Spontaneous Emergence of Periodotopic Map through Neuronal Interference in Auditory Cortex

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Abstract

Pitch perception, the ability to detect the periodicity of a harmonic sound envelope, is a fundamental auditory function that enables the recognition of speech and music. While it is clear how the mechanical filtering of the cochlea extracts frequency information into a tonotopic map, it remains unclear how periodicity is extracted along the auditory pathway. Here, we propose that periodicity processing can spontaneously emerge through interference between the tonotopic maps of the ipsilateral and contralateral auditory pathways. We demonstrated that the chiasm of the bilateral tonotopic maps with tilting generates wiring for two different frequencies. We showed that periodicity coding emerges from the interference of these two frequency components. Next, we simulated the tonotopic and periodotopic maps as a result of this interference and compared them with optical recording data from the primary auditory cortex of cats. Our model can explain the relative organization between tonotopic and periodotopic maps, such as the high-frequency preference of high-pitch areas. These results suggest how a periodotopic map simply develops through neuronal interference within a tonotopically organized auditory pathway.

Keywords: pitch perception; periodotopic map; developmental model; auditory cortex

Introduction

Natural sounds including human voices and musical instruments are harmonic, composed of multiple frequency components that are integer multiples of a fundamental frequency (f_0) (Figure 1a). Pitch perception, the ability to identify the periodicity of harmonic sound, is a fundamental and essential function that enables auditory-related behaviors such as speech and music recognition (McPherson & McDermott, 2018). This ability to extract periodicity or fundamental frequency is thought to originate from neuronal tuning within the auditory pathway (Bendor & Wang, 2005).

Regarding the neuronal processing of pitch in the auditory cortex, previous studies have proposed hypothetical mechanisms, such as the autocorrelation model, which requires temporal delay (Cariani & Delgutte, 1996). However, no neural mechanisms to accomplish a temporal delay have been identified (Plack, Oxenham, & Fay, 2006). This raises a question of how the auditory system extracts the periodicity of harmonic sound without a temporal delay mechanism.

Notably, recent experimental findings suggest that the auditory cortex processes pitch through a map with a spatial gradient of periodicity (Langner, Dinse, & Godde, 2009; Baumann et al., 2011; Barton, Venezia, Saberi, Hickok, & Brewer, 2012). However, there is no clear explanation for how this periodotopic map develops within the tonotopically organized auditory cortex. Here, we propose a mechanism for the development of a periodotopic map in the auditory cortex, which underlies the pitch perception of harmonic sound.
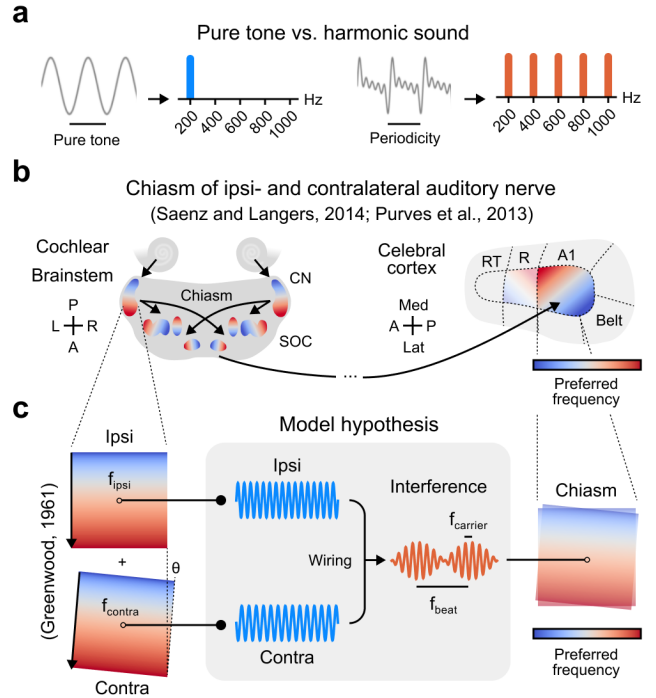

Figure 1: Periodicity coding through neuronal interference between ipsilateral and contralateral cochlear tonotopic maps. (a) Frequency components of a pure tone and harmonic sound. (b) Chiasm of ipsi- and contralateral auditory nerves in the brainstem (Saenz & Langers, 2014; Purves et al., 2013). (c) Model hypothesis that considers the periodotopic map as resulting from the interference between tonotopic maps.

Results

Our model

To explain the development of the periodotopic map in the auditory cortex, we proposed a mechanism based on the interference between the ipsilateral and contralateral tonotopic maps. We focused on the chiasm of the bilateral tonotopic maps, which are located in the brainstem (Figure 1b).

First, we modeled the tonotopic map in each cochlear nucleus (CN) using the Greenwood function (Greenwood, 1961, 1990), which correlates the position of the hair cell along the basilar membrane with the frequency of the sound (Figure 1c, left). The Greenwood function is given by

$$f = A(10^{ax} - K)$$

where f is the characteristic frequency of the sound, and x is the fractional length along the cochlear spiral from the apical end. A, a, and K are constants depending on the species.

Using the tonotopic maps from both the ipsilateral and contralateral cochlear nuclei (CN), we simulated the auditory map after the chiasm (Figure 1c, right). We assumed that the chiasm of the bilateral tonotopic maps has a small angle of tilting, which induces diverse mapping of the small difference between f_ipsi and f_contra. Physically, the superposition of pure
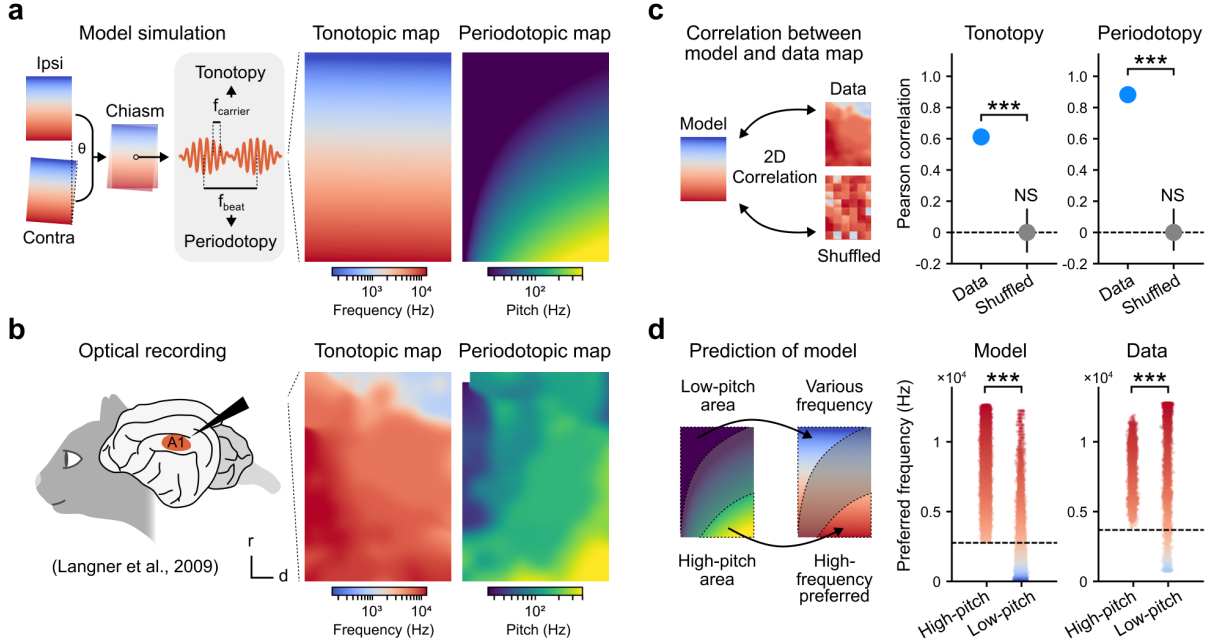
Figure 2: Tonotopic and periodotopic map of simulated model and cat A1 (a) Model tonotopic and periodotopic map. (b) Calculated tonotopic and periodotopic maps from optical recording data of cat A1. r and d indicate the dorso-ventral and rostro-caudal axes in the cat's primary auditory cortex, respectively. (c) Correlation between model and data of tonotopic and periodotopic maps. (d) Corresponding frequency preference of high-pitch and low-pitch areas in both model and cat data.

sounds with different frequencies generates amplitude modulation through temporal interference, i.e., acoustic beat.

$$\cos\left(2\pi f_{\text{ipsi}}t\right) + \cos\left(2\pi f_{\text{contra}}t\right) =$$
$$2\cos\left(2\pi\frac{f_{\text{ipsi}} + f_{\text{contra}}}{2}t\right)\cos\left(2\pi\frac{f_{\text{ipsi}} - f_{\text{contra}}}{2}t\right)$$

We modeled the tonotopic map and periodotopic map using the carrier frequency ($\frac{f_{\text{ipsi}} + f_{\text{contra}}}{2}$) and the modulated envelope frequency ($\frac{f_{\text{ipsi}} - f_{\text{contra}}}{2}$), respectively (Figure 1c, middle).

Periodotopic map as result of interference between ipsilateral and contralateral tonotopic maps

We simulated the superposition of two frequency components from bilateral tonotopic maps and investigated their temporal interference to calculate the tonotopic and periodotopic maps after the chiasm (Figure 2a). We confirmed that the emerged periodotopic map displays a diverse range of periodicity coding, while the tonotopic map preserves the frequency gradient.

To support the model results, we also calculated the tonotopic and periodotopic maps from the optical recording data (Langner et al., 2009) of the primary auditory cortex (A1) in cats (Figure 2b). We filtered out the high-frequency artifacts from the raw optical recording data.

Next, we compared the model and data of the tonotopic and periodotopic maps (Figure 2c). First, the model and data of the tonotopic map show a significant correlation (Figure 2c, middle; Pearson correlation, Data, $r = 0.602$, $P < 0.001$; one-sample t-test, Data vs. Shuffled, $^{*}P < 0.001$; Shuffled vs.

Zero, NS, $P = 0.098$). Similarly, the model and data of the periodotopic map also show a significant correlation (Figure 2c, right; Pearson correlation, Data, $r = 0.890$, $P < 0.001$; one-sample t-test, Data vs. Shuffled, $^{*}P < 0.001$; Shuffled vs. Zero, NS, $P = 0.452$).

Model predicts the relative organization between tonotopic and periodotopic maps

In our model, periodicity can be encoded by the frequency difference between the bilateral tonotopic maps. According to the model, the high-pitch area, which is achieved by wiring with a large frequency difference, should have a preference for high frequencies in the tonotopic map (Figure 2d, left).

To validate this prediction, we confirmed that the high-pitch area shows a preference for high frequencies, while the low-pitch area does not show a significant frequency preference in both the model (Figure 2d, middle; Welch's t-test, High pitch vs. Low pitch, $P < 0.001$) and cat data (Figure 2d, right; Welch's t-test, High pitch vs. Low pitch, $P < 0.001$).

Conclusion

We proposed a mechanism for the development of the periodotopic map in the tonotopically organized auditory cortex. This simulation suggests that extracting periodicity from harmonic sounds can simply be achieved through neuronal interference by encoding frequency differences between bilateral tonotopic maps. Furthermore, our model can explain the relative organization between tonotopic and periodotopic maps observed in the brain.

Acknowledgments

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