An auditory illusion in tamarin monkeys

Astrocytes spontaneously excite neurons

Computing with noisy population codes

Brain responses to other-race faces

Amodal completion of acoustic signals by a nonhuman primate

Cory T. Miller, Elizabeth Dibble and Marc D. Hauser

Primate Cognitive Neuroscience Laboratory, Department of Psychology, Harvard University, 33 Kirkland Street,Cambridge, Massachusetts 02138, USA

Correspondence should be addressed to C.T.M. (ctmiller@wjh.harvard.edu)

Evidence of amodal completion exists for both visual and auditory stimuli in humans. The importance of this mechanism in forming stable representations of sensory information suggests that it may be common among multiple modalities and species. Here we show that a species of nonhuman primate amodally completes biologically meaningful acoustic stimuli, which provides evidence that the neural mechanism mediating this aspect of auditory perception is shared among primates, and perhaps other taxonomic groups as well.

The brain organizes sensory information according to a set of basic principles that facilitate the formation of stable representations of the world. For example, humans represent visual objects as continuous bounded units in space and time. This continuity principle allows our visual system to perceive partially occluded objects as whole objects, an illusion referred to as amodal completion[1]. Comparable illusions are observed in the auditory domain for tones[2] and phonemes[3,4]; humans can understand the meaning of a word even if a phoneme within the word is masked with noise.

Our sensory systems are often provided with incomplete information about the boundaries of units such as visual objects or auditory signals. However, most of the work investigating amodal completion focuses on humans. It is thus uncertain whether this phenomenon occurs in other species[5], and, more generally, whether parallels in basic sensory principles exist between humans and other animals. Here we found evidence of amodal completion of auditory stimuli in a nonhuman primate, the cotton-top tamarin (*Saguinus oedipus*), by performing experiments based on their natural vocal response to species-specific vocalizations.

When separated from group members, cotton-top tamarins produce a species-specific combination long call (CLC; **Fig. 1**, top) consisting of two syllable types, chirps and whistles[6,7]. Experiments show that tamarins call back ('antiphonally respond') more frequently to complete CLCs than to either isolated chirps or isolated whistles[8]. A response was defined as antiphonal if a subject produced a long call within five seconds of stimulus presentation (A.A. Ghazanfar and M.D.H., unpublished data). Subjects never responded to stimuli by producing only part of the call (a single chirp or whistle). Rather, following stimulus presentation, subjects typically either made no response, or responded with a complete long call[8].

We used the tamarin's natural antiphonal calling response to examine amodal completion of auditory representations. In each condition, we presented subjects with 20 stimuli consisting of 5 exemplars of 4 stimulus types, 2 unmanipulated signals (whole CLCs and isolated whistles) and 2 experimentally manipulated whistles, and we counted the number of antiphonal calls. Subjects were tested twice for each condition, with stimuli and order of conditions counterbalanced. Eight subjects participated in both conditions 1 and 2, and two others participated only in condition 2. (One subject died, and another stopped responding to stimuli.)

In condition 1, the whistle was manipulated by inserting either white noise (middle noise) or silence (middle silence) in the middle portion of the whistle; the first and final 150 ms of the whistle were unchanged (**Fig. 1**, middle). Subjects' antiphonal calling pattern did not differ between sessions ($F_{1,7} = 0.13$, $p = 0.73$), but we found a significant effect of stimulus type ($F_{3,21} = 14.45$, $p < 0.0001$). Analyses of antiphonal calling to individual stimuli revealed that subjects responded equally to unmanipulated and middle-noise whistles

Fig. 1. Evidence of amodal completion of acoustic signals in cotton-top tamarins. Top left, an adult cotton-top tamarin. Top right, spectrogram (above) and an amplitude waveform (below) of a whole call, labeled with the different syllable types (chirps and whistles). Middle, representative amplitude waveforms for the three test stimuli used in Conditions 1 and 2 (isolated whistle, middle noise, middle silence, begin noise, end noise). The black areas depict segments of the naturally produced whistle; the gray areas depict inserted white noise. Bottom, the mean number (± s.e.m.) of antiphonal calls per session for each stimulus in conditions 1 and 2. In each condition, the second whistle was extracted from each whole call and used as the isolated whistle stimuli as well as both manipulated whistles. Each CLC and isolated whistle was normalized to peak amplitude. The mean (± s.e.m.) root mean square amplitude was 3.25 ± 0.41 for CLCs and 4.38 ± 0.46 for isolated whistles. The white noise used in both conditions was a constant 11.25 root mean square amplitude. Stimuli were randomized in each test session and presented to subjects at 15-s intervals. The alpha-level for paired statistical comparisons between unmanipulated and manipulated whistles are Bonferroni adjusted to $p < 0.0167$. Asterisk denotes statistically significant difference.
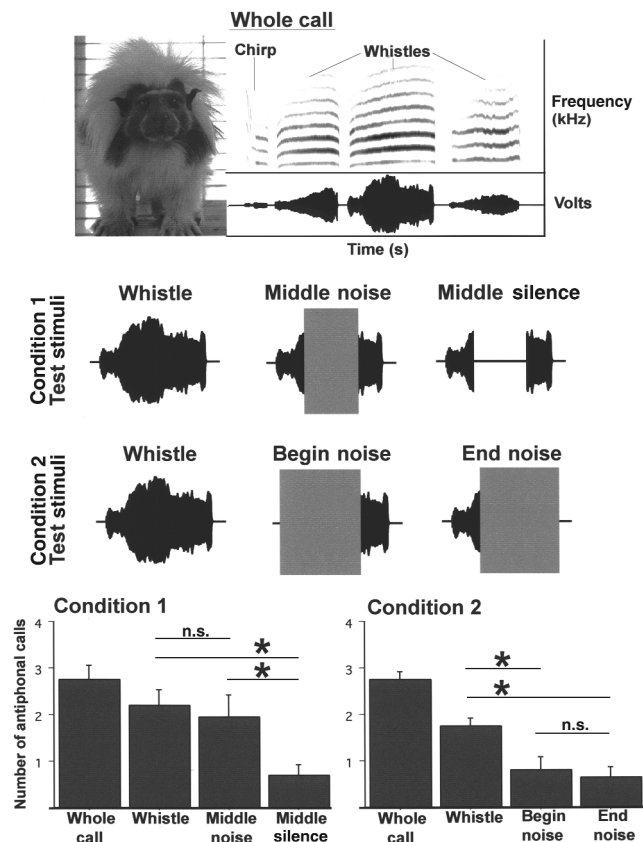
($t_{1,7} = 0.88$, $p = 0.41$), but responded significantly less frequently to middle-silence whistles than to unmanipulated whistles ($t_{1,7} = 3.31$, $p = 0.013$, **Fig. 1**, bottom). This either suggests that tamarins amodally complete the whistle unit or respond more to signals with continuous acoustic energy. Condition 2 distinguished between these hypotheses.

We designed two whistle manipulations in condition 2. In the first, white noise began at the onset of the whistle and ended 150 ms before the end of the whistle (begin noise); in the second, white noise began 150 ms after the onset of the whistle and terminated at the end of the syllable (end noise; **Fig. 1**, middle). Antiphonal calling did not differ between sessions ($F_{1,9} = 0.01$, $p = 0.93$), but we found a significant effect of stimulus type ($F_{3,27} = 26.34$, $p < 0.0001$). Subjects responded significantly more often to unmanipulated whistles than to both begin-noise ($t_9 = 3.1$, $p = 0.013$) and end-noise whistles ($t_9 = 6.736$, $p = 0.0001$), but responded at equal rates to both types of manipulated whistles ($t_9 = 0.43$, $p = 0.67$, **Fig. 1**, bottom). These results show that signals with continuous acoustic energy are not sufficient to drive the antiphonal response to whistles. Rather, the placement of white noise must be located in a way that bridges the start and end of the whistle unit. In conclusion, tamarins amodally complete the middle-noise whistle unit, and thus, in the absence of training, are susceptible to this auditory illusion.

Although auditory illusions are rarely investigated[9], such phenomena provide insights into how the brain organizes perceptual information. Given the phylogenetic relatedness of humans and cotton-top tamarins, these results suggest that the neural mechanisms mediating auditory continuity may have evolved in a common ancestor at least 40 million years ago, before the divergence of these two primate clades, and possibly earlier[5]. If true, then similar principles may facilitate the organization of sensory information in human and nonhuman primate brains[10,11,12]. Future work will explore whether cotton-top tamarins and humans use similar principles to organize sensory information in other modalities. Such data are critical to a more complete understanding of brain evolution.

1. Palmer, S. E. *Vison Science: Photons to Phenomenology* (MIT Press, Cambridge, Massachusetts, 1999).
2. Bregman, A. S. *Auditory Scene Analysis* (MIT Press, Cambridge, Massachusetts, 1990).
3. Warren, R. M. *Science* **147**, 392–393 (1970).
4. Samuel, A. R. *Lang. Cog. Proc.* **11**, 647–653 (1996).
5. Regolin, L. & Vallortigara, G. *Percept. Psychophys.* **57**, 971–976 (1995).
6. Cleveland, J. & Snowdon, C. T. *Z. fur Tierpsychol.* **58**, 231–270 (1982).
7. Weiss, D., Garibaldi, B. & Hauser, M. D. *J. Comp. Psychol.* (in press).
8. Ghazanfar, A. A., Flombaum, J. I., Miller, C. T. & Hauser, M. D. *J. Comp. Physiol. A* **187**, 27–35 (2001).
9. Shams, L., Kamitani, Y. & Shimojo, S. *Nature* **408**, 788 (2000).
10. Heffner, H. E. & Heffner, R. S. *Science* **226**, 75–76 (1984).
11. Rauschecker, J. P., Tian, B. & Hauser, M. D. *Science* **268**, 111–114 (1995).
12. Wang, X., Merzenich, M. M., Beitel, R. & Schreiner, C. E. *J. Neurophysiol.* **74**, 2685–2706 (1995).

Category specificity in reading and writing: the case of number words

Brian Butterworth[1], Marinella Cappelletti[1,2] and Michael Kopelman[1,2]

[1] *Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1 6BT, UK*

[2] *University Department of Psychiatry and Psychology, St. Thomas Hospital, Kings' College, Lambeth Palace Road, London SE1 7EH, USA*

All authors contributed equally to this work

Correspondence should be addressed to B.B. (b.butterworth@ucl.ac.uk)

In standard models, word meanings contribute to reading words aloud and writing them to dictation[1–3]. It is known that categories of knowledge and the associated word meanings can be spared or impaired selectively[4], but it has not been possible to demonstrate that category-specific effects apply to reading and writing. Here we report the case of a neurodegenerative patient with selectively spared numerical abilities whose brain damage left him able to read and write only number words.

Although reading aloud can be achieved by mapping letters directly on to sounds and sounds directly on to letters[5], there is evidence that word meanings (semantics) interact with these processes[2,3]. When knowledge of letter–sound mappings is lost, and the meaning of the target word is intact, models allow that accurate reading and spelling can be achieved on the basis of the meaning-mediated process alone. This account has been applied specifically to reading and writing numbers, with essentially the same prediction[6]. Under these conditions, selective preservation of a single semantic category should result in the patient being able to read only words in the preserved category.

The patient we describe, I.H., had temporal lobe atrophy mainly on the left with relative sparing of the hippocampus, which resulted in a severe decline in his linguistic abilities and his general knowledge. (Detailed information about the patient's neuroanatomy and references for the standard neuropsychological tests are available on the *Nature Neuroscience* website, http://neurosci.nature.com/web_specials.) Nevertheless, his memory for people and personal events remained relatively good[7]. This combination of focal temporal lobe atrophy and lexical–semantic symptoms has been labeled 'semantic dementia'[8,9].

A first set of experiments showed that I.H.'s mathematical ability was remarkably well preserved, despite his severe impairment in all the other domains of knowledge (**Tables 1** and **2**). A second set of experiments showed that he was still able to read and write almost all number words, despite being severely impaired at reading and writing non-number words matched by frequency, spelling regularity and length (**Table 3**). His performance, unlike other cases of semantic dementia[10], was not affected by spelling regularity. His performance was flawless in reading and spelling regularly spelled (ten) and irregularly spelled (two) number words, but equally impaired in reading and spelling regular and irregular non-number words such as 'table' or 'flat.' This pattern of performance plus his inability to read novel letter strings ('non-words'), is standard evidence that I.H. was unable to use letter-sound knowledge in reading or spelling.