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.

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

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 crossmodal 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

larger than the N1 in the out-of-synchrony and, possibly, the silence condition.

The phase of associated cortical oscillations was assessed for the beta band by averaging the phase values in a pre-image time window. Because of evidence that the beta band supports rhythm perception (Fujioka et al., 2012; Iversen et al., 2009; Snyder and Large, 2005), visual attention, and crossmodal processing (Gross et al., 2004; Naue et al., 2011), we considered the beta band a good candidate for our study. Moreover, we expected differences in the alignment of beta oscillations with the visual stimulus onset as a function of the auditory background and for these differences to be related to the above mentioned ERP effects.

Materials and methods

Participants

We recruited 28 participants for the experiment. The data from four participants were discarded because of excessive movement artifacts. The data from 24 participants (9 females, 22 right-handed, mean age = 21.7, SD = 1.3) were analyzed. The duration of their formal musical training ranged from 0 to 10 years (mean = 3.0, SD = 3.5). All participants gave written informed consent in accordance with the Declaration of Helsinki (2008).

Stimuli

A 12 s rhythm composed of snare and bass drum sounds served as the auditory stimulus (see Fig. 1, and Escoffier et al., 2010, for stimulus validation). The rhythm consisted of four measures with a four-beat structure designed to create expectations for a regular beat at 750 ms intervals (1.3 Hz, 80 beats per minute). The snare and bass drum sounds were drawn from the Ableton live software sample library (Ableton, Germany). The bass drum sound was 224.5 ms long and its peak frequency in the Fourier frequency spectrum was 31.8 Hz. The snare drum sound was 214.5 ms long and its peak frequency was 188.6 Hz. The first beat of the sequence was marked by a bass drum and

the second beat was marked by a snare drum sound. The third beat, was preceded and followed by a snare drum sound, a figure known as syncopation (Fitch and Rosenfeld, 2007). To limit the possibility that the two snare drum sounds marking the syncopation disrupted the meter established by the first two beats, we decreased their amplitude relative to those beats. This rendered the first two beats accented and able to drive attending processes (see Jones and Boltz, 1989; Large and Kolen, 1994). Importantly, the fourth beat in each measure was silent. It occurred in a 1098 ms silent interval between the offset of the last sound and the onset of the bass drum marking the first beat of the next measure. The actual position of the silent beat within this interval was suggested by the rhythm's global structure, but was not marked by a sound cue. Through this, the present study dissociated rhythmic expectations for a beat from stimulus expectations for a sound.

Grey-scale photographs of 40 terrace houses (Escoffier et al., 2010) and 40 emotionally neutral, full-front Asian faces (Gao et al., 2008) served as visual stimuli.

Experimental design

The experiment comprised three main conditions presented in separate blocks (Fig. 1). In the silence condition, images were presented without the auditory rhythm. In the in-synchrony condition, image onsets occurred synchronously with the silent beat in the auditory rhythm. In the out-of-synchrony condition, image onsets occurred 250 ms before the silent beat position.

Duration and pace of image presentations were identical across conditions. The time interval between two consecutive images was thus constant and only the temporal alignment of the images to the auditory rhythm changed. Images were presented on black background for 250 ms at the center of a CRT monitor (apparent size = 7.8° × 5.6°; refresh rate = 72 Hz). Each image was followed by a 5.75 s fixation cross (0.35°) resulting in a stimulus onset asynchrony of 6 s. For each condition, 40 upright houses, 40 upright faces, 4 inverted houses and 4 inverted faces were presented in random order. Inverted images served as targets in the present go/no-go task, which was used to ensure sustained attention. Upright images were repeated across conditions,
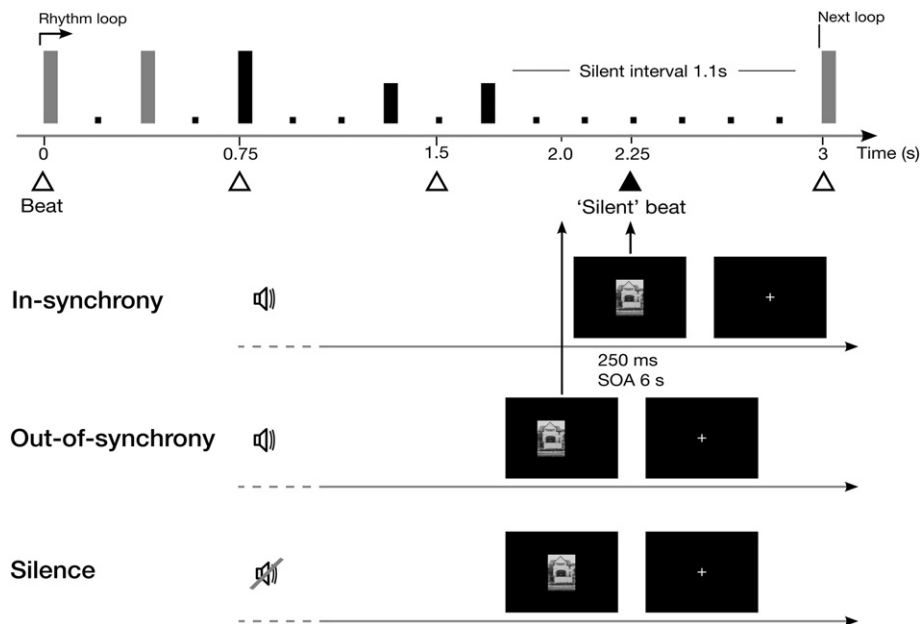
Fig. 1. The upper part of the figure illustrates the auditory rhythm that was looped throughout experimental blocks. The lower part of the figure illustrates the timing of visual stimulus presentations once every two measures. Arrows indicate their relation to the auditory rhythm. In the silence condition, visual stimuli were presented without auditory rhythm. The interval between images was identical across conditions. Gray bars represent bass drum sounds; black bars represent snare drum sounds. Bar height represents relative sound amplitude. SOA: stimulus onset asynchrony. Note, the sounds in this sequence give rise to a metric structure as indicated by the black dots. This structure promotes an expectation for the silent beat at 2.25 s that was leveraged here for image presentations.

whereas inverted images were randomly drawn without replacement from the set of 80 upright images.

As mentioned earlier, the auditory rhythm comprised a silent beat that was used as a reference for image presentations. One concern was that the sound preceding the silent beat may have triggered EEG activity that was still present at image onset thereby creating spurious crossmodal effects. To control for this, images were presented every other silent beat/off-beat and the remaining silent intervals were left empty. In other words, images occurred once every two measures. The empty epochs were then used as a no-image control condition for subtraction from the image conditions in our analyses. A similar procedure was applied in the silent condition. Here, an equivalent time window between consecutive images was used as a no-image control.

Another concern was that the sound preceding the silent beat served as a warning signal and triggered local temporal preparation. Such an effect, also known as foreperiod effect, has been shown to depend on the overall temporal structure of stimuli within a block. When foreperiod durations vary within blocks, longer foreperiods facilitate target processing relative to shorter foreperiods (Jennings et al., 1998; Loveless, 1975). However, when foreperiods within a block are held constant, shorter foreperiods facilitate target processing relative to longer foreperiods (Jennings et al., 1998).

To address the possibility of foreperiod effects potentially confounding the global rhythmic processing that was of interest there, we carefully considered the properties of the in- and out-of-synchrony conditions. Compared to the in-synchrony condition, the out-of-synchrony condition had a shorter time interval between the last sound and the image such that its foreperiod was shorter. Thus, if both conditions were intermixed, the foreperiod effect should produce results in line with the predicted global rhythmic effects making them impossible to separate. If both conditions were blocked, however, the foreperiod effect should produce results opposite to the predicted global rhythmic effects. Because of this, we opted for the blocked design.

Procedure

Participants were seated in front of a computer screen and performed a visual go/no-go task. They were instructed to respond to rare upside-down images (target probability ~ 10%) by pressing a key on a response pad (Cedrus RB-730) using their right hand. This task was employed simply to ensure sustained attention to the images. It was intentionally modified from our previous publication to avoid motor processes contaminating the EEG/ERP effects of interest. The auditory rhythm was presented at a comfortable hearing level through insert earphones (ER-4P, Etymotic Research) and a Sound blaster X-fi audio card (44.1 kHz, 16 bit, 10.4 ms latency). Participants were informed about the rhythm and asked to ignore it. The session began with a silent practice task including 20 images not used in the main experiment. During this practice only, participants were given accuracy feedback. The main experiment was divided into 6 blocks with 88 trials each, including 8 trials showing targets and hence not relevant for statistical analysis. There were two blocks each for the in-synchrony, the out-of-synchrony, and the silence conditions, resulting in 160 relevant trials per condition. Block order was counterbalanced. There was a mandatory break of 20 s between blocks. At the end of the experiment, participants completed a questionnaire, which recorded their age, sex, handedness, and length of formal musical training.

EEG recording and pre-processing

The EEG was recorded from 64 Ag/AgCl electrodes mounted in an elastic cap according to the modified 10/20 system. The electro-occulogram was recorded using three electrodes attached below the left eye and at the outer canthus of each eye. The data was recorded at 512 Hz using a Biosemi Active2 system with a common mode sense active electrode as recording reference.

The EEG data was preprocessed with EEGLAB (Delorme and Makeig, 2004). The recording was first down-sampled to 256 Hz, band-pass filtered between 0.015 and 30 Hz and re-referenced to a 64-channels average reference. During visual examination, epochs with drifts, movement or muscle artifacts were removed. The EEG was then subjected to an Independent Component Analysis algorithm to isolate and remove independent components associated with eye movement artifacts (Jung et al., 2000). The back-projected data was epoched time-locked to image onset or the equivalent timepoint for the no-image silent beat epochs. Epochs comprised a 350 ms pre-stimulus interval and an 800 ms post-stimulus interval. These intervals were selected to enable the analysis of both ERPs and evoked oscillations. For the ERP analysis only, epochs were baseline corrected using a 200 ms pre-stimulus window. All epochs were then visually examined and discarded if residual artifacts were identified. After this procedure, an average 141 of trials per condition remained. Participants were excluded from analysis if more than 30% of the trials in any one condition had been rejected. As already mentioned under "Participants", four individuals were excluded following this procedure.

Subtraction approach

Prior to the ERP and oscillatory analysis, the no-image control epochs were subtracted from the image epochs in the in-synchrony, out-of-synchrony, and silence conditions. Again, control epochs were defined for each condition separately as the equivalent duration time window situated between two consecutive images. In the two auditory conditions, this time window covered exactly the same auditory input as the time window used for image analysis and was thus different for the in- and out-of-synchrony conditions. For the silent condition, this time window covered the same relative position between images as the time window in the auditory conditions. However, the interval was completely empty. EEG epochs in the silent condition were treated similarly to EEG epochs in the auditory background conditions to ensure that effects associated with the subtraction approach left these conditions comparable.

The subtraction approach applied here served two important goals. First, it enabled us to remove signal differences between silence, in-, and out-of-synchrony conditions resulting from differences in auditory stimulus history. Second, it allowed us to isolate visual processing and its modulation by the auditory background manipulations. Specifically, we reasoned that visual processing was tied to image presentations and that associated visual expectations should emerge around the time that images were presented but be absent during control epochs without images. Thus, subtracting control epochs from image epochs should remove auditory processing and associated auditory phase alignment. However, it should retain the influence of such processing on visual perception.

Although the subtraction approach is not entirely without problems (e.g., assumed additivity), it is well established in the literature (Donohue et al., 2011; Giard and Peronnet, 1999; Mathewson et al., 2009) and was necessary for the present purpose.

ERP analysis

Visual inspections of the ERPs revealed effects on a small component elicited at the time of stimulus onset and henceforth referred to as a stimulus onset potential (SOP). SOP-like potentials have been previously associated with effects in the alpha band (Barry et al., 2003, 2004). In addition to the SOP, we observed a modulation of the N1, an established index of attentional and discriminatory visual processes (Luck et al., 1990; Mangun and Hillyard, 1991; Vogel and Luck, 2000). We examined the SOP in a time window ranging from − 15 to 15 ms around stimulus onset. Because SOP polarity differed between

conditions, mean rather than peak voltages in the SOP time window were used for analysis. We analyzed the N1 in a time window ranging from 150 to 170 ms following stimulus onset. Because the N1 had a negative polarity irrespective of condition, the analysis was performed on voltage minima.

The same electrodes of interest were used to analyse both components. They covered posterior, occipito-temporal regions (O1, PO7 and P7 in the left hemisphere and O2, PO8 and P8 in the right hemisphere). Mean values derived from these electrodes entered ANOVAs with Rhythmic Expectations (in-synchrony, out-of-synchrony, silence) and Hemisphere (left, right) as repeated measures factors.

Power and phase analysis

We investigated condition differences in the power and phase of evoked oscillations. Evoked oscillations emerge in trial averages and are thus comparable to ERPs (Klimesch et al., 2007). They are time-locked to stimulus onset such that their phase with respect to stimulus onset is consistent across trials. In contrast, the phase of induced oscillations varies across trials (Galambos, 1992; Tallon-Baudry and Bertrand, 1999). Notably, stimuli in our study included not only images, but also ongoing background sounds that generated rhythmic expectations before, at, and after image onsets. As such, we expected evoked responses not only in association with the images, but also in association with the auditory rhythm. Moreover, we focused our analysis on evoked rather than induced oscillations because the consistent time-locking of evoked oscillations across trials seemed more relevant for the temporally predictive function of rhythmic expectations. Additionally, evoked but not induced oscillations allowed us to use the subtraction approach described above. A single trial analysis required to investigate induced oscillations would have prevented any subtractions to be performed because, unlike for trial averages, these subtractions would produce complex and non-transparent consequences on both power and phase values (Senkowski et al., 2006).

Oscillation analyses were performed using EEGLAB (Delorme and Makeig, 2004), the CircStat toolbox (Berens, 2009), and in-house developed Matlab functions (The Mathworks). They were done on the same set of electrodes as selected for the ERP analysis described above. The EEG data recorded at these electrodes was averaged and subjected to a complex Morlet wavelet transform, which allowed us to evaluate condition differences in phase before stimulus onset (Tallon-Baudry et al., 1997). We used a series of wavelets covering frequencies from 5 Hz to 30 Hz (c = 2–6, increasing linearly; σ_f = 1.7–5.0 Hz; σ_t = 94–32 ms; wavelet window lengths decreased linearly from 400 at low frequencies to 200 ms at high frequencies).

In classical wavelet analysis, data from both before and after each data point is used to estimate local wavelet parameters. These parameters are therefore estimated in an *acausal* manner, meaning that they are affected by signal changes that occur later in time (Zoefel and Heil, 2013). This is problematic when examining signal in the vicinity of a stimulus onset because the post-stimulus ERPs can bias pre-stimulus power and phase estimates, producing spurious relationships between pre-stimulus estimates and post-stimulus signal. To prevent this possibility we used a novel *causal* technique that eliminates the influence of post-stimulus signals on the estimation of pre-stimulus wavelet parameters (Lakatos et al., 2013). For every trial, the post-stimulus data that overlapped with the pre-stimulus wavelet time-window was replaced by a line interpolating the signal in this interval. Lakatos et al. (2013) have shown that this procedure returns unbiased wavelet parameter estimates.

From the complex wavelet transforms, we computed the average power and the average phase over electrodes and over a −100 to 0 ms time window before image onset. This window was chosen to capture oscillatory effects occurring just prior to stimulus onset that could be linked to potential expectations for an upcoming visual

stimulus. Power and phase values were averaged for four frequency bands. These bands comprised theta (5–7 Hz), alpha (8–12 Hz), low beta (13–20 Hz) and high beta (21–30 Hz). High and low beta bands were immediately relevant for our predictions. Oscillations in the other bands were explored due to their potential interest for the oscillation literature (Gross et al., 2004; Mathewson et al., 2009; Rohenkohl and Nobre, 2011; Sauseng et al., 2007).

For each of these frequency bands, we first determined whether phase alignment had occurred. To this end, we analyzed phase consistency for each condition and each frequency band using a Rayleigh test of uniformity (Fisher, 1993; Lakatos et al., 2008; Mardia and Jupp, 2000). This test allowed us to infer whether the phases in the prestimulus analysis window were uniformly distributed. In conditions and frequency bands showing a significant phase consistency, we further examined average phase using large sample, non-parametric two-sample tests (Fisher, 1993). Additionally, we explored oscillatory power using an ANOVA.

The relationship between phase changes related to rhythmic expectations and subsequent ERPs was also investigated. To this end, the difference between in- and out-of-synchrony conditions in phase and in ERP amplitudes was computed and subjected to a linear–circular correlation (Mardia and Jupp, 2000).

As the phase analysis relied on multiple comparisons, we sought to reduce the chance of false positive results by controlling the False Discovery Rate (FDR; Benjamini and Hochberg, 1995; Gavrilov et al., 2009). Unless noted otherwise, the reported phase results passed the 5% FDR criterion. All statistical analyses were performed in R (R Core Team, 2013) using the circular package (Agostinelli and Lund, 2011).

Results

Behavioral analysis

An analysis of detection rates (96%, SD = 5) indicated that the behavioral task effectively engaged the participants' attention. As was expected due to the low response frequency in this task, the Rhythmic Expectations effect was non-significant for both accuracy ($p > .1$) and response times ($p = .08$). Moreover, response times were more variable and about 170 ms slower than in our previous study (Escoffier et al., 2010).

ERP analysis

ERP traces are presented in Fig. 2. Visual inspection suggested condition effects not only for the N1, but also for a stimulus onset potential (SOP). Both seemed more negative for the in- as compared to the out-of-synchrony and silence conditions. To probe these visual impressions, we conducted two ANOVAs.

Analysis of the SOP revealed a significant effect of Rhythmic Expectations ($F_{(2,46)} = 4.13$, $p = .02$, $\eta^2 = .068$) indicating that the SOP was more negative for the in-synchrony as compared to the out-of-synchrony ($F_{(1,23)} = 5.33$, $p = .03$, $\eta^2 = .12$) and silence conditions ($F_{(1,23)} = 5.62$, $p = .03$, $\eta^2 = .096$). The difference between the out-of-synchrony and silence conditions was non-significant ($p = .63$) as were all other effects ($ps > .26$). For the N1, the overall effect of Rhythmic Expectations was significant ($F_{(2,46)} = 5.08$, $p = .01$, $\eta^2 = .022$) and moderated by an interaction with Hemisphere ($F_{(2,46)} = 3.3$, $p = .046$, $\eta^2 = .003$). Follow-up analyses for right hemisphere electrodes revealed an enhanced N1 for the in-synchrony as compared to the out-of-synchrony ($F_{(1,23)} = 4.35$, $p = .048$, $\eta^2 = .021$) and silence conditions ($F_{(1,23)} = 10.83$, $p = .003$, $\eta^2 = .070$). The N1 was tendentially larger in the out-of-synchrony as compared to the silence condition ($F_{(1,23)} = 3.65$, $p = .07$, $\eta^2 = 0.014$). The Rhythmic Expectations effect was non-significant for left hemisphere electrodes ($p > .1$).
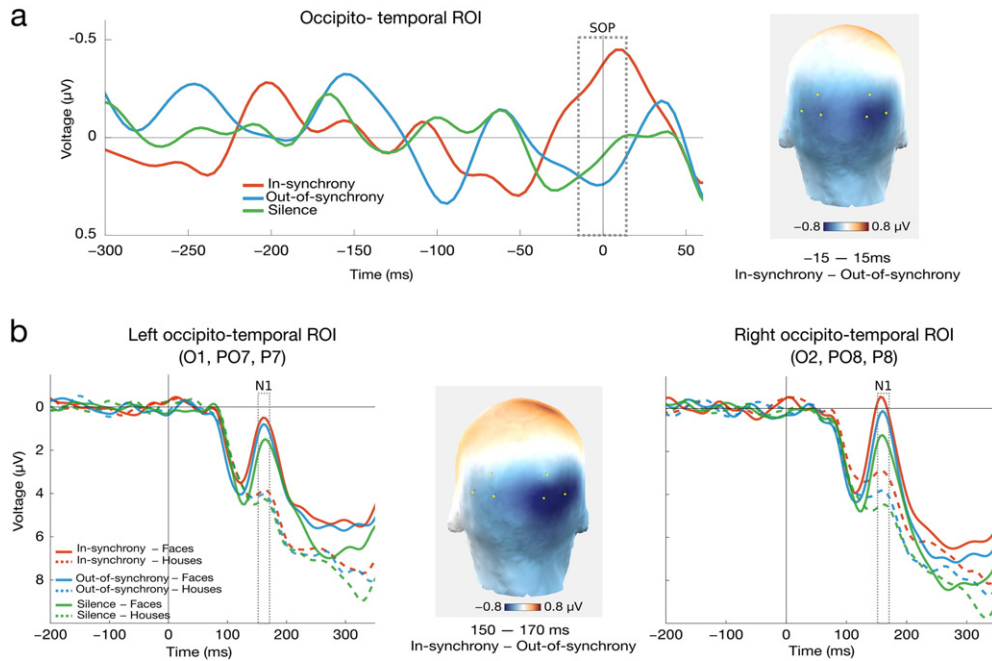
Fig. 2. Effect of crossmodal rhythmic expectation on evoked pre-stimulus activity and visual ERPs. (a) Pre-stimulus evoked activity and stimulus onset potential (SOP; left), and topography of the effect of rhythmic expectation on the SOP (right). (b) ERP traces for left and right hemisphere and topography of the effect of rhythmic expectation on N1. Yellow dots indicate the location of electrodes used for analysis and trace display; dashed boxes represent the time windows used for data analysis and topography display. ROI: region of interest. Zero indicates the onset of the visual stimulus.

For each ERP component, an ANOVA with Rhythmic Expectation and Hemisphere as repeated measures factors and Condition Order as the between subjects factor indicated that the interaction of Rhythmic Expectation and Condition Order was non-significant (all ps > .11).

Oscillation analysis

Oscillatory phase at image onset

Because an analysis of average phase is only meaningful if phase across trials and participants is non-uniformly distributed, we first explored phase consistency (R; illustrated in Fig. 3). High beta failed to show significant phase consistency in all three conditions (Rayleigh test, ps > .13). Low beta oscillations showed significant phase consistency

in all conditions (ps < .03). Alpha showed significant phase consistency in the in-synchrony condition (p < .004; other ps > .30). Theta showed significant phase consistency in the in-synchrony and silence conditions (ps < .001; other p > .25). Because phase consistency was present across all conditions only in the low beta band, only low beta oscillations were further investigated.

An analysis of oscillatory phase before image onset revealed phase differences between the in-synchrony and out-of-synchrony conditions ($\chi^2(1) = 5.48$, $p = .019$) and between the in-synchrony and silence conditions ($\chi^2(1) = 4.33$, $p = .037$). Phase was comparable for the out-of-synchrony and silence conditions ($\chi^2(1) < 0.01$, $p = .97$).

A series of correlation analyses further explored whether the phase difference between conditions predicted the subsequent ERP effects.
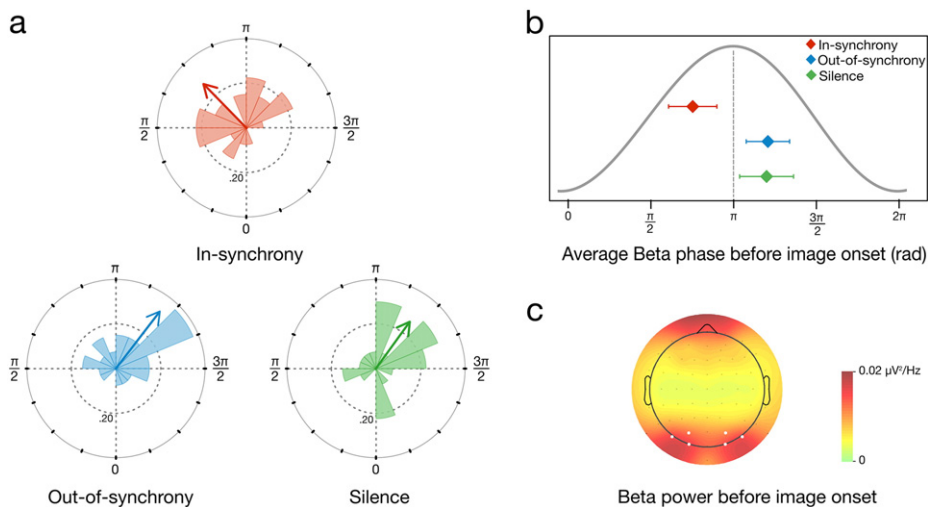
Fig. 3. Effect of crossmodal rhythmic expectations on evoked beta (13–20 Hz) phase in the 100 ms interval before image onset. (a) Pre-stimulus phase distribution changes across conditions. Arrow direction indicates the average phase; arrow length indicates phase consistency across participants (R). (b) Average phase. The gray trace represents an example oscillation (negativity plotted upwards) that can be used to gauge the average phase values for each condition. Error bars indicate the circular standard error of the average phase (Fisher, 1993). (c) Topography of beta power in the pre-stimulus interval. White dots indicate the location of the electrodes used for phase analysis and display.

We found that the phase difference between the in-synchrony and the out-of-synchrony conditions predicted the enhancement for the N1 ($R^2 = .19$, $F_{(2,21)} = 5.05$, $p = .016$), but not for the SOP ($R^2 = .02$, $F_{(2,21)} = 0.49$, $p = .62$). The phase difference between in-synchrony and silence conditions predicted the enhancement for the SOP ($R^2 = .15$, $F_{(2,21)} = 3.56$, $p = .047$), but not for the N1 ($R^2 = .04$, $F_{(2,21)} = 0.80$, $p = .46$).

The pre-stimulus phase effects could be the consequence of a broadband phase-reset phenomenon triggered by the last sound preceding the visual stimulus. Because this sound appeared with different time lags in the in- and out-of-synchrony conditions, it may have evoked activity with different phase lags between these conditions that would then be captured in the subsequent pre-stimulus interval. In order to address this possibility, we performed another analysis of the pre-stimulus phase without subtracting the no-image control condition. This fully preserved the sound-related phase-reset activity, making its potential influence on pre-stimulus phase maximal. The type of phase differences that would be triggered by sound-related phase reset could then be observed, and compared with the initial results obtained from the subtraction approach.

The analysis revealed different patterns. In the presence of the sound, the phase differences reported above were non-significant (ps > .08). Therefore, our initial findings are unlikely to be due to a phase reset triggered by the last sound preceding the visual stimulus.

Oscillatory power

Because external rhythms may affect phase results by inducing oscillations at specific frequencies rather than by changing the phase of existing ones, we supplemented the above phase analyses with an exploration of oscillatory power in the low beta band within a 100 ms time window prior to stimulus onset (Fig. 4). Power values from the same occipital sites were averaged and analyzed using a one-way ANOVA with Rhythmic Expectations (in-synchrony, out-of-synchrony, silence) as the repeated measures factor. The results of this analysis were non-significant ($p = .91$).

Discussion

The present study explored the neural correlates of rhythmic expectations. It identified a range of effects both in the ERP and in the phase of EEG oscillations. How these effects inform our understanding of rhythmic expectations and shed light on more general neurofunctional principles is detailed below.

ERP correlates for rhythmic expectations

The present study revealed an effect of rhythmic expectations on a stimulus onset potential (SOP) and the N1 suggesting that these expectations modulated early sensory and later perceptual stages of stimulus processing. A modulation of an early sensory stage was indexed by the SOP. In the past, potentials evoked at or before stimulus onset were treated as baseline artifacts and attracted little theoretical interest. More recently, however, evidence emerged that marks them as correlates of preparatory processes (Potter et al., 2009; Stefanics et al., 2010). The present work furthers this development by showing that rhythmic expectations produce a negative onset potential for rhythmically expected as compared to less expected stimuli (i.e., in- vs out-of-synchrony, in-synchrony vs silence). Thus, in line with previous studies, we link condition differences at stimulus onset to the preparation for an upcoming event. Additionally, we suggest that SOPs may serve as tools in the study of rhythmic expectations and, more generally, in the study of timing and time perception.

A modulation of later perceptual processes by rhythmic expectations was indexed by the N1, a negative component that peaks between 150 and 200 ms following stimulus onset (Luck et al., 1990). The N1 comprises several cortical sources that may contribute differently depending on stimulus properties. For example, a source in the fusiform gyrus enhances the N1 for faces relative to other non-face images (Bentin et al., 1996; Bötzel et al., 1995). For the present purpose, however, we do not consider these different contributions separately as our effects were not stimulus specific and thus seem to tap on more general aspects of the N1.

Several studies have linked the N1 to endogenous and exogenous changes in attention. Among others, it has been demonstrated that temporally or spatially cued stimuli elicit a larger N1 than non-cued stimuli (Doherty et al., 2005; Griffin et al., 2002; Zanto et al., 2011; Hsu et al., 2013) and that task-relevant stimuli elicit a larger N1 than task-irrelevant stimuli (Luck et al., 1990, 1993; Vogel and Luck, 2000). Here we observed a larger N1 to images presented synchronously with an auditory rhythm as compared to images presented asynchronously or in silence. This extends previous findings by showing that rhythmic expectations, independently of local stimulus expectations, modulate the N1.

Apart from revealing ERP correlates of rhythmic expectations, the present findings contribute to the debate of whether ERPs are caused by changes in the strength of ongoing neural activity or their temporal structure (Makeig et al., 2002; Fellinger et al., 2011). Some research suggests the latter possibility indicating that the N1 arises in part from a phase reset of alpha oscillations (Makeig et al., 2002; Hanslmayr
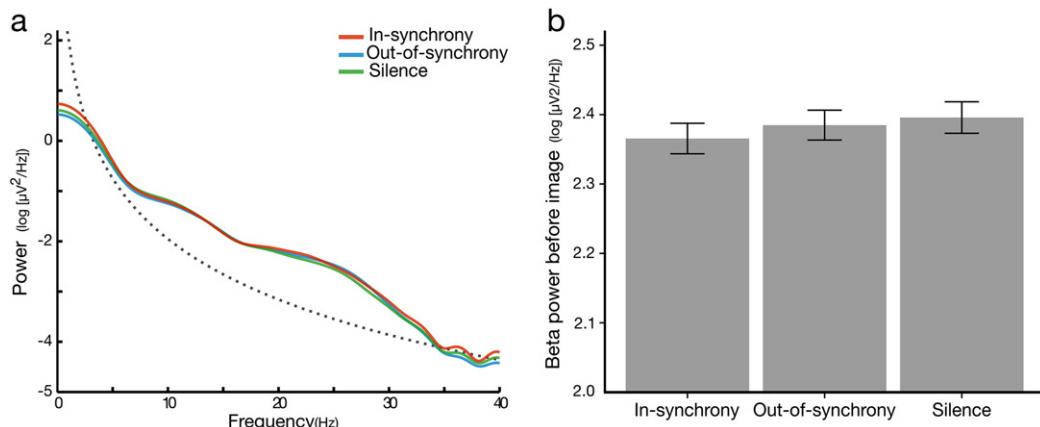

Fig. 4. (a) Average power spectrum, showing power in the low and high beta bands over a 1/f trend (dotted line). (b) Average power in the low beta band (13–20 Hz) in the 100 ms interval before image onset. Error bars indicate 95% within participant confidence intervals.

et al., 2005, 2007). Our results accord with this. Specifically, the coincidence and correlation of ERP effects with the oscillatory effects described below suggest that the former are closely tied to the latter.

Oscillation correlates for rhythmic expectation

Previous work suggests that regular external events drive cortical oscillations into a "preferred" phase such that, across trials, this phase relatively consistently overlaps with event onsets (Barry et al., 2003, 2004; Fellinger et al., 2011). As images presented in the present study were also regular, we expected them to similarly affect the ongoing EEG. This was confirmed in an analysis of phase consistency. Low beta showed significant phase consistency irrespective of the auditory background. Thus, all conditions entrained low beta allowing us to conclude that the temporal regularities in these conditions aligned evoked cortical oscillations around a preferred phase value.

As expected, however, this value differed across conditions. Changes in the temporal alignment between the auditory background rhythm and the images were reflected in changes in the phase of beta oscillations at image onset. These beta effects concur with existing research on auditory, visual, and audiovisual processing. Past auditory studies showed that beta oscillations entrain to stimulus periodicities (Will and Berg, 2007) and that their power is modulated by imagined or actual changes in auditory rhythms (Fujioka et al., 2012; Iversen et al., 2009; Snyder and Large, 2005). Past visual studies, furthermore, indicate that beta power and phase distribution can determine the distribution of visual attention over time and affect perception performance (Arnal et al., 2014; Gross et al., 2004; Hanslmayr et al., 2007). In addition, there is evidence that audiovisual stimuli evoke beta oscillations in visual areas and that an auditory input can trigger a reorganization of their phase (Naue et al., 2011). Thus, together, existing work highlights the beta-band as particularly important for the rhythmic and perceptual processes examined here.

In line with this, the present study found beta effects and added to existing work by using an entrainment rhythm outside the beta range, by showing that the resulting phase reorganization may occur in the absence of power modulations, and by linking beta-phase alignment to rhythmic expectations and visual processing. When image presentations occurred synchronously with an auditory rhythm, they were preceded by a positive going wave in the beta band. When image presentations occurred in silence or out-of-synchrony with the auditory rhythm, they were preceded by a negative going wave in the beta band. At the participant level, these phase differences predicted SOP and N1 effects in the ERP pointing to a link between phase reorganization and stimulus perception. This link is further corroborated by a comparison between the present study and previous behavioral work using the same procedure (Escoffier et al., 2010). This work identified parallel condition differences whereby images in the in-synchrony condition were judged faster than images in the silence and out-of-synchrony conditions. Thus, we consider beta phase as a substrate for rhythmic visual expectations and visual attention. Moreover, we suggest that task-irrelevant and possibly unattended auditory rhythms drive beta phase thereby benefiting the processing of visual information that is rhythmically aligned as compared to misaligned.

Although our main interest was the beta band, we also explored the alpha and theta bands. Like beta, alpha and theta were previously implicated in the processing of stimulus regularity, albeit relevant evidence is relatively rare. For example, studies have found both alpha and theta phase alignment with stimulus onset to be enhanced during periodic as compared to aperiodic auditory stimulation (Will and Berg, 2007; Mathewson et al., 2012). Alpha and theta phase have also been related to visual processing efficiency (Busch et al., 2009; Mathewson et al., 2009) and to the perceptual binding of audiovisual information (Kösem et al., 2014). Additionally, the temporal properties of crossmodal stimuli were found relevant for the phase of EEG frequencies below beta (Thorne et al., 2011; Kösem et al., 2014) giving rise to the

possibility that these frequencies underpin cross-modal rhythmic expectations.

The present findings support this possibility by showing alpha and theta phase consistency to images presented synchronously with an auditory background rhythm. However, due to a lack of phase consistency in the other background conditions, as well as suboptimal parameter estimation in the case of theta, no conclusions could be made as to whether the auditory rhythm could entrain oscillations below the beta range.

In sum, the present oscillation findings further the discussion of how the brain represents predictions about "what" is going to happen "when" (for a review see Arnal and Giraud, 2012). Additionally, they corroborate the notion that phase reorganization contributes to cross-modal rhythmic expectations. An external auditory rhythm was shown to drive oscillatory phase of visual preparatory processes within the beta band such that image presentations occurred at different phase angles in the in- as compared to the silence and out-of-synchrony condition. In line with previous research and based on our ERP results, we suggest that the in-synchrony phase angle was more preferred for resource allocation than the phase angle in the other two conditions.

The preferred phase value found in this study differs from that observed in other studies. This difference could be due to the different frequency bands that have been implicated suggesting that these bands have different processing modes or functional roles. Alternatively, the actual value of the preferred phase may be a meaningless surface feature that varies with the transmission speed from the sensory organs to respective neuronal generators. Evidence for this comes from studies demonstrating that visual stimulus properties such as luminance or spatial frequency content affect the latency of subcortical and cortical activations (Maunsell and Gibson, 1992; Maunsell et al., 1999; Parker and Salzen, 1977). As a consequence, the optimal phase of cortical oscillations in relation to stimulus presentation must vary. Moreover, because the same frequency oscillations may have different neuronal sources, their phase differences may be a function of variation in distance between these sources and the sensory organs.

Although condition differences between in- and out-of-synchrony confirmed our predictions, this was not the case for the silence condition. Specifically, we predicted comparable oscillatory phases for the silence and the in-synchrony conditions because rhythmic expectations, although differently strong, should fall on the same temporal grid. That we failed to observe this pattern may be because the preferred phase differed between the cross-modal and the unimodal conditions. In line with the argument raised above, auditory and visual stimulations likely traveled at different speeds through the nervous system such that visual only processing may benefit from a different preparatory phase than audiovisual processing. This interpretation accords with the fact that phase differences involving the silence condition related differently to the ERP than did phase differences involving the out-of-synchrony condition. The former were associated with the SOP, whereas the latter were associated with the N1. Thus, the same phase value predicted different modes of temporal preparation.

Beyond unimodal stimulus expectations

Apart from the results highlighted above, the present paper makes important theoretical contributions that deserve special emphasis. For one, this is one of the first oscillation studies to dissociate rhythmic or global expectations from stimulus or local expectations. To our knowledge, only two other groups have attempted this before (Iversen et al., 2009; Rohenkohl and Nobre, 2011). First, Iversen et al. (2009) raised the importance of a "silent beat" and examined this notion using syncopated rhythms similar to the one used here. Specifically, in a preliminary test with seven musically trained participants they found that induced oscillations were marked by increased beta-power shortly before beat onset. Notably, and in line with the present observations, similar

power differences were absent for evoked oscillations. No explorations were made concerning the phase of either induced or evoked beta.

Rohenkohl and Nobre (2011) pursued the idea of a physically unmarked beat using a visual entrainment paradigm in which a dot appeared along a diagonal at regular or irregular intervals. Importantly, one part of the screen was obscured by a rectangle giving the impression that, although invisible, the dot appeared once behind it. Thus, at this point, rhythmic expectations dissociated from explicit stimulus expectations, albeit implicit stimulus expectations could not be ruled out. Shortly before rhythmically or physically marked events, alpha power in the EEG was modulated by the regularity of stimulus presentations.

The present study adds to this work in several ways. First, using a larger sample of non-musicians and removing the possibility of implicit stimulus expectations we found robust evidence for a role of oscillations in rhythmic expectations. Moreover, our results point to the reorganization of oscillatory phase as a supporting mechanism.

A second contribution is that we found phase reorganization for neuronal frequencies that differed drastically from the external stimulus rhythm. A slow rhythm comparable to the biological rhythms we encounter in daily life (Schirmer, 2004; Voss and Clarke, 1975) successfully entrained the phase of fast cortical oscillations in the beta-band. This study, therefore, establishes oscillatory phase as an important mechanism through which humans exploit natural regularities in the environment. Moreover, it agrees with an influential model of time perception that incorporates cortical oscillatory phase as a mechanism for temporal representations (Buhusi and Meck, 2005; Matell and Meck, 2004).

Finally, our results contribute to the literature on how information from the different modalities is integrated into a unified percept. In the absence of stimulus expectations, rhythmic expectations were shown to influence the temporal organization and efficiency of visual processing. Because our auditory rhythm effectively entrained slower paced visual expectations despite being uninformative and irrelevant for the task, its cross-modal influence appears to operate relatively spontaneously. Furthermore, because visual processing was enhanced in the in-synchrony condition and left unimpaired (i.e., not different from silence) in the out-of-synchrony condition, one may infer that, at least in the context of rhythmic expectations, cross-modal auditory rhythms have a primarily beneficial effect. Last, because facilitation relative to the silence condition was found for rhythmic cues present in the in-synchrony condition, but not for stimulus cues (i.e., foreperiod) present in the out-of-synchrony condition, our results suggest that cross-modal stimulus preparatory processes are more dependent on global as compared to local structure.

Taken together, our research sheds light on the neural underpinnings of rhythmic expectations and elucidates their importance as a fundamental organizing principle of perception and, possibly, thought.

Acknowledgments

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