



Auditory rhythms entrain visual processes in the human brain: Evidence from evoked oscillations and event-related potentials[☆]



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ABSTRACT

Temporal regularities in the environment are thought to guide the allocation of attention in time. Here, we explored whether entrainment of neuronal oscillations underpins this phenomenon. Participants viewed a regular stream of images in silence, or in-synchrony or out-of-synchrony with an unmarked beat position of a slow (1.3 Hz) auditory rhythm. Focusing on occipital recordings, we analyzed evoked oscillations shortly before and event-related potentials (ERPs) shortly after image onset. The phase of beta-band oscillations in the in-synchrony condition differed from that in the out-of-synchrony and silence conditions. Additionally, ERPs revealed rhythm effects for a stimulus onset potential (SOP) and the N1. Both were more negative for the in-synchrony as compared to the out-of-synchrony and silence conditions and their amplitudes positively correlated with the beta phase effects. Taken together, these findings indicate that rhythmic expectations are supported by a reorganization of neural oscillations that seems to benefit stimulus processing at expected time points. Importantly, this reorganization emerges from global rhythmic cues, across modalities, and for frequencies significantly higher than the external rhythm. As such, our findings support the idea that entrainment of neuronal oscillations represents a general mechanism through which the brain uses predictive elements in the environment to optimize attention and stimulus perception.

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Introduction

Many events are periodic: the ticking of a clock, ocean waves washing against a shore, or two individuals talking to each other are only a few examples. In each of these examples, sensory events occur at relatively regular intervals and together form a rhythm. Do humans exploit such rhythms to develop expectations about the future and, if so, what is the underlying neural mechanism?

A popular framework for addressing the first part of this question is Dynamic Attending Theory (Jones, 1976). It holds that attention and processing resources are not distributed evenly across time but follow endogenous attending rhythms (Jones and Boltz, 1989; Large and Jones, 1999). Regular external events, such as the ticking of a clock, can entrain these rhythms and thereby determine when attention or processing resources are at their peak or trough. If other events then

coincide with aligned attentional peaks, they create better mental or neural representations.

Dynamic Attending Theory has been supported by behavioral findings. Unimodal investigations provided evidence that rhythmic streams facilitate the perception of and behavioral responses to synchronously as compared to asynchronously occurring events both in the auditory and visual modalities (Doherty et al., 2005; Jones et al., 2002; Mathewson et al., 2010). In a typical paradigm investigating dynamic attending, participants listen to an isochronous rhythmic tone sequence followed by a target tone. The interval between the sequence and the target is manipulated such that the target is either consistent or inconsistent with the rhythm suggested by the sequence. Detection performance is maximal for consistent targets and decreases the larger the temporal offset between the target and the rhythm (Jones et al., 2002). Similar results are obtained when targets and rhythmic sequences occur in different modalities (Escoffier et al., 2010; Miller et al., 2013; Kösem and van Wassenhove, 2012; Ten Oever et al., 2014) indicating that rhythmic expectations span across the different senses and that they rely on a shared neural mechanism.

Electrophysiological research revealed clues as to what this mechanism might be. Specifically, it produced two lines of evidence that point to the phase of neuronal oscillations and associated changes in

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neuronal excitability or processing readiness (Bishop, 1932, cited by Drewes and VanRullen, 2011; Buzsaki, 2006; Jacobs et al., 2007; Schroeder and Lakatos, 2009; Schroeder et al., 2010).

The first line of evidence entails insights into the effect of external rhythms on the organization of neuronal oscillations. A number of studies explored this organization in the electroencephalogram (EEG) and found that besides amplifying the power of certain EEG frequencies (Herrmann, 2001; Iversen et al., 2009; Neher, 1961; Nozaradan et al., 2011; Rees et al., 1986; Regan, 1966; Snyder and Large, 2005) external rhythms can shift EEG phase (Barry et al., 2003, 2004; Lakatos et al., 2008; Will and Berg, 2007). Specifically, external rhythms were shown to align the phase of oscillatory activity with the onset of rhythmic events—with the aligned or “preferred” phase angle varying between studies (Barry et al., 2004; Fellinger et al., 2011).

The second line of evidence emerged from research on the relationship between EEG oscillatory phase and stimulus processing. This research showed that the phase angle before or at stimulus onset correlates with stimulus-related perceptual awareness (Busch et al., 2009; Busch and VanRullen, 2010; Mathewson et al., 2009; Valera et al., 1981), reaction times (Dustman and Beck, 1965; Stefanics et al., 2010), and event-related potentials (ERPs; Busch et al., 2009; Mathewson et al., 2009; Stefanics et al., 2010). For example, the phase of beta oscillations before the onset of a visual stimulus was shown to predict stimulus detection accuracy (Fiebelkorn et al., 2013). Furthermore, the phase of low frequency oscillations at the onset of an auditory event was shown to predict the amplitude of the N1 component in the ERP (Barry et al., 2003, 2004), a known correlate of attention (Luck et al., 1990).

Together, existing electrophysiological work raises the possibility that external rhythms drive the phase of cortical oscillations, which in turn modulates the ups and downs of perceptual processing and awareness. However, a thorough test of this possibility is still lacking. Most published research failed to clearly link external rhythms to both neuronal oscillations and perceptual processing. Moreover, the few studies that did (Henry and Obleser, 2012; Mathewson et al., 2012; Rohenkohl and Nobre, 2011; Kösem et al., 2014), found inconsistent results and employed paradigms that generated stimulus expectations alongside rhythmic expectations.

Stimulus expectations differ from rhythmic expectations in that they may arise from temporal processes that are non-rhythmic. In other words, participants may time intervals between successive events without generating an overall rhythmic representation that imposes a perceptual structure on sensory input—a structure comprising strong and weak elements that may or may not map onto the sensory input. Thus, to explore rhythmic expectations independently from stimulus expectations, it does not suffice to establish a temporal regularity and to present stimuli that converge or diverge from this regularity. In this case, responses reflect the participants' expectation for a stimulus to occur at a particular point in time alongside potential modulations of rhythmic attending. To avoid this, rhythmic points need to be developed and tested independently from stimulus regularity, for example, by using physically unmarked subdivisions of a regular sequence or by developing a metric structure in which not all rhythmic points are physically marked (Escoffier et al., 2010). Unless this is done, one cannot tell whether sequence effects on the target have something to do with rhythmic entrainment or simply arise from the expectation of a scheduled physical event.

Another shortcoming of existing work is a focus on neuronal oscillations at frequencies that match the frequency of an external stimulation. For example, external rhythms in the beta band have been shown to drive cortical oscillations in the beta band (Nozaradan et al., 2011) and external rhythms in the alpha band have been shown to drive cortical oscillations in the alpha band (Mathewson et al., 2012; Kösem et al., 2014). Few studies have tackled entrainment for non-matching frequencies and those that did restricted their analysis to oscillatory power (Herrmann, 2001; Tierney and Kraus, 2014; Snyder and Large,

2005; Iversen et al., 2009; for a review see Schroeder and Lakatos, 2009) leaving the potential effect on oscillatory phase unexplored.

Last, existing EEG studies explored rhythmic expectations in a mostly unimodal context. Participants were presented with an auditory or visual entrainment sequence and performed an auditory or visual task, respectively. Yet, Dynamic Attending Theory predicts that rhythmic expectations drive attention regardless of entrainment modality. Auditory entrainment, for example, should benefit not only the processing of a rhythmically expected sound—but also the processing of a rhythmically expected visual, tactile, or olfactory stimulus. The possibility of such crossmodal entrainment is suggested by recent behavioral evidence (Brochard et al., 2013; Escoffier et al., 2010). Additionally, it is corroborated by electrophysiological research in monkeys and humans. In both species, stimulation in one modality was shown to reset the phase of ongoing oscillations in the sensory areas of another modality (Lakatos et al., 2007; Naue et al., 2011; Thorne et al., 2011; Kösem et al., 2014). However, a possible entrainment of such a phase effect by an external rhythmic as opposed to stimulus structure has not yet been established.

With these issues in mind, we designed the present study. Specifically, we investigated rhythmic expectations, while keeping stimulus expectations constant, and sought to test whether rhythmic expectations drive the alignment of neural oscillations with target onsets and facilitate target processing. Additionally, we employed an auditory sequence with a low beat frequency comparable to that of music, speech, and biological motion (Oullier et al., 2008; Schirmer, 2004; Van Noorden, and Moelants, 1999) and explored the alignment of faster neuronal oscillations. Last, we examined whether the oscillatory changes found for task-relevant and unimodal rhythmic stimulation extend to task-irrelevant and crossmodal rhythmic stimulation.

We pursued these objectives using a recently established paradigm (Brochard et al., 2013; Escoffier et al., 2010). In this paradigm, participants are presented with a regularly spaced stream of visual stimuli for which they perform a simple discrimination task. The timing of stimulus presentations is held constant across different rhythmic expectation conditions to ensure that only rhythmic, but not stimulus expectations vary. To manipulate rhythmic expectations, these visual stimuli are presented in silence or in conjunction with a task-irrelevant 1.3 Hz auditory rhythm that is temporarily aligned or misaligned. Notably, the auditory rhythm comprises a silent beat that serves as reference point for the presentations of visual stimuli and that produces rhythmic expectations in the absence of an auditory event.

In line with Dynamic Attending Theory, we predicted that both the visual and the auditory rhythm entrain attention and produce visual rhythmic expectations. To ensure that the auditory rhythm had a stronger influence than the visual rhythm on visual expectations, the former was set at a faster pace (Repp, 2005). This, combined with the fact that auditory, but not visual, rhythms can be processed pre-attentively and without awareness (Atienza and Cantero, 2001; Ladinig et al., 2009; Winkler et al., 2009) led us to expect the auditory rhythm to trump the visual rhythm in driving visual rhythmic expectations in the cross-modal conditions and the visual rhythm to be the basis for potential visual rhythmic expectations in the silence condition. If true, image processing should be better when auditory and visual rhythms were aligned as compared to when they were misaligned or when no auditory rhythm was present.

We tested our predictions by exploring the efficiency of image processing and the phase of associated cortical oscillations over visual cortex. The efficiency of image processing was assessed through visual ERPs recorded from occipital electrodes. Specifically, we examined the N1, an ERP component enhanced by stimulus cuing (Luck et al., 1993; Mangun and Hillyard, 1991) and, thus, a candidate marker for rhythmic cuing. In line with existing behavioral evidence (Escoffier et al., 2010), as well as electrophysiological data on temporal expectations (Hsu et al., 2013), we expected the N1 in the in-synchrony condition to be

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