Published in final edited form as:

Neurosurgery. 2015 August ; 62(0 1 0 0): 185–189. doi:10.1227/NEU.0000000000000789.

Investigating the Anterior Temporal Lobe With Direct Intracranial Recordings

Taylor J. Abel, MD^a, Ariane E. Rhone, PhD^a, Kirill V. Nourski, MD, PhD^a, Matthew A. Howard III, MD^a, and Daniel Tranel, PhD^b

^aDepartment of Neurosurgery, University of Iowa, Iowa City, Iowa

^bDepartments of Neurology and Psychology, University of Iowa, Iowa City, Iowa

Keywords

Anterior Temporal Lobe; Electrocorticography; Epilepsy Surgery; Proper Naming; Temporal Pole; Tool Naming

Anterior temporal lobectomy, also known as cortico-amygdalohippocampectomy (CAH), is one of the most effective operations for medically intractable (“pharmacoresistant”) epilepsy and can be associated with a greater than 70% chance of seizure freedom in patients with temporal lobe epilepsy¹⁻³. Despite the potential for an excellent seizure outcome after CAH, resection of language dominant anterior temporal lobe (ATL) is frequently associated with a pronounced and specific deficit in naming⁴. Neuropsychologically, deficits can be seen as a decline in visual confrontation naming (e.g., naming concrete entities as on the Boston Naming Test⁴), but the most striking deficits (and those that are most troubling to patients) are in proper naming of unique entities (e.g., famous faces as on the Iowa Famous Faces test⁵) and in learning new proper names. Lesion studies have provided consistent evidence that proper naming (e.g. of famous faces, landmarks) is dependent on the language dominant ATL^{6, 7}. Interestingly, studies comparing CAH to selective amygdalohippocampectomy (where the ATL is partially disconnected, but spared) report no significant difference in cognitive decline between the two techniques⁸. In contrast, recent reports examining naming outcomes following selective laser ablation of the amygdala and hippocampus (a technique that spares ATL connectivity) report better postoperative naming outcomes⁹. Together, these findings suggest that language dominant CAH-associated naming impairment is a result of ATL resection or disconnection.

Although the nature of CAH-associated naming impairment is well-studied, the physiologic mechanisms of naming in the ATL are poorly understood and are difficult to study using noninvasive techniques. One reason for this is the variation in ATL response patterns in functional magnetic resonance imaging¹⁰, which may be attributed at least in part to signal dropout caused by susceptibility artifact that is particularly prominent around the ATL^{11, 12}.

Correspondence: Taylor J. Abel, MD, University of Iowa Hospitals and Clinics, 200 Hawkins Drive, Iowa City, Iowa 52242, taylor-abel@uiowa.edu.

Disclosure: The authors have no personal, financial, or institutional interest in any of the drugs, materials, or devices described in this article.

Positron emission tomography has also been used^{7, 13}, but is limited by low temporal resolution that cannot resolve the exquisite timing of language processes. Therefore, studying the physiologic correlates of cognition in the ATL is technically challenging, and noninvasive techniques to map ATL language cortex with high spatial and temporal resolution are not yet available.

Recently, there has been increasing use of intracranial electrodes, which are implanted in patients with medically intractable epilepsy for localization of epileptic foci, to directly study the physiology of the ATL with excellent spatial and temporal resolution. An emerging body of literature¹⁴⁻¹⁷ demonstrates the utility of intracranial recordings for studying ATL physiology and has yielded important results that have increased knowledge about ATL function. Traditionally, coverage of the ATL has been achieved with an anteromedial strip electrode that provides sparse coverage of ATL cortex¹⁸. Recently, we developed a specialized electrode array that fits within the middle cranial fossa to provide dense and consistent coverage of ATL cortex for localization of both epileptogenic and eloquent cortex¹⁴. In this manuscript, we describe our preliminary work studying physiologic responses of the ATL during proper naming.

The functional role of the ATL

Anterior temporal cortex has been implicated in a wide variety of higher order cognitive processes including face perception¹⁹, voice recognition²⁰, semantic processing²¹, social processing²², and naming^{6, 15, 23}. The role of the ATL in naming is most obvious to clinicians since deficient name retrieval is a frequent complaint after language-dominant CAH^{24, 25}. The nature of naming dysfunction after language-dominant CAH is well described by numerous studies^{6, 7, 23, 26, 27}. Naming dysfunction after language-dominant CAH is specific to naming (word retrieval) and dissociated from recognition (semantic knowledge retrieval)²³. This means that an affected patient retains knowledge for the entity to be named (i.e. can describe specific identifying information about a person), but cannot produce the specific proper name. For example, when presented with a picture of Barack Obama, a patient with this naming deficit would know and be able to express that Barack Obama is the President, but would not be able to say his name. Another property of the naming deficit associated with language-dominant CAH is that it is more pronounced for retrieving proper nouns than common nouns⁶. For example, studies demonstrate that patients have a more significant deficit for naming famous faces^{6, 7} or specific landmarks²⁷, than for animals or tools⁶.

An additional characteristic of language-dominant CAH-associated naming impairment is that it is transmodal, meaning it applies not only to naming visually presented entities, but also famous voices²⁸ or famous melodies²⁹. Although the transmodal nature of language-dominant ATL naming deficits has been documented in several recent studies^{28, 29}, there is an intense debate regarding the neurophysiologic and anatomical basis for these transmodal naming deficits^{21, 30, 31}. One possibility is that the left ATL contains spatially segregated cortex with unimodal response characteristics, and that these spatially segregated cortical sites mediate modality-specific name retrieval. An alternate hypothesis is that the left ATL contains cortex with heteromodal (or transmodal) response characteristics, and supports both

visual and auditory naming, as a single intermediary zone for modality-independent name retrieval. Previous anatomical studies in nonhuman primates have reported convergent inputs to the ATL from visual, auditory, and olfactory cortices³², and diffusion tensor imaging techniques have demonstrated graded convergence of visual and auditory inputs to the ATL³³. These anatomical findings support the hypothesis of functional convergence within the ATL; however, neurophysiologic evidence of convergent ATL responses is lacking.

Technical challenges of studying the ATL

Anterior temporal cortex has been exceedingly difficult to study in humans, in good measure because of technical challenges associated with noninvasive functional neuroimaging specific to the ATL¹⁰. Perhaps one of the most important examples of a technical challenge associated with studying the ATL is seen with functional magnetic resonance imaging (fMRI). fMRI is a widely available technique that has enabled neuroscientists to noninvasively study large-scale neural responses associated with higher order cognitive processes by measuring event-related alterations in blood flow and has become a mainstay in human cognitive neuroscience research^{10, 34, 35}. fMRI is advantageous because it is noninvasive, can be employed to study normal subjects, and has excellent spatial resolution compared to noninvasive electrophysiologic techniques (i.e. scalp electroencephalography)³⁶. Unfortunately, applying fMRI to study the human ATL has been challenging due to MRI susceptibility artifact present at the anterior cranial base¹⁰⁻¹². For this reason, responses from the ATL to various tasks may not be seen in the ATL when imaging with fMRI. For example, for the same semantic task a response may be seen from the ATL using positron emission tomography (PET), but not with fMRI¹². Factors contributing to ATL response variability on fMRI have been reviewed extensively by Visser and colleagues¹⁰.

Given the role of the ATL in language, particularly its potential role in integrating visual and auditory information to retrieve modality-independent neural dispositions for names, the ideal technique to study the ATL would have both excellent spatial and temporal resolution. PET and fMRI lack the temporal resolution to resolve language processes that occur on relatively rapid time scales. This is particularly true if one were to study the integration of auditory and visual processes in ATL, which is likely to be a highly time-dependent process. For example, Perrodin and colleagues have reported phase resetting of low frequency oscillations by visual face stimuli in voice sensitive ATL cortex of macaques, which in turn modulates neuronal responses³⁷. Evaluating dynamics on this temporal scale requires electrophysiologic recordings.

Intracranial recordings of the ATL: Surmounting technical challenges

Given the limitations of PET and fMRI for studying ATL physiology, we have utilized electrocorticography (ECoG) to study the large-scale electrophysiologic responses of the human ATL with temporal and spatial resolution unmatched by noninvasive techniques. Intracranial electrodes are implanted in patients with medically intractable seizures for the

purpose of localizing of the epileptic focus prior to resection, and cognitive experiments are performed over the duration of seizure localization.

Although ECoG has many advantages over noninvasive neuroimaging techniques for mapping the ATL, obtaining dense and consistent ECoG coverage of the ATL is a technical challenge. The ATL is embedded in the middle cranial fossa and has a half-spherical shape that makes reproducible and dense coverage of the ATL difficult to achieve using standard ECoG arrays. Because of the shape of the ATL, it is nearly impossible to achieve dense coverage of the ATL using standard strip or grid ECoG arrays. Specifically, because the ATL has the shape of a half-sphere, a standard grid electrode array in which electrodes are embedded within a flat continuous silicon sheet will not conform smoothly to ATL cortical surface. Additionally, even when multiple anterior subtemporal strip electrodes are placed, there are often gaps in electrode coverage.

We designed an electrode array for the specific purpose of providing dense and consistent coverage of the ATL for seizure localization and mapping of eloquent cortex¹⁴. We achieved this by adopting a ‘multi-prong’ design, in which a grid electrode design is modified to create multiple thin strip electrodes that remain connected along one border of the grid (Fig. 1A). Each strip is sufficiently malleable to contour itself along the curvature of the ATL. The points of mechanical fusion at the array edge ensure that consistent spacing is achieved between the parallel strips of the array. Multiple strip electrodes can be implanted to provide coverage of the ATL, but due to limited visualization of ATL cortex during surgery, the final positions of the strip electrode recording contacts cannot be determined at the time of implantation (Fig. 1B). Our grid design results in dense, predictable electrode coverage of the ATL that cannot be achieved using traditional grid or strip electrode arrays (Fig. 1C). We implemented this design by modifying a commercially available grid array (Ad-Tech Medical Instruments, Racine, WI). In our first 12 patients with the array, we demonstrated dense and consistent coverage across multiple patients. We have now implanted the ATL array in more than 20 patients.

Heteromodal responses of the ATL

As mentioned previously, there is an ongoing debate regarding the spatial distribution of picture and voice naming responses in the left ATL. Our hypothesis is that the left ATL is a transmodal convergence region for proper naming dispositions that contains heteromodal cortex that would demonstrate similar responses regardless of modality. Specifically, we predicted that naming either a picture or a voice clip of a famous person (e.g. Bill Clinton), would result in a similar response from the left ATL. Using the dense ATL coverage afforded by our specialized ATL ECoG array, we evaluated this hypothesis empirically by examining responses of the left ATL to picture and voice naming of American presidents.

We performed picture and voice naming experiments with patients who had intracranial electrodes placed for localization of medically intractable epilepsy. Using an IRB-approved protocol, patients were presented 50 pictures each of three American presidents (Barack Obama, George W. Bush, and Bill Clinton) and asked to name the president (Fig. 2A). In a separate experimental block, patients performed a similar task in which they named 50 voice

clips of each of the presidents while focusing on a fixation cross. Time-frequency analysis was performed using multitaper spectral analysis³⁸ to assess response at individual electrode sites (Fig. 2B). To determine statistically significant cortical responses to conditions of interest (specifically, picture and voice naming), event-related band power (ERBP) was measured in the beta (14-30 Hz) and high gamma (70-150 Hz) ECoG bands in a 700 ms window (300 – 1000 ms from stimulus onset).

Using this approach, we found cortical sites in the left ATL with similar response properties to both picture and voice naming tasks (Fig. 3). Examining significant ERBP in the beta band, we found that 50% of cortical sites in the left ATL demonstrated significant responses to both picture and voice naming tasks (Fig. 3A). Interestingly, when we examined high gamma band ERBP in the same time epoch, there were no cortical sites that showed responses to both picture and voice naming tasks (Fig. 3B). These findings demonstrate convergent and robust large-scale neurophysiologic responses to picture and voice naming in the human left ATL. It is interesting to note that convergent responses were seen when examining lower frequency ERBP, but not high gamma ERBP. It is possible that anterior temporal cortex uses lower frequency rhythms to integrate convergent neural inputs from distant cortex. As observed by Perrodin and colleagues, phase resetting of low frequency rhythms by visual stimuli in voice-sensitive anterior temporal cortex plays a role in the integration of visual and auditory information³⁷. A similar process may be involved during our picture and voice naming tasks in language-dominant ATL. Ultimately, our finding provides further evidence in support of heteromodal (i.e. transmodal) dispositions for proper naming in the left ATL.

Conclusion

The work reviewed in this manuscript demonstrates that in using ECoG arrays specialized for coverage of anterior temporal cortex, the ATL can be mapped with excellent temporal and spatial resolution for clinical and research purposes. While the role of the ATL in human cognition remains poorly understood, its importance for naming is clear from the naming deficits seen in patients after language-dominant CAH and the responses generated from the ATL seen on the ECoG experiments reviewed in this manuscript. Given the importance of the language-dominant ATL in naming, in the future, mapping language function in the ATL may play a role in guiding more selective epilepsy resections in which naming function can be preserved. The results reviewed here show that naming functions in the ATL can be mapped, but the clinical significance of ECoG responsive sites in the ATL will only be determined by studies comparing ECoG responses to lesion data.

Using dense coverage of the ATL, we demonstrate similar responses from ATL cortex in the beta band for both picture and voice naming tasks. This finding supports the hypothesis that the left ATL is a transmodal convergence region for proper naming dispositions. While the role of the ATL in human cognition remains poorly understood, future work of this nature will shed light on the functional architecture and electrophysiology of the ATL.

Acknowledgments

Funding: This work was supported through grants by the National Institutes of Health (NIH F32-NS087664, NIH RO1-DC004290, NIH UL1RR024979), the Hoover Fund, and Hearing Health Foundation. Also supported in part by a McDonnell Foundation Collaborative Award to D.T. (#220020387).

References

1. Josephson CB, Dykeman J, Fiest KM, Liu X, Sadler RM, Jette N, Wiebe S. Systematic review and meta-analysis of standard vs selective temporal lobe epilepsy surgery. *Neurology*. 2013; 80(18): 1669–1676. [PubMed: 23553475]
2. Tanriverdi T, Olivier A, Poulin N, Andermann F, Dubeau F. Long-term seizure outcome after mesial temporal lobe epilepsy surgery: corticamygdalohippocampectomy versus selective amygdalohippocampectomy. *J Neurosurg*. 2008; 108(3):517–524. [PubMed: 18312099]
3. Clusmann H, Schramm J, Kral T, Helmstaedter C, Ostertun B, Fimmers R, Haun D, Elger CE. Prognostic factors and outcome after different types of resection for temporal lobe epilepsy. *J Neurosurg*. 2002; 97(5):1131–1141. [PubMed: 12450036]
4. Ives-Deliperi VL, Butler JT. Naming outcomes of anterior temporal lobectomy in epilepsy patients: a systematic review of the literature. *Epilepsy Behav*. 2012; 24(2):194–198. [PubMed: 22569529]
5. Yucus CJ, Tranel D. Preserved proper naming following left anterior temporal lobectomy is associated with early age of seizure onset. *Epilepsia*. 2007; 48(12):2241–2252. [PubMed: 17645534]
6. Damasio H, Grabowski TJ, Tranel D, Hichwa RD, Damasio AR. A neural basis for lexical retrieval. *Nature*. 1996; 380(6574):499–505. [PubMed: 8606767]
7. Grabowski TJ, Damasio H, Tranel D, Ponto LL, Hichwa RD, Damasio AR. A role for left temporal pole in the retrieval of words for unique entities. *Hum Brain Mapp*. 2001; 13(4):199–212. [PubMed: 11410949]
8. Tanriverdi T, Dudley RW, Hasan A, Al Jishi A, Al Hinai Q, Poulin N, Colnat-Coulbois S, Olivier A. Memory outcome after temporal lobe epilepsy surgery: corticoamygdalohippocampectomy versus selective amygdalohippocampectomy. *J Neurosurg*. 2010; 113(6):1164–1175. [PubMed: 19961307]
9. Drane DL, Loring DW, Voets NL, Price M, Ojemann JG, Willie JT, Saindane AM, Phatak V, Ivanisevic M, Millis S, Helmers SL, Miller JW, Meador KJ, Gross RE. Better object recognition and naming outcome with MRI-guided stereotactic laser amygdalohippocamptomy for temporal lobe epilepsy. *Epilepsia*. 2014
10. Visser M, Jefferies E, Lambon Ralph MA. Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. *J Cogn Neurosci*. 2010; 22(6):1083–1094. [PubMed: 19583477]
11. Ojemann JG, Akbudak E, Snyder AZ, McKinstry RC, Raichle ME, Conturo TE. Anatomic localization and quantitative analysis of gradient refocused echo-planar fMRI susceptibility artifacts. *Neuroimage*. 1997; 6(3):156–167. [PubMed: 9344820]
12. Devlin JT, Russell RP, Davis MH, Price CJ, Wilson J, Moss HE, Matthews PM, Tyler LK. Susceptibility-induced loss of signal: Comparing PET and fMRI on a semantic task. *Neuroimage*. 2000; 11(6):589–600. [PubMed: 10860788]
13. Grabowski TJ, Damasio H, Tranel D, Cooper GE, Ponto LL, Watkins GL, Hichwa RD. Residual naming after damage to the left temporal pole: a PET activation study. *Neuroimage*. 2003; 19(3): 846–860. [PubMed: 12880813]
14. Abel TJ, Rhone AE, Nourski KV, Granner MA, Oya H, Griffiths TD, Tranel DT, Kawasaki H, Howard MA 3rd. Mapping the temporal pole with a specialized electrode array: technique and preliminary results. *Physiol Meas*. 2014; 35(3):323–337. [PubMed: 24480831]
15. Abel TJ, Rhone AE, Nourski KV, Kawasaki H, Oya H, Griffiths TD, Howard MA, Tranel D. Direct physiologic evidence of a heteromodal convergence region for proper naming in human left anterior temporal lobe. *J Neurosci*. 2015; 35:1513–1520. [PubMed: 25632128]

16. Chan AM, Baker JM, Eskandar E, Schomer D, Ulbert I, Marinkovic K, Cash SS, Halgren E. First-pass selectivity for semantic categories in human anteroventral temporal lobe. *J Neurosci*. 2011; 31(49):18119–18129. [PubMed: 22159123]
17. Shimotake A, Matsumoto R, Ueno T, Kunieda T, Saito S, Hoffman P, Kikuchi T, Fukuyama H, Miyamoto S, Takahashi R, Ikeda A, Lambon Ralph MA. Direct Exploration of the Role of the Ventral Anterior Temporal Lobe in Semantic Memory: Cortical Stimulation and Local Field Potential Evidence From Subdural Grid Electrodes. *Cereb Cortex*. 2014
18. Cohen-Gadol AA, Spencer DD. Use of an anteromedial subdural strip electrode in the evaluation of medial temporal lobe epilepsy. Technical note. *J Neurosurg*. 2003; 99(5):921–923. [PubMed: 14609175]
19. Rajmehar R, Young JC, Tootell RB. An anterior temporal face patch in human cortex, predicted by macaque maps. *Proc Natl Acad Sci U S A*. 2009; 106(6):1995–2000. [PubMed: 19179278]
20. Andics A, McQueen JM, Petersson KM, Gal V, Rudas G, Vidnyanszky Z. Neural mechanisms for voice recognition. *Neuroimage*. 2010; 52(4):1528–1540. [PubMed: 20553895]
21. Lambon Ralph MA. Neurocognitive insights on conceptual knowledge and its breakdown. *Philos Trans R Soc Lond B Biol Sci*. 2014; 369(1634):20120392. [PubMed: 24324236]
22. Olson IR, Plotzker A, Ezzyat Y. The Enigmatic temporal pole: a review of findings on social and emotional processing. *Brain*. 2007; 130(Pt 7):1718–1731. [PubMed: 17392317]
23. Tranel D. The left temporal pole is important for retrieving words for unique concrete entities. *Aphasiology*. 2009; 23(7-8):867–884. [PubMed: 20161625]
24. Drane DL, Ojemann GA, Aylward E, Ojemann JG, Johnson LC, Silbergeld DL, Miller JW, Tranel D. Category-specific naming and recognition deficits in temporal lobe epilepsy surgical patients. *Neuropsychologia*. 2008; 46(5):1242–1255. [PubMed: 18206185]
25. Griffin S, Tranel D. Age of seizure onset, functional reorganization, and neuropsychological outcome in temporal lobectomy. *J Clin Exp Neuropsychol*. 2007; 29(1):13–24. [PubMed: 17162718]
26. Drane DL, Ojemann JG, Phatak V, Loring DW, Gross RE, Hebb AO, Silbergeld DL, Miller JW, Voets NL, Saindane AM, Barsalou L, Meador KJ, Ojemann GA, Tranel D. Famous face identification in temporal lobe epilepsy: support for a multimodal integration model of semantic memory. *Cortex*. 2013; 49(6):1648–1667. [PubMed: 23040175]
27. Tranel D. Impaired naming of unique landmarks is associated with left temporal polar damage. *Neuropsychology*. 2006; 20(1):1–10. [PubMed: 16460217]
28. Waldron EJ, Manzel K, Tranel D. The left temporal pole is a heteromodal hub for retrieving proper names. *Front Biosci (Schol Ed)*. 2014; 6:50–57. [PubMed: 24389260]
29. Belfi AM, Tranel D. Impaired Naming of Famous Musical Melodies Is Associated With Left Temporal Polar Damage. *Neuropsychology*. 2013
30. Rogers TT, Lambon Ralph MA, Garrard P, Bozeat S, McClelland JL, Hodges JR, Patterson K. Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychol Rev*. 2004; 111(1):205–235. [PubMed: 14756594]
31. Skipper LM, Ross LA, Olson IR. Sensory and semantic category subdivisions within the anterior temporal lobes. *Neuropsychologia*. 2011; 49(12):3419–3429. [PubMed: 21889520]
32. Moran MA, Mufson EJ, Mesulam MM. Neural inputs into the temporopolar cortex of the rhesus monkey. *J Comp Neurol*. 1987; 256(1):88–103. [PubMed: 3819040]
33. Binney RJ, Parker GJ, Lambon Ralph MA. Convergent connectivity and graded specialization in the rostral human temporal lobe as revealed by diffusion-weighted imaging probabilistic tractography. *J Cogn Neurosci*. 2012; 24(10):1998–2014. [PubMed: 22721379]
34. Logothetis NK. What we can do and what we cannot do with fMRI. *Nature*. 2008; 453(7197):869–878. [PubMed: 18548064]
35. Visser M, Embleton KV, Jefferies E, Parker GJ, Ralph MA. The inferior, anterior temporal lobes and semantic memory clarified: novel evidence from distortion-corrected fMRI. *Neuropsychologia*. 2010; 48(6):1689–1696. [PubMed: 20176043]
36. Cabeza R, Nyberg L. Imaging cognition II: An empirical review of 275 PET and fMRI studies. *J Cogn Neurosci*. 2000; 12(1):1–47. [PubMed: 10769304]

37. Perrodin C, Kayser C, Logothetis NK, Petkov CI. Natural asynchronies in audiovisual communication signals regulate neuronal multisensory interactions in voice-sensitive cortex. *Proc Natl Acad Sci U S A*. 2015; 112(1):273–278. [PubMed: 25535356]
38. Thomson D. Spectral estimation and harmonic analysis. *Proceedings of the IEEE*. 1982; 7(9): 1055–1096.
39. Nourski KV, Howard MA. Invasive recordings in the human auditory cortex. *Handb Clin Neurol*. 2014; 129:225–244. [PubMed: 25726272]

Figure 1.

Intracranial recording from the human ATL. A: Customized 30-contact electrode array providing dense coverage of the human ATL. B: Intraoperative photograph depicting placement of recording arrays including the ATL array (bottom right). C: CT-MR co-registered brain renderings demonstrating location of the implanted electrode arrays. Contacts of the lateral temporal, frontoparietal and ATL grid are shown in purple, orange and teal, respectively. Modified with permission from Abel et al.¹⁴ and Nourski & Howard.³⁹

Figure 2. ECoG recorded from the human ATL during picture and voice naming. Example from a representative recording site. **A:** Schematic of picture-naming (left) and voice-naming (right) experiments. **B:** CT-MR co-registered brain renderings demonstrating location of a representative recording site on the left ATL (asterisk). **C:** Time-frequency plots of cortical activity recorded from the ATL during picture and voice naming tasks (left and right plots, respectively). Modified with permission from Abel et al.¹⁵

Figure 3. Spatial distribution of beta (14-30 Hz; panel A) and high gamma (70-150 Hz, panel B) ERBP responses on the ATL. Data from three subjects (left, right and middle panels, respectively). Sites that exhibited significant responses during picture naming and voice naming are shown in magenta and cyan, respectively. Open circles represent recording sites that were included in the analysis on anatomical grounds, but did not feature significant response to either stimulus. Modified with permission from Abel et al.¹⁵