word recognition. *J. Cognit. Neurosci.* **17**, 884-892 (2005).

20. Belin, P., Zatorre, R. J., Lafaille, P., Ahad, P. & Pike, B. Voice-selective areas in human auditory cortex. *Nature* **403**, 309-312 (2000).

21. Specht, K. & Reul, J. Functional segregation of the temporal lobes into highly differentiated subsystems for auditory perception: an auditory rapid event-related fMRI-task. *Neuroimage* **20**, 1944-54 (2003).

22. Lewis, J. W. et al. Human brain regions involved in recognizing environmental sounds. *Cereb. Cortex* **14**, 1008-1021 (2004).

23. Wheeler, M. E., Petersen, S. E. & Buckner, R. L. Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proc. Natl. Acad. Sci. U.S.A.* **97**, 11125-11129 (2000).

24. Kraemer, D. J., Macrae, C. N., Green, A. E. & Kelley, W. M. Musical imagery: sound of silence activates auditory cortex. *Nature* **434**, 158 (2005).

25. Zatorre, R. J., Halpern, A. R., Perry, D. W., Meyer, E. & Evans, A. C. Hearing in the mind's ear: A PET investigation of musical imagery and perception. *J. Cognit. Neurosci.* **8**, 29-46 (1996).

26. Kellenbach, M. L., Brett, M. & Patterson, K. Large, colorful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cogn. Affect. Behav. Neurosci.* **1**, 207-221 (2001).

27. James, T. W. & Gauthier, I. Auditory and action semantic features activate sensory-specific perceptual brain regions. *Curr. Biol.* **13**, 1792-1796 (2003).

28. Clarke, S., Bellmann, A., Meuli, R. A., Assal, G. & Steck, A. J. Auditory agnosia and auditory spatial deficits following left hemispheric lesions: evidence for distinct processing pathways. *Neuropsychologia* **38**, 797-807 (2000).

29. Damasio, A. R. Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition* **33**, 25-62 (1989).

30. Hauk, O. Keep it simple: A case for using classical minimum norm estimation in the analysis of EEG and MEG data. *Neuroimage* **21**, 1612-1621 (2004).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements

This research was supported by grants of the German Research Community and of the European Social Foundation to M.K. The authors thank Cornelia Müller, Florian Diehl and Gerwin Müller for their help with data acquisition.

Author information

Reprints and permissions information is available at npg.nature.com/reprintsandpermissions. The authors declare no competing financial interests.

Correspondence and requests for materials should be sent to M.K. (markus.kiefer@uni-ulm.de)

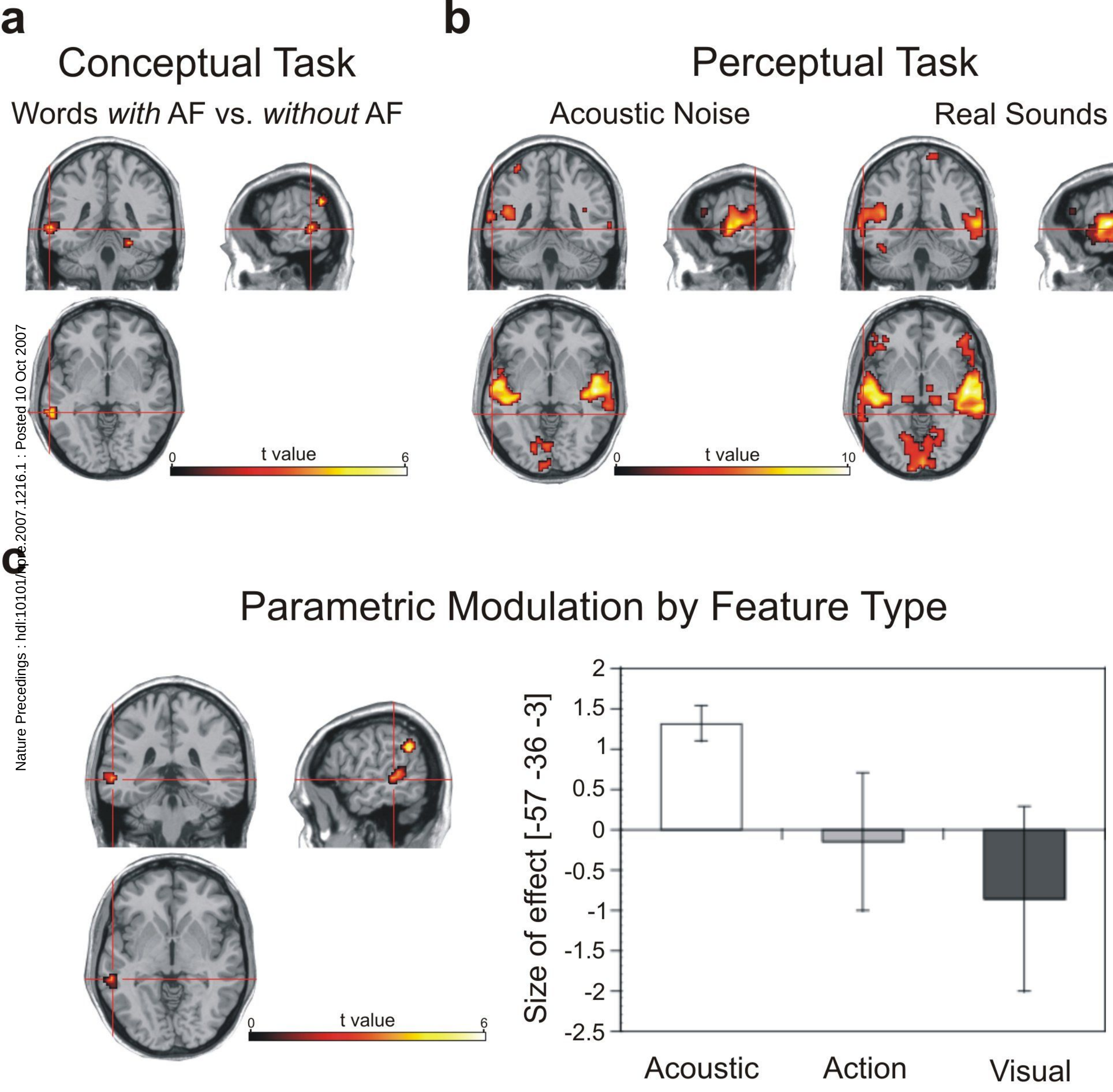
Figure captions

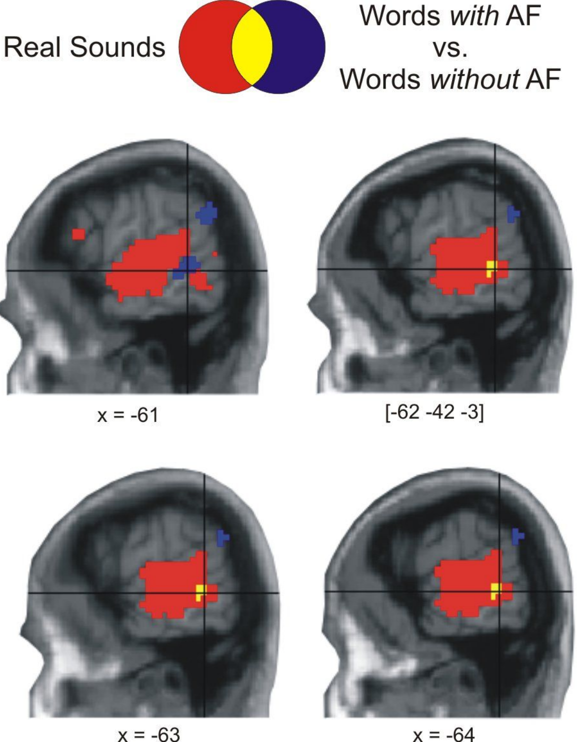
Figure 1 Functional brain activation during the conceptual and the perceptual tasks. a, Conceptual task: Increased functional activation for lexical decisions to words with vs. words without acoustic features (AF), $p < .05$, corrected. **b**, Perceptual task: Increased functional activation during listening to acoustic noise and real sounds, respectively, $p < .01$, corrected. **c**, Parametric modulation of brain activity by conceptual feature relevance: Brain regions showing a parametric modulation of the MR signal by acoustic feature relevance (left part), $p < .05$ corrected. The bar chart (right part) depicts the effect size for the contributions of acoustic, action-related, and visual conceptual features at the peak voxel within the pSTG/MTG cluster. Small vertical bars indicate the standard error of means (s.e.m.). All functional group activation maps are displayed with a spatial extend threshold of 10 voxels and overlaid on the MNI reference brain.

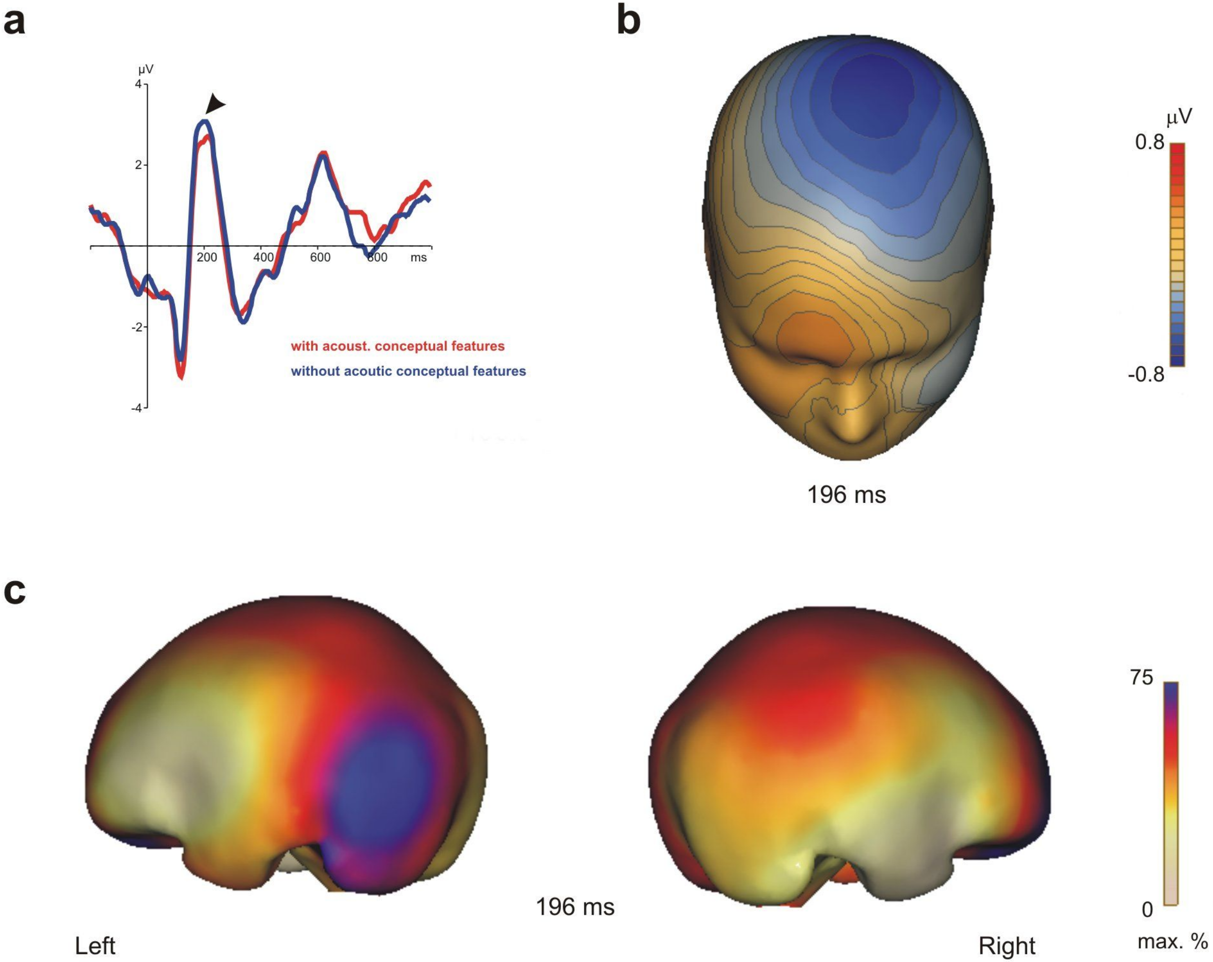
Figure 2 Functional-anatomical overlap between conceptual and perceptual processing of acoustic features. Increased functional activation to words with acoustic features ($p < .05$, corrected) overlaps with brain activation during listening to real sounds ($p < .01$, corrected) in pSTG/MTG. Functional contrast maps are color coded and overlaid on the MNI reference brain. Shown are contiguous slices centered on the peak coordinates.

Figure 3 Time course of conceptual processing of acoustic features. a, Event-related scalp potentials to words with vs. without acoustic features: The arrow indicates the onset of the effect related to conceptual acoustic processing at 150 ms. **b**, Topography of the ERP effect related to conceptual acoustic processing at its maximum global field power. Shown is the interpolated potential difference between conditions (with minus without acoustic features) using spherical splines projected on the rendered head surface of the MNI reference brain. **c**, Brain electrical sources of scalp ERPs to acoustic conceptual processing: Maps of cortical currents calculated according to the minimum norm algorithm from the ERP difference waves. Maps are shown for the respective maxima in global field power and projected on the cortical surface of the MNI reference brain.

Figure 4 Summary of findings from previous imaging studies on the role of pSTG/MTG in sound processing. Peak activations (red symbols) are overlaid on the MNI reference brain. Posterior STG/MTG has been found activated during voice listening (Belin et al. 2000, ◇), sound recognition (Lewis et al., 2004, ×; Specht et al., 2003, ■), word recognition (Specht et al., 2003, ●), sound retrieval (Wheeler et al. 2000, ○), sound imagery (Zattore et al. 1996, ◆, □), and sound verification (Kellenbach et al., 2001, +). Peak activation of acoustic conceptual processing from the present study (blue diamond) is located within this cluster of previously reported activations in pSTG/MTG.


a
Conceptual Task
Words with AF vs. without AF
t value
0
6
b
Perceptual Task
Acoustic Noise
Real Sounds
t value
0
10
c
Parametric Modulation by Feature Type
t value
0
6
Size of effect [-57 -36 -3]
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
Acoustic
Action
Visual


Real Sounds
Words *with* AF
vs.
Words *without* AF
x = -61
[-62 -42 -3]
x = -63
x = -64


a
µV
4
2
-2
-4
200
400
600
800
ms
with acoust. conceptual features
without acoutic conceptual features
b
µV
0.8
-0.8
196 ms
c
196 ms
Left
Right
75
0
max. %