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REVIEW

EEG Frequency-Tagging and Input–Output Comparison in Rhythm Perception

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Abstract The combination of frequency-tagging with electroencephalography (EEG) has recently proved fruitful for understanding the perception of beat and meter in musical rhythm, a common behavior shared by humans of all cultures. EEG frequency-tagging allows the objective measurement of input–output transforms to investigate beat perception, its modulation by exogenous and endogenous factors, development, and neural basis. Recent doubt has been raised about the validity of comparing frequency-domain representations of auditory rhythmic stimuli and corresponding EEG responses, assuming that it implies a one-to-one mapping between the envelope of the rhythmic input and the neural output, and that it neglects the sensitivity of frequency-domain representations to acoustic features making up the rhythms. Here we argue that these elements actually reinforce the strengths of the approach. The obvious fact that acoustic features influence the frequency spectrum of the sound envelope precisely justifies taking into consideration the sounds used to generate a beat percept for interpreting neural responses to auditory rhythms. Most importantly, the many-to-one relationship between rhythmic input and perceived beat actually validates an approach that objectively measures the input–output transforms underlying the perceptual categorization of rhythmic inputs. Hence, provided that a number of potential pitfalls and fallacies are avoided, EEG frequency-tagging to study input–output relationships appears valuable for understanding rhythm perception.

Keywords EEG · Frequency-tagging · Rhythm and beat perception · Auditory system · Perceptual categorization · Neural transform

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Introduction

Evolution has endowed animals with the ability to interact in real-time with external signals that continuously stimulate their sensory organs. This interaction is well illustrated by the common behavior of moving to a musical rhythm, a form of auditory-motor entrainment shared by humans of all cultures. In particular, the beat, i.e., perceived periodic pulses in music, can be considered a cornerstone of entrainment to music. Even when music is not periodic, humans spontaneously organize the constituent complex sound sequences according to a periodic pulse-like beat and experience the urge to move to it (e.g., bobbing the head, tapping the hand when listening to music). Moreover, beats are usually perceived within meters (e.g., a waltz, which is a three-beat meter, or a march which is a two-beat meter, or any inclusionally related set of isochronous pulses) corresponding to grouping or subdivision of the beat period, and these multiple metrical levels are nested hierarchically. Musical beat and meter thus structure the perception of musical rhythm and serve as a mental framework for synchronized movement to music. Typically, beat and meter are perceived

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within a specific frequency range corresponding to the musical tempo (approx. 0.5–5 Hz, peaking around 2 Hz) (London 2004; van Noorden and Moelants 1999; Repp 2005; McAuley 2010).

Beat perception can be induced by simple metronomic pulses or by complex rhythmic structures, thus indicating that the beat itself is not an objective property of the stimulus but rather the product of endogenous processes that are driven by the stimulus (e.g., Lerdahl and Jackendoff 1983; Povel and Essens 1985; London 2004). In other words, the beat is a *perceptual* phenomenon, as it goes beyond the sensory stimulus and shows some degree of *invariance* and *flexibility* with respect to the physical characteristics of the input (Helmholtz 1866; Bruner 1957). In fact, a single musical rhythm can lead to different perceived beat frequencies and phases (e.g., Desain and Honing 2003) and, in turn, various rhythmic patterns can give rise to a similar perceived beat frequency and phase (Povel and Essens 1985). Hence, beat perception can be considered a form of *perceptual categorization*, according to which different physical stimuli are categorized according to their currently experienced properties. Such a many-to-one relationship between inputs and outputs, also called *degeneracy*, has not only been described between physical inputs and perceptual outputs, but also as an ubiquitous property of biological systems, allowing for invariance and flexibility at different levels of organization, from neurons to behavior and interpersonal communication (Edelman 1978; Edelman and Gally 2001) (Fig. 1). Without this critical brain function, we would be overwhelmed by the sheer diversity of the sensory inputs we experience. That is, if every auditory rhythm allowed only a single perceptual interpretation, we would be unable to cope with the wide variety of rhythms in our environment, encode and

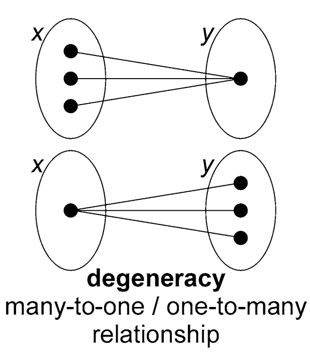

Fig. 1 Degeneracy is the ability of structurally different elements (x) to perform the same function or yield the same output (y) (and vice versa, also referred to as pluripotentiality). This ubiquitous biological property has been observed between different entities such as brain structures and functions, or sensory input and perceptual output. According to EEG frequency-tagging studies in the context of beat perception, this relationship could also apply to rhythmic inputs and neural outputs

remember these rhythms and communicate them efficiently when producing music and during our social interactions.

The EEG Frequency-Tagging Approach

A promising approach to understand the perceptual representation of rhythm is the combination of *electroencephalography* (EEG), the recording of brain electrical activity at the millisecond time scale, with *frequency-tagging* (Nozaradan 2014). The EEG frequency-tagging approach was initially developed as a technique to measure "low-level" sensory processes in the visual modality (e.g., a flickering light or a contrast reversed grating; Regan 1966, 1989). The approach was further extended to the auditory modality, based on electrophysiological evidence that neural populations can synchronize their activity with the temporal envelope of acoustic streams (see, e.g., Galambos et al. 1981; Galambos 1982; Pantev et al. 1996; Picton et al. 2003; Ross et al. 2003). Recently, the technique has been extended to characterize higher-level processes such as the perceptual categorization of complex stimuli in vision (Rossion and Boremanse 2011; e.g.; Rossion 2014; Norcia et al. 2015 for reviews) and other sensory modalities (e.g., Moungou et al. 2016).

Frequency-tagging is based on the long-standing observation that repetition of a stimulus, or modulation of the property of a stimulus, at a fixed rate (i.e., periodically) generates a periodic change in EEG signal amplitude (Adrian and Matthews 1934). This periodic change can be objectively identified in the EEG frequency spectrum by Fourier Transform (Regan 1966). In the EEG frequency-tagging approach, the stimulus frequency determines the frequency content of the response, consisting of narrow-band peaks at the frequencies that are directly related to the stimulation frequency. For instance, listening to a rhythmically modulated sound elicits responses in the EEG spectrum at frequencies corresponding to those of the acoustic envelope spectrum (Nozaradan et al. 2012b, 2016a, c) (Fig. 2). An important advantage of this approach is its *objectivity* in relating stimuli (i.e., inputs) and neural responses (i.e., outputs) (Regan 1989; Rossion 2014). Yet, even a pure sinusoidal input, represented in the frequency domain as a single peak corresponding to the frequency of stimulation, generates frequencies in the EEG spectrum that are not present in the stimulus (that is, the brain response is not a pure sinusoid), demonstrating the presence of nonlinear neural mechanisms responsible for an input–output transform (e.g., firing threshold; see Regan 1989; Fig. 1 in Norcia et al. 2015). In addition, this input–output transform is limited to specific frequency bandwidths (i.e., resonance frequency bands, or frequency-tuning functions) based on temporal constraints inherent to

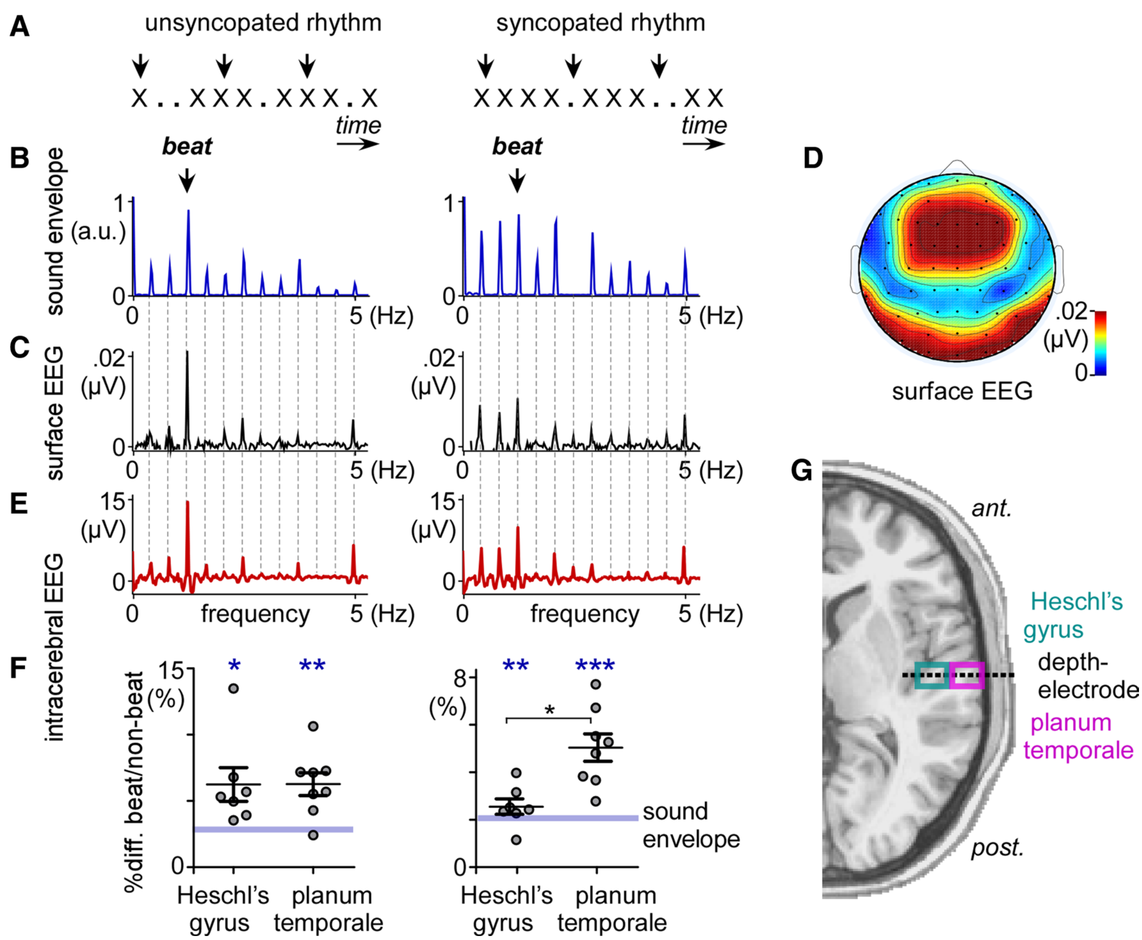

Fig. 2 **a** Example of two rhythmic patterns ('X': 200 ms tone; dots: 200 ms silent interval). The pattern on the left has a regular beat marked by periodically occurring sound onsets, while the pattern on the right is a syncopated rhythm, as some beats coincide with silent intervals instead of sounds. **b** Spectrum of the sound envelope of the repeated patterns (extracted with the Hilbert function implemented in Matlab). Note that in the syncopated rhythm presented on the right, the beat frequency is relatively less prominent in the sound envelope spectrum as compared to the unsyncopated rhythm on the left. **c** Frequency spectrum of surface EEG (average across nine participants and across 64 EEG electrodes). Neural activity was observed at frequencies corresponding to the spectrum of the rhythm envelope (dotted lines), with a relative enhancement of the frequency-tagged activities at beat and meter frequencies compared to frequencies unrelated to beat and meter. **d** Topography of the neural responses at beat and meter frequencies. **e** Frequency spectrum of intracerebral EEG averaged across 55 depth-electrode contacts located within the auditory cortex of eight patients (Heschl's gyrus and planum temporale). Note that the spectra are markedly similar to those recorded with surface EEG in healthy participants. **f** Percentage of difference between the amplitude of the EEG response at beat frequency versus non-beat frequencies. The intracerebral EEG responses at beat frequency were larger than the responses elicited at frequencies unrelated to the beat (percentage of difference higher than 0%). The percentage of difference between beat and non-beat frequencies was also higher than the corresponding value obtained from the sound envelope (blue line; one-sample *t*-test, $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$). This relative enhancement at beat frequency was sharper in the planum temporale as compared to the Heschl's gyrus, especially for the syncopated rhythm, suggesting that this auditory area shapes the neural representation of rhythmic inputs in favor of the emergence of a periodic beat. **g** Structural image depicting the location of the implanted depth-electrode. Adapted from Nozaradan et al. (2012b, 2016c)

the responding neural system (see, for example, Alonso-Prieto et al. 2013, showing a frequency-tuning function for individual face perception). Therefore, the mapping between the stimulus and the neural response is not one-to-one, and the frequency-tagging approach offers a unique opportunity to objectively measure and investigate these input–output transforms.

Frequency-Tagging to Investigate Rhythm Processing

To explore the internal representation of beat and meter with EEG, we developed a new application of the frequency-tagging approach based on the hypothesis that beat perception is supported by a synchronization of large pools of neurons at the beat frequency (see Nozaradan 2014 for a review). This synchronized periodic neural activity is expected to elicit an EEG response that can be identified in the EEG spectrum as a peak of activity at the beat frequency and its harmonics. When the frequencies of the beat and meter percept coincide with prominent frequencies of the envelope of the rhythmic input, the frequency-tagged EEG activity measured at these frequencies can be expected to reflect both *exogenous* processes in response to the rhythmic input and *endogenous* processes possibly supporting beat perception and playing a role in predicting the timing of upcoming sounds and synchronizing movements with the beat (Nozaradan et al. 2016a). Conversely, in instances where the frequencies of the beat and meter percept do *not* coincide with frequencies contained in the stimulus, neural activity may still be elicited at beat and meter frequencies due to the endogenous processes underlying rhythm and meter perception (see for example the study of Nozaradan et al. 2011 in which mental imagery was used to elicit an endogenous meter percept; see also Celma-Miralles et al. 2017; Stupacher et al. 2017; Tal et al. 2017).

In a specific study (Nozaradan et al. 2012b), five different rhythmic patterns consisting of sounds alternating with silent intervals were used to induce the spontaneous perception of beat and related metric levels based on a preferential periodic grouping by four intervals (Povel and Essens 1985) (Fig. 2). Three patterns were syncopated, i.e., some beats coincided with silent intervals instead of sounds, whereas the two other patterns were unsyncopated, i.e., the beat was marked by periodically occurring sound onsets. Beat perception was confirmed by a behavioral task performed after the EEG recording, in which participants tapped along with each pattern. Based on prior assumptions concerning the beat periodicity estimated from the distribution of sound and silent intervals for each rhythm (Povel and Essens 1985) as well as the results of the tapping task, the multiple frequencies constituting the envelope spectrum of the five sound patterns could be categorized as related or unrelated to beat and meter frequencies. This study thus brought together physical measures of the inputs, physiological measures of neural outputs, and behavioral measures of entrainment to the beat. Comparison of the frequency spectra of the sound envelope (i.e., the input) with the frequency spectra of the EEG (i.e., the output) revealed a relative increase of magnitude of the responses elicited at frequencies coinciding with perceived beat and meter-related frequencies, compared to neural responses at frequencies unrelated to beat and metric periodicities (Fig. 2; see also Fig. 3 in Nozaradan et al. 2012b).

The relative enhancement of neural responses at beat and meter-related frequencies was observed even for rhythmic patterns in which the acoustic energy at the beat frequency was not prominent. Conversely, frequencies with prominent acoustic energy in the sound envelope that were unrelated to the beat and meter were markedly reduced in the EEG. Moreover, this selective enhancement at beat and meter frequencies was not observed for rhythms that failed to elicit a stable and unequivocal beat frequency, or for rhythms that were presented above the upper tempo limit for inducing beat and meter perception (Nozaradan et al. 2012b). This latter observation suggests that the input–output transformation of the sound envelope is restricted to a critical frequency bandwidth, or resonance frequency range, matching the range of musical tempo at which a beat can be perceived.

Together, these observations corroborate the hypothesis that beat and meter perception involves neural mechanisms that support the selection of beat-related frequencies in the processing of rhythmic patterns, and that these processes can be captured with EEG frequency-tagging. These results have, over the past few years, led to a research program involving the comparison of acoustic inputs with their neural outputs (i) across different conditions in which the internal representation of the beat is manipulated while the rhythmic input remains identical (Chemin et al. 2014), (ii) across different brain regions with intracerebral depth-electrodes recordings in humans (Nozaradan et al. 2016c) (Fig. 1f, g), or (iii) across different groups of patients with lesions in specific areas of the brain (Nozaradan et al. 2017b). The observations made to date also raise a number of novel research questions, asking for instance (i) whether the neural transforms of rhythm result from ongoing neural activities resonating at the frequency of the stimulation or whether they result from the superposition of independent transient event-related potentials elicited by the rhythmic stimulus, (ii) whether these neural representations rely on nonlinear processes arising along the ascending auditory pathway and/or involving higher-level areas such as associative and motor areas, (iii) how these neural transforms emerge over the course of human development (Cirelli et al. 2016) and (iv) across animal species (Rajendran et al. 2016), (v) how they are shaped by exogenous versus endogenous factors (e.g., by manipulating the rhythmic inputs or the beat internal representation respectively) and (vi) are linked to the subjective experience of the beat.

What Can We Learn About Beat Perception by Comparing EEG Signals to Sound Envelopes?

A recent paper (Henry et al. 2017) questioned the validity of comparing the frequency spectrum of EEG signals to the frequency spectrum of the sound envelope of rhythmic stimuli in the context of beat perception. While we agree with the authors that the relationship between rhythmic inputs and perceptual outputs is important to study, the arguments raised against the validity of our approach are moot points, and in fact demonstrate the opposite of their conclusion regarding the input–output comparison, thus rather highlighting the strengths of the approach.

In their first key point, Henry et al. (2017) highlight the fact that the frequency spectrum of the envelope of a rhythmic auditory sequence does not only depend on the structure of sound onsets, but also on acoustic properties of the auditory events used to generate the rhythm, such as tone duration and onset/offset ramp duration. This is stating the obvious, as can be readily ascertained by examining the equation for computing the Fourier coefficients of a train of pulses according to the duty cycle, i.e., the fraction of the time the pulse is high (see also Zhou et al. 2016 for a recent discussion on the Fourier representation of waveforms of different shapes). It is, nevertheless, important to note that the fact that acoustic features influence the frequency spectrum of the sound envelope does not undermine the sound-EEG frequency spectrum comparison. Instead, it is precisely for this reason that the sound patterns used to generate beat percepts need to be taken into consideration when interpreting neural responses to auditory rhythms. Indeed, the input–output comparison aims to measure whether there is an increase of the EEG response at beat and meter-related frequencies, regardless of whether these frequencies coincide with a prominent frequency component of the sound envelope (note also that in studies using the input–output comparison method, low-level acoustic properties were held constant across different rhythms; see Nozaradan et al. 2012b, 2016c).

Second, Henry et al. (2017) conducted a behavioral experiment in order to demonstrate that the strength of the beat percept generated by a rhythmic pattern (measured by asking the participants to give a score of perceived beat strength on a rating scale from 1 to 9) is largely independent of the low-level acoustic properties of the events used to generate the sound patterns. Specifically, the authors showed that changes to acoustic features affecting the frequency representation of a rhythmic input do not affect the strength of the beat percept. Conversely, differences in the strength of the beat percept could be induced using different rhythms having identical frequency representations of their envelope. This many-to-one relationship, or dissociation, between frequency-domain representations of rhythmic inputs and perceived beat strength is, in fact, an example of *perceptual categorization*, as defined above (Fig. 1). That is, the perceived beat shows some degree of *invariance* and *flexibility* with respect to the strict physical characteristics of the input.

Crucially, contrary to the authors' claim, this observed dissociation is irrelevant to invalidate the practice of input–output comparison, for two reasons. First, it represents the relationship between rhythmic input and perceptual outcome, as opposed to the relationship between rhythmic input and *neural* output that results from sound-EEG frequency spectrum comparison. More crucially, the observation that changes to acoustic features affecting the frequency representation of a rhythmic input do not affect the strength of the beat percept (many-to-one mapping) is not in contradiction with the conclusions drawn by input–output comparison in previous EEG frequency-tagging studies (Nozaradan et al. 2012b, 2016c). Instead, these studies predict that changes in these acoustic features also affect the frequency spectrum of the EEG, except for the fact that beat and meter-related frequencies would still be relatively enhanced as compared to beat and meter unrelated frequencies. Similarly, the observation that different strengths of beat percept could be induced using different rhythms having identical frequency representations of their envelope (one-to-many mapping) does not contradict the conclusions of these previous studies, which predict to find different EEG responses to different rhythms having identical frequency representations of their envelope but nevertheless inducing different beat strengths.

In fact, the dissociation between the stimulus and the perceptual outcome could invalidate the "direct comparison" approach only if one assumes a one-to-one mapping between auditory rhythms and EEG spectra, as the authors apparently do. However, this assumption is not justified. Given the infinite variety of inputs of the auditory world, such a coding scheme at the neural level, or in any biological system of recognition, would be unrealistic, since it would rapidly lead to saturation (Edelman 1978). To summarize, the dissociation between the stimulus and the perceptual outcome precisely renders the frequency-tagging approach highly valuable as it allows us to objectively measure and investigate the input–output transforms underlying the many-to-one mapping. For instance, a systematic investigation of the input–output transform while gradually changing acoustic features could provide direct insights on the capacity of the responding neural system to extract perceptual invariants according to a many-to-one mapping and its underlying neural mechanisms.

Finally, in their behavioral task, Henry et al. (2017) instructed participants to rate the perceived beat strength instead of, for instance, requiring participants to tap along with the beat for each rhythm, claiming that the rating measure is a *direct index of beat perception*. However, as for most high-level perceptual processes, there is probably no unequivocal single method to behaviorally measure beat perception. Indeed, while tapping on the beat might (as they point out) alter beat processing due to kinematic feedback, ratings of beat strength may be subject to the influence of other cognitive processes inherent to explicit judgments using ordinal rating scales. Moreover, ratings of beat strength alone are not informative about beat periodicity and phase relative to the auditory pattern, and such measures are therefore not a comprehensive measure of beat perception (and are also not comparable to measures that take periodicity and phase into account). In fact, it is not possible to know what beat period was perceived by participants in the Henry et al. (2017) study, and how consistent this was across individuals. This uncertainty effectively limits the contribution of studies investigating the effects of low-level acoustic features of tones on beat perception. Most critically, it makes the contribution of these studies irrelevant to the issue of the validity of input–output comparisons involving brain data.

Studying Input–Output Transforms to Understand Beat Perception: Pitfalls and Significance

Since the recent doubt raised about the validity of input–output comparisons involving brain data in the context of beat perception reveals misinterpretations, we take the opportunity to offer a note of caution on a number of pitfalls related to such comparisons, and also to highlight the main benefits of this relatively new approach to understanding rhythm processing.

First, it should be noted that the stimulus spectrum is not an absolute reference but a relative one. Indeed, it is the relative enhancement of the various peaks of the stimulus spectrum that is germane to understanding the processes by which the brain transforms the stimulus into a categorized percept (i.e., related to a beat percept). The measure of input–output transform is also relative rather than absolute, as it is compared across different conditions, brain areas, or groups of participants. Moreover, this input–output comparison is driven by theoretical and/or empirical knowledge about the frequency of the target perceptual phenomenon (here beat and meter frequencies), thus taking into account relations between three elements: stimulus properties, neural activity, and the perceptual experience of beat.

In addition, as in most signal analysis contexts, the algorithms used to process the acoustic and neural signals can affect the utility of the physical-physiological comparison. For example, in most EEG frequency-tagging studies of rhythm (Nozaradan et al. 2016a, b, c, 2017; Cirelli et al. 2016), the sound envelope was obtained using the Hilbert function implemented in Matlab (as endorsed by Henry et al. 2017). However, this procedure is not exclusive. There are other options that can be employed to address specific questions, such as models of cochlear filters for rhythmic sequences comprised of different tone frequencies (e.g., Ding et al. 2016; Nozaradan et al. 2017a).

Finally, an input–output transform of rhythm characterized by a significant relative enhancement of neural responses at the beat frequency does not necessarily imply beat perception. Indeed, this neural measure may be correlated, and may perhaps even be necessary, but nevertheless not sufficient to fully perceive the beat in musical rhythms. We therefore recommend caution in making invalid assumptions based on such a reverse inference. However, and although the approach was not originally proposed to provide a neural marker of beat perception, it paves the way for future research to investigate how input–output transforms relate to the perceptual experience and motor entrainment to the beat across individuals. For example, this question could be addressed by recording neural responses to rhythm at different levels of the ascending auditory pathway, to investigate how the selective neural enhancement at beat and meter frequencies emerges across these different stages of auditory processing and how this relates to behavior. Using a recent extension of the frequency-tagging method, it is possible to concomitantly sample with EEG and distinguish auditory cortical and lower-level sources of activity in the form of slow (<20 Hz) and fast (>150 Hz) responses to auditory rhythms, respectively (Nozaradan et al. 2016b). This method offers a unique way to test how features of the acoustic stimulus might influence the cortical processing of beat and meter frequencies and to compare this to lower-level auditory activity that can be expected to be more directly driven by the stimulus. Gradual dissociation from the acoustic features of the stimulus, with enhanced representation of beat and meter frequencies reflecting perception and motor entrainment, could also be investigated in higher-level associative and/or motor cortices using the same approach combined with more spatially resolved neuroimaging techniques such as magnetoencephalography or human intracranial EEG (see Fig. 2f for a first evidence for this gradual dissociation from the input between Heschl's gyrus and the planum temporale, with enhanced response at the beat frequency; Nozaradan et al. 2016c).

Following on from these future prospects, it is also important to stress that the frequency-tagging approach is not restricted to frequency domain analysis of power on long temporal windows as described above. For example, frequency-tagged activity lends itself well to time domain analysis of latency and amplitude (see Retter and Rossion 2016; Fig. 5 in; Nozaradan et al. 2016b), estimation of the phase retrieved from frequency domain analysis (e.g., Fig. 3 in Nozaradan et al. 2016b), or estimation of the dynamics of activity over the sequence using time–frequency decompositions (e.g., short-term Fourier transform; see Fig. 6 in Nozaradan et al. 2017a). These time-resolved methods also provide valuable information about the relation between the stimulus and brain activity.

To summarize, the use of EEG frequency-tagging to study input–output relationships appears valuable for understanding beat perception provided that certain potential pitfalls are avoided. There is accumulating experimental evidence demonstrating that this approach can be used to study the neural processing involved in rhythm processing and beat perception. Indeed, a number of studies have shown that the neural responses tagged by this approach do not only depend on the physical properties of the rhythmic auditory sequences, but also on contextual factors influencing rhythm perception. First, imposing a higher-order metrical grouping on a metronomic sequence of beats leads to the appearance of additional peaks in the EEG frequency spectrum at the frequency of the imagined meter (Nozaradan et al. 2011; Stupacher et al. 2017; Celma-Miralles et al. 2017). Second, movements to the beat of an auditory rhythm selectively shape the neural responses to the rhythm, illustrating how the role of motor representations in rhythm perception could be used as a way to disentangle the contribution of low-level acoustic features from an integrated percept of beat (Chemin et al. 2014; Nozaradan et al. 2015, 2016b). Third, there is an inter-individual correlation between measures of relative amplitude of the EEG response at beat frequency and behavioral measures of motor entrainment, especially the accuracy of beat tapping and temporal prediction abilities (Nozaradan et al. 2016a).

Conclusions

Understanding the relationship between stimulus content and brain activity is a major goal of cognitive neuroscience. A comparison of stimulus and response spectra in the context of rhythmic stimuli constitutes a unique opportunity to attain this goal, as it allows an objective and straightforward quantification of the signal content based on the expected set of frequencies at which the response will be concentrated. However, this comparison does not imply a one-to-one mapping between stimulus input and EEG output, which would be unrealistic in terms of neural coding. In reality, stimulus-EEG comparison aims at characterizing the computational *transformations*, i.e. the neural *processes* between the input and the output. While input–output nonlinearities have been extensively investigated in the auditory system for processes underlying envelope and pitch extraction from acoustic inputs (e.g., Eggermont 2001; Joris et al. 2004; Wang et al. 2008; Town and Bizley 2013; Plack et al. 2014), little is known about the nonlinear input–output transformation of rhythmic patterns and how it relates to perceptual aspects of beat and meter. Hence, establishing systematic relationships between sound inputs and neural outputs is a valuable means to uncover the neural mechanisms contributing to perceptual representations of sensory stimuli.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interests.

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