LETTER

REPLY TO NOVEMBRE AND IANNETTI: Conceptual and methodological issues

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In a recent study in PNAS on musical rhythm (1), we show that EEG responses at beat- and meter-related frequencies are selectively enhanced when conveyed by low-frequency sounds, especially in complex syncopated rhythms with no prominent acoustic energy at beat- and meter-related frequencies in the stimulus. In their letter, Novembre and Iannetti (2) discuss ongoing questions about the nature of EEG responses as neural entrainment vs. event-related potentials (ERPs).

While we are pleased that our paper attracted attention and provoked a thoughtful response, a point of clarification is in order. Novembre and Iannetti (2) state that we interpret our findings as indicative of "an entrainment of sensory-motor networks." This is incorrect; our mention of "sensory-motor entrainment in widespread musical traditions" in the conclusion to our paper refers to overt (behavioral) sensorimotor synchronization, not the coupling of activity across different brain regions. Relatedly, it is puzzling that Novembre and Iannetti claim that our study reported evidence for "neural entrainment," "sustained oscillatory activity," and "steady-state responses." The basis for this claim is unclear, as none of these terms are used in our paper when describing our results and their implications, simply because the study was not designed to demonstrate sustained neural oscillations vs. ERPs.

In their letter, Novembre and Iannetti (2) also advocate the use of conventional time-domain EEG analyses. There is no doubt that time-domain analyses can be useful and complementary to frequency-domain analyses for investigating EEG responses to auditory sequences. The relationship between time- and frequency-domain analyses and their advantages and disadvantages have already been discussed extensively in the EEG literature, including in the context of rhythm processing (e.g., refs. 3–6). Frequency-domain analyses were employed in our study (1) because they offered an appropriate and straightforward way to quantify the amplitude of EEG responses to assess the effects of low-frequency sounds at beat- and meter-related frequencies.

Lastly, at a conceptual level, and independent of the specific content of the target paper, it is unclear in what sense an explanation based on ERPs is more parsimonious than an explanation based on neural entrainment, as argued by Novembre and Iannetti (2). It is likewise unclear how the shape of the waveforms observed in time-domain analyses (periodic sine waves vs. periodic nonsinusoidal waveforms), as proposed by Novembre and Iannetti in figure 1 of ref. 2, demonstrates, in itself, evidence for neural entrainment vs. ERPs.

Questions concerning the nature of EEG responses and their neurophysiological substrates remain a lively area of related research. However, for the reasons given above, the issues raised in the letter by Novembre and Iannetti (2) do not appear to be informative with regard to the results of our study and the conclusions we draw about the low-tone benefit in musical rhythm processing.

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 Novembre G, Iannetti GD (2018) Tagging the musical beat: Neural entrainment or event-related potentials? *Proc Natl Acad Sci USA* 115:E11002–E11003.

3 Nozaradan S, Schönwiesner M, Caron-Desrochers L, Lehmann A (2016) Enhanced brainstem and cortical encoding of sound during synchronized movement. *Neuroimage* 142:231–240.

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.

5 Rajendran VG, Harper NS, Garcia-Lazaro JA, Lesica NA, Schnupp JWH (2017) Midbrain adaptation may set the stage for the perception of musical beat. *Proc Biol Sci* 284:20171455.

6 Nozaradan S, Keller PE, Rossion B, Mouraux A (2018) EEG frequency-tagging and input–output comparison in rhythm perception. *Brain Topogr* 31:153–160.

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