

REPLY TO RAJENDRAN AND SCHNUPP:

Frequency tagging is sensitive to the temporal structure of signals

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In PNAS, we (1) report that neural responses to musical rhythms conveyed by low-frequency sounds are characterized by greater relative prominence of beat and meter frequencies in EEG amplitude spectra. Rajendran and Schnupp (2) challenge whether this prominence is indicative of selective locking to the beat and meter periodicities.

Greater Relative Prominence of Meter Frequencies with Low Tone Corresponds to Periodic Amplitude Increase Locked to the Beat

We first address the critique by showing that there were no significant differences between low- and high-tone conditions in the phase of neural responses across the frequencies of interest [see online code (3)]. Even with random phases, if these phases are constant across two conditions, an increase in amplitude at meter frequencies in one of the conditions corresponds to periodic increases in magnitude of responses selectively locked onto the beat and meter (with the exact latency and shape dependent on the specific phase relationship between meter frequencies) (Fig. 1A). This lack of phase difference between low- and high-tone conditions was not due to weak phase locking of the responses (i.e., random phase across trials), as calculated using mean vector length [see online code (3)]. Therefore, the lack of phase differences combined with selective increases of EEG amplitude at meter frequencies in the low-tone condition observed in our study (1) are likely to correspond to amplitude increases locked onto the beat and meter periodicities, thus corroborating our original conclusions about low-tone benefit.

Frequency Tagging Is Sensitive to the Stability of Phase Locking at Beat and Meter Frequencies

Rajendran and Schnupp (2) also provide examples of time domain signals with equal-magnitude spectra and distinct-phase spectra (see figure 1B–D in ref. 2), intended to illustrate different degrees of locking to the beat. However, if beat locking is defined as stability of the phase relationship between the beat and an output signal across time (e.g., indexed by phase-locking values), the three examples do not differ, because phase relations are constant throughout the sequence. In contrast, if we construct signals with weaker locking at the beat and meter frequencies throughout the sequence (Fig. 1B), we obtain, as expected, not only reduced phase-locking values at the beat frequency but also reduced z-scored amplitude at the meter frequencies, as measured with frequency tagging [Fig. 1C; see also online code (3) for simulation of 50 experiments with standard and jittered conditions].

The final example leveled against the frequency-tagging method by Rajendran and Schnupp (2) is a signal containing transient amplitude deflections aligned with beat positions, which is without energy at the beat frequency in its amplitude spectra but contains prominent peaks at other meter-related frequencies. This scenario is precisely one of the reasons why, in our recent studies, we have consistently used the composite measure at meter frequencies (while assessing the z score at the beat frequency only in a complementary fashion) (1, 4).

To summarize, frequency tagging offers high sensitivity to assess the stability of neural phase locking at beat and meter frequencies, as well as increases in the magnitude of beat-locked signal variation.

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Data deposition: Files containing processed data and code associated with the analyses reported in this paper have been deposited in GitHub and Zenodo (available at https://github.com/TomasLenc/XPLOWHIGH/tree/v1.0.2/PNAS_response2Rajendran and <https://doi.org/10.5281/zenodo.2548487>, respectively).

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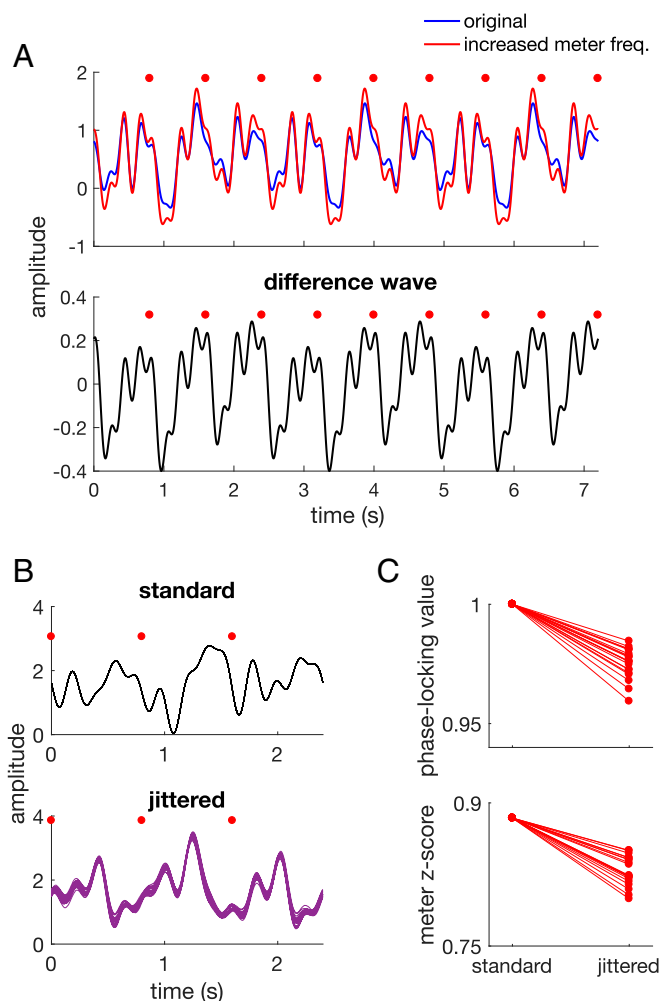


Fig. 1. (A) Time domain signal reconstructed using original amplitudes of the 12 frequencies of interest from the unsyncopated rhythm used in ref. 1, with phases set randomly. Red dots mark beat times at positions suggested by Rajendran and Schnupp (2). (B) Plot of one simulated trial from standard and jittered conditions (with all 2.4-s cycles overlaid). (C) Plot of phase-locking values and meter z scores obtained in standard and jittered conditions in one simulated experiment.

- 1 Lenc T, Keller PE, Varlet M, Nozaradan S (2018) Neural tracking of the musical beat is enhanced by low-frequency sounds. *Proc Natl Acad Sci USA* 115:8221–8226.
- 2 Rajendran VG, Schnupp JWH (2019) Frequency tagging cannot measure neural tracking of beat or meter. *Proc Natl Acad Sci USA* 116:2779–2780.
- 3 Lenc T, Keller PE, Varlet M, Nozaradan S (2019) Code related to Lenc et al. 2018. Zenodo. Available at <https://doi.org/10.5281/zenodo.2548487>. Deposited January 24 2019.
- 4 Nozaradan S, Schönwiesner M, Keller PE, Lenc T, Lehmann A (2018) Neural bases of rhythmic entrainment in humans: Critical transformation between cortical and lower-level representations of auditory rhythm. *Eur J Neurosci* 47:321–332.