number may not be closely related to the actual number of individuals, but the mathematical theories of genetic drift could still work. But unfortunately, the randomness associated with recombination has different mathematical properties to the random sampling of gametes (Figure 1). With background selection or hitchhiking, if an allele frequency increases in one generation, it is likely to increase again in the next. This is because recombination does not completely mix things up every generation. With genetic drift, what happens in one generation has no connection to what happens in the next. Successive generations of genetic drift mostly cancel each other out, so that over the long term, an allele undergoing genetic drift has much less variation in its success than it would if it were linked to other genes under selection.

Do these differences matter? If genetic drift is not important, then evolution doesn't depend so much on population size. The two theories also predict different distributions of allele frequencies. There may be many more consequences that we don't know about yet: the theory of selection at linked sites is still being worked out.

Can we test whether drift is less important than selection at linked sites? To test this directly in a setup like Buri's, one could look for a correlation between one generation and the next in terms of the magnitude and direction of change in allele frequency. In natural populations, there is lots of indirect evidence supporting the view that selection at linked sites is more important than genetic drift. For example, it is otherwise very hard to explain why patterns of genetic variation depend so little on population size, and so much on differences in the recombination rate along the chromosome.

Where can I find out more?

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Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA.
E-mail: masel@u.arizona.edu

Correspondence

Right temporal TMS impairs voice detection

Patricia E.G. Bestelmeyer[1], Pascal Belin[2,3], and Marie-Helene Grosbras[2]

Functional magnetic resonance imaging (fMRI) research has revealed bilateral cortical regions along the upper banks of the superior temporal sulci (STS) which respond preferentially to voices compared to non-vocal, environmental sounds [1,2]. This sensitivity is particularly pronounced in the right hemisphere. Voice perception models imply that these regions, referred to as the temporal voice areas (TVAs), could correspond to a first stage of voice-specific processing in auditory cortex [3,4], after which different types of vocal information are processed in interacting but partially independent functional pathways. However, clear causal evidence for this claim is missing. Here we provide the first direct link between TVA activity and voice detection ability using repetitive transcranial magnetic stimulation (rTMS). Voice/non-voice discrimination ability was impaired when rTMS was targeted at the right TVA compared with a control site. In contrast, a lower-level loudness judgement task was not differentially affected by site of stimulation. Results imply that neuronal computations in the right TVA are necessary for the distinction between human voices and other, non-vocal sounds.

The human voice carries important non-linguistic messages about the emotional state, identity or gender of a speaker. This information is essential for everyday social interaction and thus makes vocal sounds the most common and meaningful of our environment. Neuroimaging studies have identified regions along the middle and anterior part of the STS with a preferential neural response to vocal compared to non-vocal sounds (the TVAs) [1]. Their early development [5], ancient phylogenetic history [6], and crucially, preferential response to vocalisations, even those devoid of linguistic content [1,7], suggest that the TVAs might constitute a critical node of the cerebral network involved in voice cognition abilities. However, the exact functional role of the TVAs and, particularly, whether their greater fMRI response to voice indicates a specific role in cerebral voice processing, remains unclear. Our aim was to test a causal link between the right TVA and the ability to discriminate voices from other sounds. To this end, we first localised the right TVA in each subject with

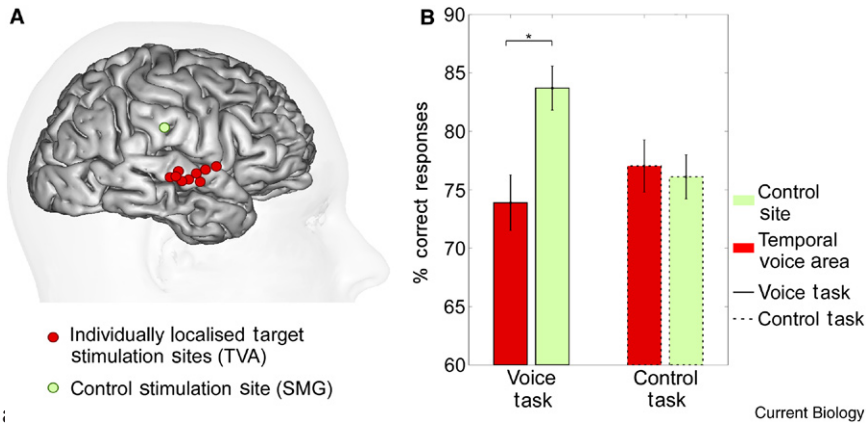

Figure 1. Functional role of the TVA in voice/non-voice discrimination.
(A) Illustration of stimulation sites. Individually localised right temporal voice area (TVA) in red; control site (supramarginal gyrus, SMG) in green. (B) Bar graph illustrates results of both tasks when stimulating the TVA or the control site. Stimulating the TVA caused significantly poorer performance compared with the control site on the voice/non-voice discrimination task. The control task was not affected by rTMS at either stimulation site. Error bars represent standard error of the mean.

fMRI before disrupting its activity with rTMS while participants performed a voice/non-voice and a control (loudness) discrimination task.

Nine volunteers participated in two experimental sessions; first, the localization of the TVA plus behavioural threshold tests and second, the TMS session. Participants were scanned using the established fMRI 'voice localizer' (see Supplemental Information); a blocked design in which participants listened passively to vocal and non-vocal sounds. Contrasting neural activity elicited when listening to vocal compared to non-vocal sounds reliably localised the TVA in each individual (Figure 1A). After the scan volunteers participated in behavioural threshold tests. We employed two alternative forced choice tasks: (1) a voice/non-voice discrimination task during which participants had to differentiate between vocal versus environmental sounds; and (2) a loud/quiet discrimination task in which we manipulated the amplitude of the same category of sounds and presented them at two different loudness levels.

To ensure the tasks were both challenging and therefore sensitive to possible disruption by rTMS, we titrated each individual's performance level to approximately 80% correct before the actual TMS session. These performance thresholds were obtained by adjusting the duration of all sound samples in the voice/non-voice task (longer sounds resulted in better performance) and the amplitude difference in the loudness discrimination task. Performance thresholds were assessed in the presence of the magnetic discharge noise (but without stimulation or contact with the head). In the second session, using the individually established performance thresholds, we stimulated the right TVA while participants performed these tasks with four pulses of rTMS at 10 Hz, the first pulse coinciding with stimulus onset (110% intensity of motor threshold; see Supplemental Information for more details). We delivered four pulses at 100 ms intervals in order to disrupt neuronal activity during the entire voice-related processing window based on findings in the event-related potentials literature assessing voice processing speed [8,9].

As a control site we stimulated the right supramarginal gyrus (SMG). The order of TVA and SMG blocks was counterbalanced across participants. We chose the SMG as the control site because it is close to the ear but is not known to be involved in auditory source or loudness discrimination. Based on previous fMRI findings and voice perception models, we predicted that rTMS targeted at the TVA but not SMG would interfere with the ability to discriminate between voices and environmental sounds. If the TVA is involved in higher-level auditory cognition, rTMS targeted at the TVA should not interfere with the ability to perform a low-level task such as loudness discrimination and performance of the loudness task should therefore not be affected by stimulation site. Specifically, we predicted an interaction between task and site of stimulation.

We obtained a significant interaction between task (voice/non-voice, loudness) and site (TVA, SMG) ($F(1, 8) = 12.244$, $p = 0.008$). Voice/non-voice discrimination ability was significantly impaired when rTMS was targeted at the right TVA compared with the control site ($t(8) = -3.274$; $p = 0.011$) while performance of the control loudness task was not differentially affected by site of stimulation ($t(8) = 0.540$; $p = 0.604$; Figure 1B). Notably, eight out of nine participants showed this effect. The participant who was not affected by rTMS displayed the most medial TVA and was thus less susceptible to rTMS compared to the remaining participants. We found no reaction time differences.

Our result has important implications for understanding the involvement of high-level auditory cortex in voice perception. Disrupting the activity of the right TVA impaired voice/non-voice discrimination compared to the control site. No such effect of rTMS was observed for a lower-level loudness discrimination task, indicating that rTMS of the right TVA did not disrupt any auditory perception ability. It is important to mention that our result is unlikely due to peripheral effects of the TMS stimulation because participants who experienced them did not report greater discomfort for one site or the other. Moreover, if the voice detection impairment we observed was related to greater peripheral effects of TVA stimulation, then both tasks should have been significantly impaired during TVA stimulation, when in fact performance of the control task was not differentially affected by site of stimulation. We note that our finding does not suggest that the TVA is only involved in voice perception but that it could subserve other higher-order auditory functions, nor does it imply that the TVA is the only area necessary for voice/non-voice discrimination. However, this result is the first clear evidence that neuronal computations in the right TVA are necessary for the distinction between human voices and other, non-vocal sounds and that the TVA's preferential response to voice as observed in fMRI studies is likely to be causally related to voice cognition.

Supplemental Information

Supplemental Information contains Supplemental Experimental Procedures and Results and can be found with this article online at doi:10.1016/j.cub.2011.08.046.

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[1]School of Psychology, Bangor University, Bangor, Gwynedd, UK. [2]Institute of Neuroscience and Psychology, University of Glasgow, Glasgow, UK. [3]International Laboratory for Brain, Music and Sound Research, University of Montréal and McGill University, Montréal, Canada.
E-mail: p.bestelmeyer@bangor.ac.uk