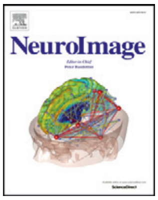
NeuroImage 132 (2016) 148–156

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



# Perceived time and temporal structure: Neural entrainment to isochronous stimulation increases duration estimates

Ninja K. Horr, Maria Wimber, Massimiliano Di Luca *

*Department of Psychology, Centre for Computational Neuroscience and Cognitive Robotics, University of Birmingham, Edgbaston, Birmingham B15 2TT, United Kingdom*

ARTICLE INFO

*Article history:*
Received 4 November 2015
Accepted 7 February 2016
Available online 13 February 2016

*Keywords:*
Temporal perception
Perceived duration
Filled duration illusion
Isochrony
Entrainment

ABSTRACT

Distortions of perceived duration can give crucial insights into the mechanisms that underlie the processing and representation of stimulus timing. One factor that affects duration estimates is the temporal structure of stimuli that fill an interval. For example, regular filling (isochronous interval) leads to an overestimation of perceived duration as compared to irregular filling (anisochronous interval). In the present article, we use electroencephalography (EEG) to investigate the neural basis of this subjective lengthening of perceived duration with isochrony. In a two-interval forced choice task, participants judged which of two intervals lasts longer – one always being isochronous, the other one anisochronous. Response proportions confirm the subjective overestimation of isochronous intervals. At the neural level, isochronous sequences are associated with enhanced pairwise phase consistency (PPC) at the stimulation frequency, reflecting the brain's entrainment to the regular stimulation. The PPC over the entrainment channels is further enhanced for isochronous intervals that are reported to be longer, and the magnitude of this PCC effect correlates with the amount of perceptual bias. Neural entrainment has been proposed as a mechanism of attentional selection, enabling increased neural responsiveness toward stimuli that arrive at an expected point in time. The present results support the proposed relationship between neural response magnitudes and temporal estimates: An increase in neural responsiveness leads to a more pronounced representation of the individual stimuli filling the interval and in turn to a subjective increase in duration.

## Introduction

An interesting distortion in the subjective estimate of duration for intervals in the millisecond-to-second range is the filled duration illusion: intervals that are filled with either a sequence of short stimuli (e.g., Adams, 1977; Buffardi, 1971; Horr and Di Luca, 2015a; Thomas and Brown, 1974) or with one continuous stimulus (e.g., Hasuo et al., 2014; Horr and Di Luca, 2015a; Rammsayer and Lima, 1991) are perceived to last longer than empty intervals that only consist of a beginning and an end marker. Filled duration and related illusions are good examples of how distortions of perceived duration can foster the formulation of hypotheses regarding the conceptual and neural mechanisms underlying the brains' ability to estimate interval duration. There are several possible explanations for the filled duration illusion. Most straightforwardly, the illusion is in line with a neural magnitude approach of perceived duration. The fundamental assumption of a magnitude approach is that the degree of neural activity concurrent with the stimulation during an interval is directly related to the interval's perceived duration (e.g., Eagleman and Pariyadath, 2009; Matthews et al., 2014). This approach is not only able to explain how higher magnitude, e.g., higher stimulus intensity (e.g., Berglund et al., 1969), bigger stimulus size (e.g., Xuan et al., 2007), and higher number of stimuli in the interval (e.g., Buffardi, 1971), leads to increases in perceived duration. It also explains a decrease in perceived duration with stimulus repetitions or extended presentation (e.g., Efron, 1970; Birngruber et al., 2014; Chen and Yeh, 2009; Kim and McAuley, 2013; Pariyadath and Eagleman, 2008; Tse et al., 2004), as repeated stimulation leads to a more efficient neural representation of the stimulus (e.g., Wiggs and Martin, 1998; Grill-Spector et al., 2006) and therefore repetition suppression, that is, decreased neural activation concurrent with repeated stimulation (e.g., Fahy et al., 1993; Rainer and Miller, 2000).

Horr and Di Luca (2015b, 2015c) recently showed that not only the amount of filling in an interval, but also the temporal structure of fillers can influence perceived duration: For example, regularly spaced (isochronous or rhythmic) tone sequences cause intervals to be perceived as longer compared to those with a random (anisochronous) filler spacing. A tendency that isochronously filled intervals are overestimated as compared to anisochronously filled intervals has also been reported by Thomas and Brown (1974) and Grimm (1934). Consistent with these findings, a recent study by Matthews (2013) showed that isochronously filled intervals are perceived longer than intervals filled with accelerating or decelerating sequences. Horr and Di Luca (2015b) further demonstrated that the bias toward overestimating isochronous intervals

---

* Corresponding author.
*E-mail address:* m.diluca@bham.ac.uk (M. Di Luca).

http://dx.doi.org/10.1016/j.neuroimage.2016.02.011
1053-8119/

increases with the number of stimuli per interval. They also showed that the isochrony bias is specific to regularity in time, as no distortions in duration are induced when varying regularity in non-temporal filler characteristics (e.g., sound intensity or pitch), as long as the average characteristics of sounds in irregular sequences are the same as for regular ones.

Although not as immediately obvious as for the filled duration illusion, the overestimation of isochronous stimulation may as well be in line with a neural magnitude approach of perceived duration. To understand why, we have to take a closer look at the phenomenon of neural entrainment: neural oscillations are assumed to adapt to the rhythm of regular stimulation, so that the expected arrival time of each stimulus consistently coincides with a specific phase of the entrained oscillation (e.g., Ding et al., 2006; Lakatos et al., 2008; Lakatos et al., 2007). The phase of neural oscillations has further been shown to modulate neural excitability (e.g., Canolty and Knight, 2010; Schroeder and Lakatos, 2009). Entrainment has been suggested to amplify the response to stimuli of interest which arrive at an expected time (and therefore during "high-excitability phases" of the oscillation) while attenuating all other stimulation (e.g., Cravo et al., 2013; Schroeder et al., 2008; Schroeder and Lakatos, 2009; Ng et al., 2012). Assuming that perceived duration increases with the neural response during the timed interval, isochronous intervals would then be overestimated because the neural response elicited by an isochronous sequence is higher than the response elicited by an anisochronous sequence. The higher neural response toward isochronous stimulation occurs because each stimulus in an isochronous sequence arrives at the point of maximal neural responsiveness, whereas in an anisochronous sequence the stimuli arrive at random points in the pattern of periodic excitability.

If the proposed entrainment mechanism is responsible for the overestimation of duration with isochronous intervals, we should be able to directly relate the amount of neural entrainment to the magnitude of overestimation in perceived duration. To test this hypothesis, we used electroencephalography (EEG) to record neural responses during a simple two-interval forced choice task in which each trial consisted of a pair of one isochronous and one anisochronous interval. We performed three tests of our specific entrainment hypothesis, using pairwise phase consistency (PPC, Vinck et al., 2010) as a measure of the degree to which the phase of the EEG consistently entrained to the regular external stimulation. First, we compared PPC between the isochronous versus the anisochronous sequences to demonstrate entrainment toward the frequency at which isochronous stimuli were presented (4 Hz). Second, we compared PPC between physically identical intervals to determine whether entrainment is higher during the presentation of intervals which subjectively appear to last longer. Third, we correlated the PPC effect of perceived duration with participants' general tendency to overestimate isochronous sequences.

## Methods

### Participants

Thirty students (25 females, 20.2 ± 3.2 years) from the University of Birmingham participated in the experiment for course credits or a payment of 6 GBP/h. Two participants were excluded due to their performance in the behavioral task (JND > 0.6). Another four participants had to be excluded because too few trials (<20) were left in at least one response condition after EEG artifact rejection. Data of 24 participants (21 females, 20.5 ± 3.5 years) were used for the analysis. As reported in the results section, behavioral data of participants excluded due to insufficient EEG trial numbers had a pattern in line with the overall behavioral findings. All participants were naive to the purpose of the experiment and reported normal auditory sensitivity. The experimental procedure and data collection followed the guidelines of the Declaration of Helsinki (2012), and the protocol was approved by the Science, Technology, Engineering and Mathematics Ethical Review Committee of the University of Birmingham.

### Experimental design and task

Participants were presented with two intervals per trial and had to decide which of the two was longer in duration (two-interval forced choice, 2IFC, Fig. 1a). Each interval consisted of five 1000 Hz 60 dB SPL tones of 10 ms duration with a 1 ms onset and offset tapering. Because the first sound marked the beginning of the interval and the last sound marked its end, a stimulus was presented on average every 250 ms, leading to an average stimulation frequency of 4 Hz. One of the two intervals to be compared within a trial was always isochronous, that is, the filler tones were equally spaced, while the other one was anisochronous, that is, had a random spacing of the filler tones. Anisochrony was created by randomly moving the onset of the filler tones in a range extending ± half the interstimulus interval in the isochronous sequence. The order of the isochronous and the anisochronous interval was pseudorandomized and counterbalanced between trials and trial types (see below). There was a random gap of 1.5 to 2 s between intervals.

In total, participants performed 272 duration comparisons arranged in four blocks of 68 trials each. In half of the trials, the isochronous and anisochronous intervals had an equal duration of 1000 ms. Only these trials were used for EEG analysis to exclude the influence of physical differences in interval durations and thus compare brain activation solely based on (1) temporal structures and (2) perceived duration. In the other half of the trials, the standard interval (either isochronous or anisochronous) was 1000 ms long, while the comparison interval lasted for 500, 700, 850, 1150, 1300, or 1500 ms (500 and 1500 ms 28 trials each, all others 20 trials each). Although EEG recordings from trials with varying interval durations were not analysed, these conditions were necessary to give participants a feasible task and assess their response proportions dependent on physical duration differences. Values for the points of subject equality (PSE) and the just noticeable differences (JND) were estimated as the first and second moment of each participants' individual data obtained with the Spearman–Kärber method (Miller and Ulrich, 2001). This was crucial to ensure that participants (1) were sufficiently able to perform the task (JND < 0.6) and (2) showed the previously observed bias (Horr and Di Luca, 2015b) toward judging isochronous intervals as longer than anisochronous intervals (PSE < 0).

### Procedure and EEG recording

Participants were seated 60 cm away from a switched-off computer screen whose centre was marked with a fixation point. Auditory stimuli were presented via one speaker positioned 20 cm underneath the fixation point. Responses were given with the right hand using the "left" and "right" buttons of a computer keyboard. Participants could begin each block by pressing the space button and every trial in a block would start randomly between 1200 and 1700 ms after they gave a response. Participants were instructed to avoid eye and muscle movements during the presentation of the auditory sequences. They were told to take a break for as long as they wanted between blocks and, if necessary, to take a short break between two trials by delaying their response. The experiment lasted between 30 and 40 min; 1.5 h were reserved to give participants detailed instructions on the task and recording procedure as well as to mount the EEG cap and electrodes.

EEG was recorded using an ActiveOne Biosemi System (BioSemi, Amsterdam, The Netherlands) with an EEG cap of 128 Ag/AgCl electrodes, including the standard locations of the extended international 10/5 system. Electrode offsets were kept below 50 mV. The signal was digitized at a rate of 2048 Hz and offline down-sampled

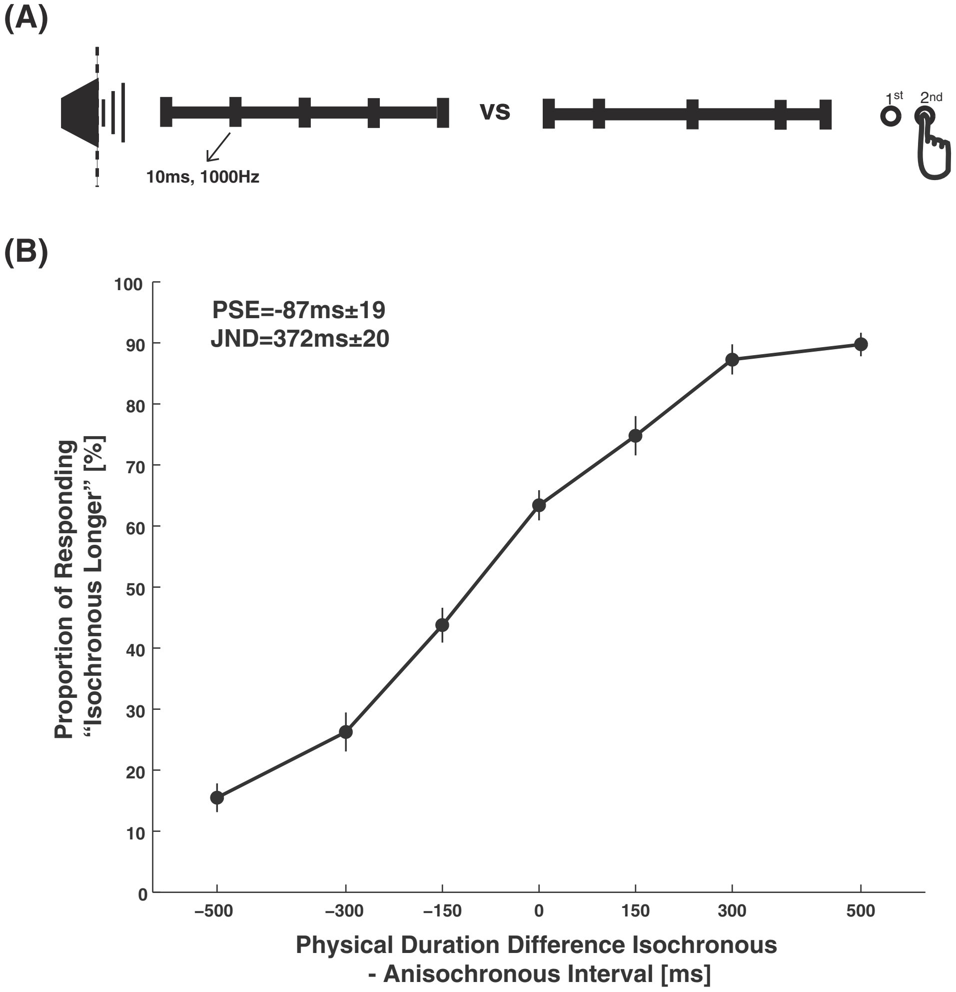


**Fig. 1.** Paradigm and behavioral results. (A) In a two-interval forced choice manner participants had to decide which of two intervals, one isochronous and one anisochronous, was longer in duration. The sequence of intervals was counterbalanced. (B) Response proportions are plotted as a function of the physical duration difference between the isochronous and anisochronous interval. Point of subjective equality (PSE) and just noticeable difference (JND) values were calculated as the first and second moment of the distribution using the Spearman–Kärber method.

to 500 Hz. Electrodes were re-referenced offline to the average over all non-rejected channels.

### *EEG Analysis*

Data were analysed using Matlab 8.1.0.604 (The MathWorks, Natick, Massachusetts) and the Matlab-based software package Fieldtrip (Oostenveld et al., 2011). The EEG signal was filtered between 1 and 30 Hz and down-sampled to 500 Hz. As explained above, only trials with two intervals of the same physical duration (1 s) were used for EEG analysis. From each trial two epochs were defined: the 1-s isochronous interval and the 1-s anisochronous interval. Each epoch contained the 1-s interval, plus pre- and poststimulus periods of 1500 ms (to allow for onset and offset effects of the filter for later time-frequency transformation). Noisy epochs and channels were rejected according to inspection of the raw data as well as semi-automatic visual inspection of outlier trials and channels. In order to compare between participants, rejected channels were interpolated by the average of their neighboring channels weighted by distance. No more than five channels had to be replaced for any participant. Eye artifacts were removed with principal component analysis using a logistic infomax ICA algorithm (Makeig et al., 1996).

Epochs were divided according to the following conditions: (1) temporal structure (i.e., isochronous or anisochronous) and (2) response (i.e., intervals perceived as longer or shorter). Participants for whom less than 20 trials per any condition remained after artifact rejection were excluded from further analysis. All four participants excluded for this reasons had too few trials in the isochronous perceived as shorter (= anisochronous perceived as longer) condition. For the remaining participants, the mean number of isochronous perceived as longer (= anichronous perceived as shorter) trials was 73.75 ± 18.8, and the mean number of isochronous perceived as shorter (= anisochronous perceived as longer) trials was 42.04 ± 13.85.

We used the measure of pairwise phase consistency (PPC, Vinck et al., 2010) in order to test for neural entrainment. The PPC is the average of the circular correlation between the phases of neural oscillations in each possible pairing of trials from two conditions. The time-frequency representation of the data and the phase angles to compute the PPC were obtained using complex Morlet wavelet convolution with 5 wavelet cycles to obtain a balanced frequency- and time-resolution (Cohen, 2014, pp. 170f), in a frequency range from 2 Hz to

20 Hz. On the basis of the respective phase angles, one PPC value can be calculated for each channel at each frequency and each point in time. With $N$ being the number of trials per condition and $\varphi$ and $\omega$ being the paired phase angles, the PPC is computed as

$$\mathrm{PPC} = \frac{2}{N(N-1)} \sum_{j=1}^{N-1} \sum_{k=j+1}^{N} \cos\left(\varphi_j\right) \cos(\omega_k) + \sin\left(\varphi_j\right) \sin(\omega_k).$$

External sensory stimulation typically leads to an increase of phase consistency between trials around stimulus onset (e.g., Brandt, 1997; Jansen et al., 2003). This increase may be due to phase reset of ongoing oscillations (e.g., Klimesch et al., 2007; Makeig et al., 2002), a neural population response leading to additive power (e.g., Jervis et al., 1983; Schroeder et al., 1995) or a combination of both (Min et al., 2007). While the phase consistency to a single stimulus rapidly decreases after stimulus onset as oscillations between trials quickly become out of phase, entrainment leads to a prolonged increase of phase coherence. This prolonged increase has been argued to reflect oscillations in the stimulus frequency being aligned to the regular stimulation (e.g., Schroeder et al., 2008).

The PPC was chosen over other measures of intertrial phase consistency since its magnitude is not affected by the number of trials per condition (Vinck et al., 2010). While other measures of intertrial phase consistency overestimate the population statistics with finite sample sizes, that is, are biased toward higher values for lower trial numbers, the PPC is independent of such bias. A bias-free measure was crucial in the present experiment, as participants' behavioral tendency toward judging isochronous intervals as longer in duration led to grossly unequal trial numbers for the two response options and equating trial numbers would have led to a substantial loss of statistical power. We present the results of the following analyses performed on the PPC data. (1) The PPC was compared between isochronous and anisochronous intervals using a cluster-based permutation test (Maris and Oostenveld, 2007) over all channels, frequencies, and time points. This allowed us to identify channels, frequencies and time points showing significant entrainment. (2) Intervals judged as longer and intervals judged as shorter (despite the same physical duration) were compared for channels and frequencies of interest as identified from the previous analysis. The two response options (longer or shorter) were compared separately for isochronous and anisochronous intervals using a running $t$-test with a moving 50 ms time window for the mean over the entrainment frequencies and channels (e.g., Schneider et al., 2008). (3) Participants' individual PPC difference between isochronous intervals judged as longer and as shorter was correlated with their PSE, that is, the overall behavioral tendency of judging isochronous intervals to last longer.

## Results

### *Behavioral results*

Participants' response proportions as a function of the physical duration difference between intervals is shown in Fig. 1b. The mean JND was 370 ms ± 20 ms, indicating a reasonable performance since the longest duration difference presented (500 ms) was reliably distinguishable. Note that data of two participants had to be excluded from analysis due to a JND higher than 600 ms.

The mean PSE was −87 ms ± 19 ms, indicating a significant overestimation in the duration of the isochronous interval (single sample $t$-test on PSE against 0: $t(23) = -4.5$, $p < 0.001$, $d = 1.87$). Note that participants excluded from analysis due to insufficient trial numbers after artifact rejection had PSEs of −11 ms, −200 ms, −155 ms and −86 ms, respectively, with a JND less than 600 ms, so each of them showed at least a slight bias toward judging isochronous intervals as longer, and excluding them did not change the conclusions from behavioral results. The overall overestimation of isochronous intervals was further confirmed by looking only at those trials in which the isochronous and anisochronous interval were of the same physical duration. For such trials participants judged, the isochronous interval as longer in 63.4% ± .4% of cases (single sample $t$-test on proportions against 50%: $t(23) = 5.4$, $p < 0.001$, $d = 2.25$).

### *EEG results*

In order to ensure that entrainment of neural oscillations toward regular auditory sequences was present in the EEG data, and to determine the channels and frequencies showing significant entrainment for our next analysis steps, we first examined the difference in PPC between isochronous and anisochronous intervals (see Fig. 2a for PPC overview over all channels; see Fig. S1a for the same contrast with the more commonly used measure of intertrial phase coherence, ITPC, that averages over all phase angle vectors within each condition). We compared isochronous and anisochronous intervals across the whole time span of interest from 250 ms (defining the average onset time of the second stimulus, and thus the earliest time at which entrainment can be expected) to 1000 ms, and frequencies from 2 to 20 Hz. As expected, the PPC for isochronous intervals is significantly increased around 4 Hz (3.5–4.5 Hz), the stimulation frequency, an effect present over 14 out of 128 channels. Furthermore, a significant PPC increase for isochronous intervals is found around 8 Hz (7.5–8.5 Hz) over 86 out of 128 channels (permutation-based statistics, cluster-corrected, $p < 0.05$, see Fig. 2b, c for topographies). The latter finding may be explained by the fact that 8 Hz is the second harmonic to the stimulation frequency. Entrainment to harmonic frequencies has been observed in previous research (e.g., Kim et al., 2007; Wimber et al., 2012). Using the mean over all entrainment channels at a given frequency, a running average $t$-test ($p > .05$, with 50 ms sliding time windows) revealed that PPC is significantly higher for isochronous as compared to anisochronous intervals from 450 to 750 ms at 3.5 to 4.5 Hz, and from 150 to 750 ms at 7.5 to 8.5 Hz (see Fig. 3a, d). Together, the contrast between isochronous and anisochronous intervals therefore produced the expected results in terms of entrainment toward isochronous auditory stimulation.

Next, we tested for an actual relation between entrainment and perceived duration, as determined by separating intervals according to participants' subjective perception. Specifically, we divided isochronous and anisochronous intervals according to whether they were perceived as longer or shorter than their respective counterpart in a given trial. Note that the two groups of trials compared here (perceived as longer and perceived as shorter) are of identical physical duration, and only differ in terms of participants' subjective estimates. When taking the mean over all significant entrainment channels, as displayed in Fig. 2b and c, we find a significantly higher PPC at the entrainment frequency (3.5–4.5 Hz) for regular intervals perceived as longer compared to regular intervals perceived as shorter. The effect is present between 550 and 700 ms after onset of the regular stimulation (running average $t$-test, $p < 0.05$ at every 50 ms time bin, mean over 3.5 to 4.5 Hz; see Fig. 3b; see Fig. S1b for the 3.5 to 4.5 Hz analysis of isochronous sequences using ITCP). This enhanced PPC with isochronous stimuli perceived to last longer hints at an increased entrainment as compared to regular intervals perceived as shorter. No significant effect between subjective judgments is found when comparing the same channels and intervals at the harmonic frequency (7.5–8.5 Hz, see Fig. 3e). With irregular intervals no differences were found either at 3.5 to 4.5 Hz or at 7.5 to 8.5 Hz (see Fig. 3c, f; see Fig. S1c for the 3.5 to 4.5 Hz analysis of anisochronous sequences using ITCP).

Given the well-known relationship between attention and perceived duration (see e.g., Grondin, 2010 for a review) and the finding that intertrial phase consistency has also been shown to be increased when voluntarily attending a stimulus sequence (Kashiwase et al., 2012; Kim et al., 2007), an additional analysis of frequency power, pre- and poststimulation, specifically focusing on alpha power, was carried out to address the possible concern that observed PPC effects

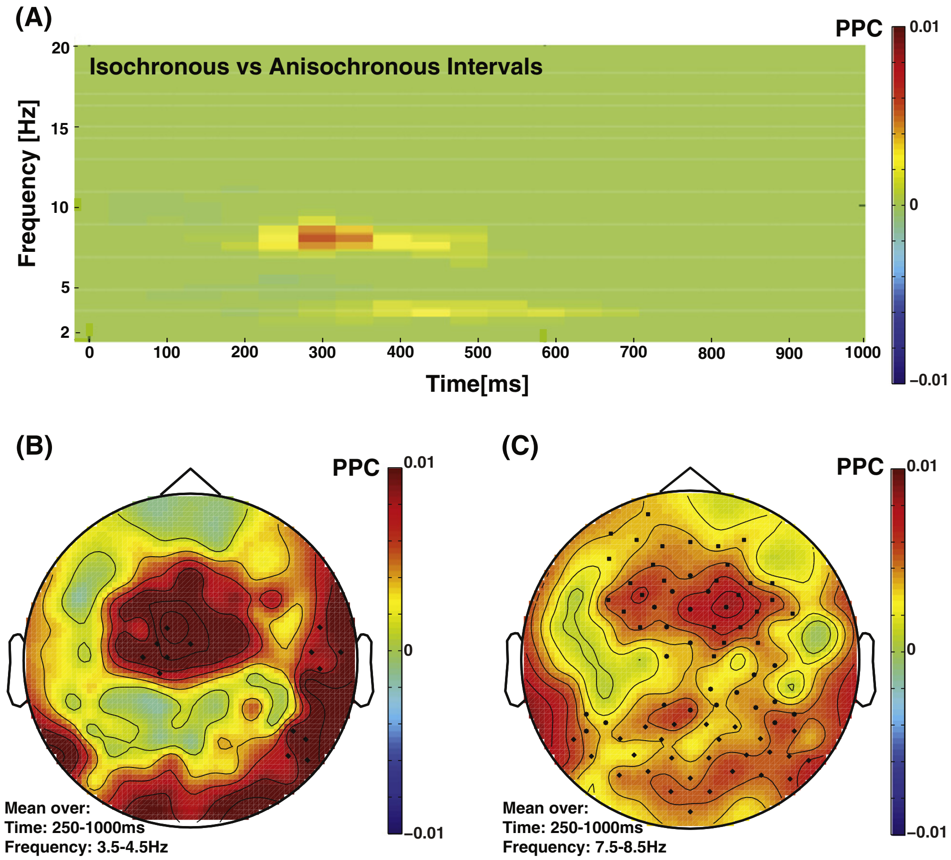


**Fig. 2.** Pairwise phase consistency (PPC) for isochronous and anisochronous intervals of the same duration. (A) Average PPC difference between isochronous and anisochronous intervals over all channels, masked so that only significantly different activation is shown ($p < 0.05$, permutation-based statistics, cluster-corrected). (B, C) Topographical plots of PPC distributions for the difference between isochronous and anisochronous intervals, between 250 and 1000 ms. Significant entrainment channels are marked with dots, (B) mean over 3.5–4.5 Hz, (C) mean over 7.5–8.5 Hz.

was based on random attentional fluctuations. This analysis is displayed in Fig. S2. Alpha power has been suggested as a neural index of top-down attention (Hanslmayr et al., 2011; Van Diepen et al., 2013). An increase in poststimulus alpha power (8 to 12 Hz) was found in the mean over entrainment channels (displayed in Fig. 2b and c) for anisochronous intervals judged as longer compared to shorter between 350 and 500 ms (see Fig. S2c). However, the contrasts with a differentiation in PPC, that is, the comparison between isochronous and anisochronous intervals (see Fig. S2a) as well as isochronous intervals judged as longer and shorter (see Fig. S2b), showed no significant difference in alpha power. Given there was a non-significant tendency of decreased prestimulus alpha power for isochronous intervals judged as longer compared to shorter, we checked for a correlation of the mean over alpha power (8 to 12 Hz) over the entrainment channels (displayed in Fig. 2b and c) between 800 and 200 ms before stimulus onset and the PPC effect in the time span of entrainment to isochronous stimulation from 450 to 750 ms. No significant correlation was found ($r(23) = -0.12, p = 0.56$).

Finally, we specifically tested whether the PPC difference dependent on participant's subjective report of stimulus duration (subjective PPC differentiation) is related to the general overestimation of isochronous sequences. To do so, we correlated participants' individual PSE values with the mean PPC difference between isochronous intervals perceived as longer and isochronous intervals perceived as shorter, over frequency-specific entrainment channels (displayed in Fig. 2b and c), and averaged across the time span of entrainment to isochronous stimulation. At the entrainment frequency (3.5–4.5 Hz, significant time span: 400–750 ms), there is a significant negative correlation between PSE and subjective PPC differentiation ($r(23) = -0.65, p < 0.001$; see Fig. 4a). At the second harmonic (7.5–8.5 Hz, significant time span: 150–750 ms) there is no correlation of the subjective PPC differentiation with the overall perceived duration bias ($r(23) = 0.12, p = 0.59$; see Fig. 4b), in accordance with the general lack of a subjective duration specific PPC effect at 7.5 to 8.5 Hz. Also the difference in prestimulus alpha power (8 to 12 Hz, 200 to 800 ms before stimulus onset) between isochronous intervals perceived as longer and isochronous intervals perceived as shorter, was not correlated with PSE ($r(23) = 0.19, p = 0.36$).

## Discussion

In the present experiment, we investigated the neural mechanisms underlying the overestimation of isochronous (temporally regular) as compared to anisochronous (temporally irregular) auditory sequences. More specifically, we tested whether neural entrainment toward stimuli that appear at regular points in time may mediate duration distortions driven by isochrony. This hypothesis arises from the proposal that perceived duration is linked to the magnitude of neural responses concurrent with the stimulation in the relevant interval (e.g., Eagleman and Pariyadath, 2009; Matthews et al., 2014). Neural entrainment has been shown to cause increased neural responsiveness toward temporally expected compared with unexpected stimuli and has been suggested as one possible neural mechanism by which temporal attention enhances stimulus processing (e.g., Lakatos et al., 2008). Based on these observations, we hypothesized that due to entrainment, higher average neural responses to stimuli presented in an isochronous than an anisochronous sequence would form the neural basis of behavioral distortions in perceived duration. The present results show an increase in pairwise phase consistency (PPC) for isochronous as compared to

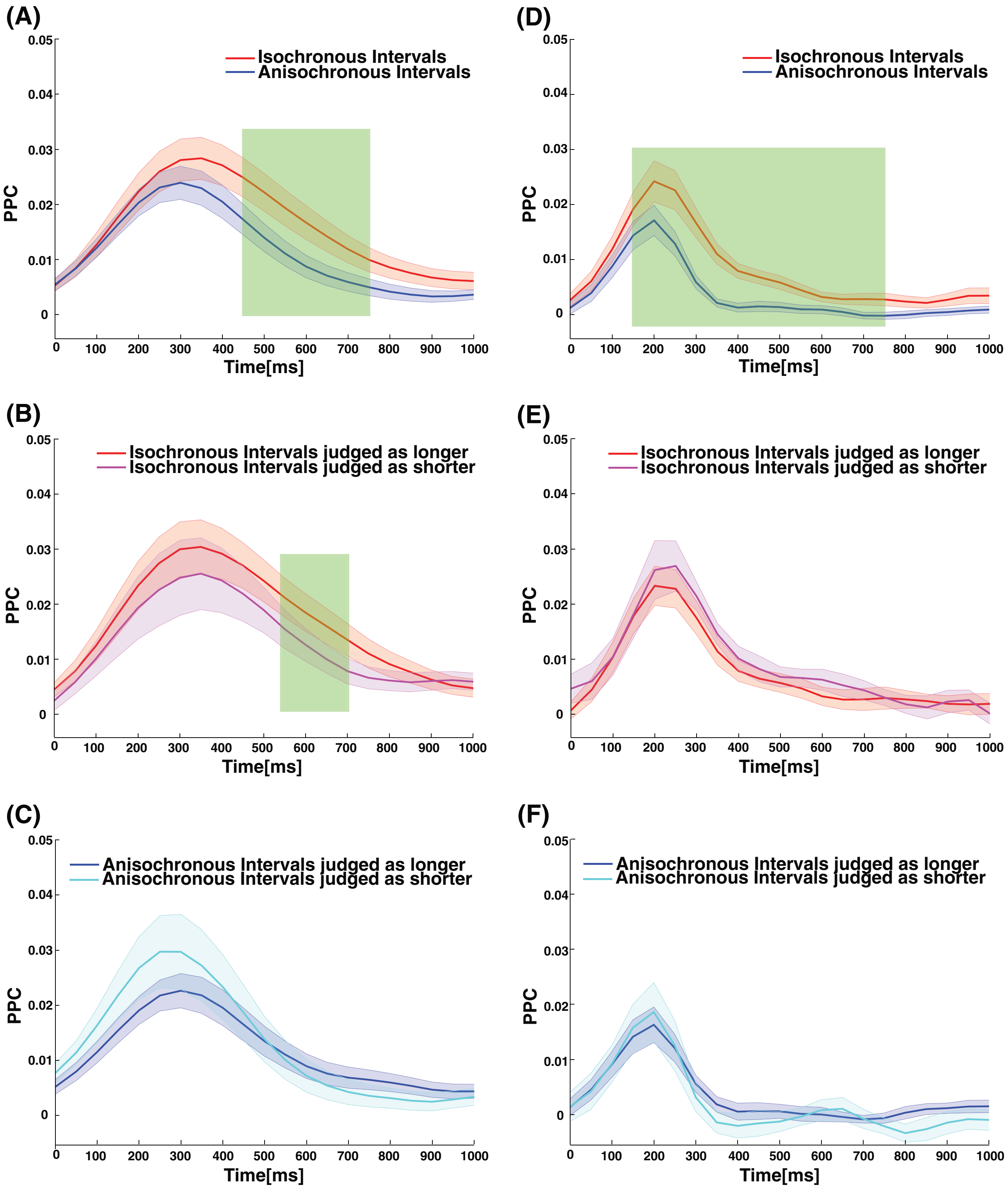


**Fig. 3.** Time course of PPC between 0 and 1000 ms, mean over all entrainment channels from the isochronous versus anisochronous contrast (see Fig. 2b and c) and the entrainment frequency (A–C) 3.5–4.5 Hz and (D–F) 7.5–8.5 Hz. (A and D) Isochronous and anisochronous intervals. (B and E) Isochronous intervals judged as longer and isochronous intervals judged as shorter than their anisochronous counterpart. (C and F) Anisochronous intervals judged as longer and anisochronous intervals judged as shorter than their isochronous counterpart. Green segments between the two conditions compared using a running average *t*-test ($p < 0.05$ at each 50 ms time bin).

anisochronous sequences around the entrainment frequency (4 Hz) and its second harmonic (8 Hz). This finding of increased oscillatory phase coherence in response to regular auditory stimulation strongly suggests that neural responses entrain toward the isochronous stimulation. Most interestingly, we found that over EEG channels showing general entrainment (in either frequency), the PPC at 3.5–4.5 Hz shows a significant increase between 500 and 750 ms for isochronous intervals that are perceived as longer compared to those that are perceived as shorter than their anisochronous counterparts. Note that latter effect can only be driven by perceptual differences, as there are no physical differences between the two intervals presented. An even stronger link to behavior is suggested by the finding that the same PPC effect

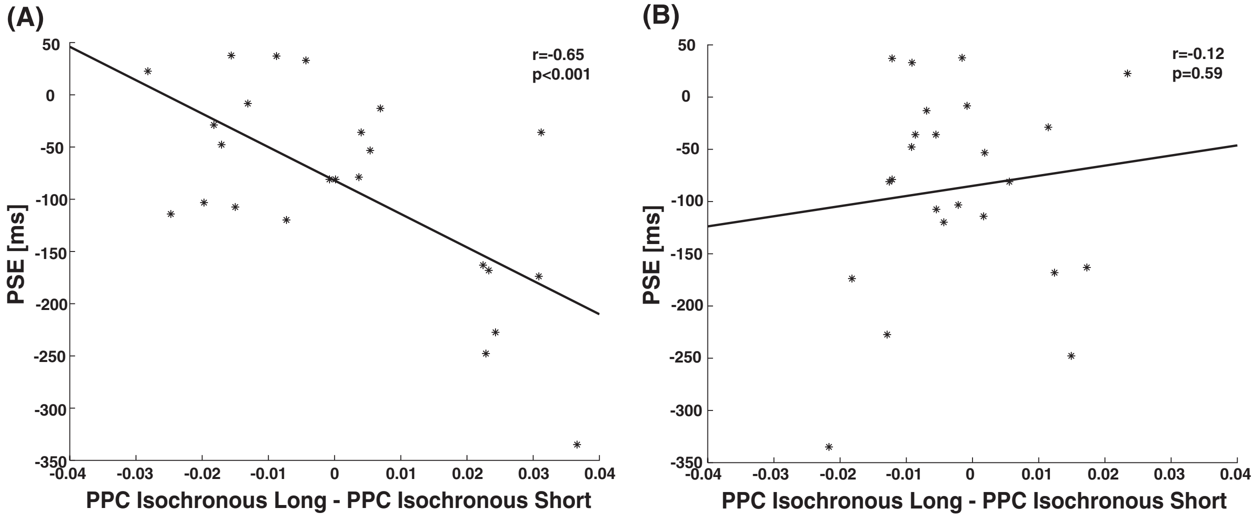


**Fig. 4.** Correlation between the PPC effect and the behavioral overestimation of the isochronous interval. The *x*-axis plots the difference between the mean PPC of isochronous intervals judged as longer versus shorter for (A) 3.5–4.5 Hz and 450–750 ms (time span of significant 3.5–4.5 Hz entrainment effect), averaged over the 3.5–4.5 Hz entrainment channels (see Fig. 2b), and (B) 7.5–8.5 Hz and 150–750 ms (time span of significant 7.5–8.5 Hz entrainment effect), averaged over the 7.5–8.5 Hz entrainment channels (see Fig. 2c). The *y*-axis represents the subject-by-subject PSE value in ms.

between isochronous intervals perceived as longer versus shorter is negatively related with a participant's point of subjective equality. That is, participants who show a larger average PPC difference between the isochronous intervals that are over- versus those that are underestimated also tend to show a larger overall bias toward overestimating isochronous (compared to anisochronous) intervals. These findings support the idea that neural entrainment, resulting in enhanced neural responsiveness, underlies our behavioral illusion of perceptually overestimating isochronous intervals.

A correlation between neural response magnitudes and perceived duration has been suggested on the basis of previous research on a behavioral as well as neural level. A plethora of behavioral findings demonstrates that the magnitude of stimulation occurring during a given interval influences its estimated duration. Such an increase of perceived duration with the magnitude of stimulation is shown in the filled duration illusion (e.g., Adams, 1977; Hasuo et al., 2014; Thomas and Brown, 1974) as well as the increase of perceived duration with an increased number of fillers in the sequence (Buffardi, 1971). Furthermore, perceived duration increases with stimulus intensity, size and number of stimuli (e.g., Berglund et al., 1969; Xuan et al., 2007) as well as with stimulus complexity (Roelofs and Zeeman, 1951; Schiffman & Bobko, 1974). Another commonly observed distortion of perceived duration is the oddball effect with deviant stimuli being perceived as longer than repeated ones (e.g., Birngruber et al., 2014; Chen and Yeh, 2009l; Kim and McAuley, 2013; Tse et al., 2004). Within a neural magnitude framework, the latter finding can be explained via a habituation of neural responses toward repeated stimulation, that is, repetition suppression (e.g., Fahy et al., 1993; Rainer and Miller, 2000), or vice versa increased attention and therefore increased neural responses to novel stimuli (e.g., Linden et al., 1999; Ranganath and Rainer, 2003). Finally, an increase of perceived duration with moving as compared to stationary stimuli has been reported (Brown, 1995) that may be explained via recruitment of additional neural networks, and therefore higher activation when perceiving motion (Dupont et al., 1994).

Behavioral findings indicating overestimation of duration for stimuli that lead to increased neural responses can only provide limited evidence toward the actual neural mechanisms underlying this perceptual bias. To confirm a neural relationship, neurophysiological studies are needed. Sadeghi et al. (2011) conducted an experimental task with moving dot stimuli. They showed that the stimuli moving in an unexpected direction (oddballs), which were overestimated in duration by human participants, elicited higher firing rates and response durations in neural recordings from middle temporal and visual cortex of awake monkeys. More direct evidence comes from Mayo and Sommer (2013) showing that neurons in the frontal eye field of monkeys, who were trained to classify an interval as longer or shorter than a reference stimulus, have higher firing rates during intervals judged as “long” as compared to those judged as “short.” Furthermore, Kononowicz and Van Rijn (2014) demonstrated that the amplitude of event-related-potentials (N1-P2 amplitude) in humans is a valid indicator for the subjective difference between target and reference stimuli and, unlike latency, amplitude difference correlates with perceived duration difference between the two stimuli. All these studies support the idea that neural response magnitudes are to some degree involved in the process leading to the estimate of duration with short intervals.

At a first glance, the overestimation of isochronous as compared to anisochronous stimulus sequences observed in the present and previous studies (Horr and Di Luca, 2015b) seems to be in conflict with magnitude-related overestimation due to, for example, novelty and complexity. If an entrained stimulus is temporally expected, why would it cause a bias similar to unexpected, deviant oddball stimuli? To answer this question, note that in traditional oddball paradigms, the deviant is embedded in a regular stimulation of repeated stimuli. The differentiation between predictability of stimulus characteristics and predictability of stimulus arrival in time is demonstrated by McAuley and Fromboluti (2014), showing that oddballs presented earlier than expected are actually underestimated in perceived duration, while overestimation is strongest for late oddballs. This influence of arrival time is diminished in an anisochronous stimulation sequence. Such results suggest that predictability in time should be investigated separately from effects of novelty and habituation. Neural entrainment has been proposed as a mechanism underlying attentional selection by modulating neural oscillations in relevant cortical assemblies to be in phase with regular stimulus presentation, and therefore enabling the highest neural responsiveness and behavioral accuracy at those points in time where the stimulus is expected (e.g., Cravo et al., 2013; Lakatos et al., 2008; Schroeder and Lakatos, 2009). This involvement, in turn, links back to the connection between neural response magnitudes and perceived duration of stimuli in an isochronous sequence.

The present study is, to our knowledge, the first to demonstrate a direct link between the strength of neural entrainment toward regular stimulation and the perceived duration of entrained intervals. It should be noted that the critical comparison in this work is based on completely identical stimulus sequences, so that the increase in PPC for isochronous sequences judged as longer relative to those judged as shorter is genuinely related to perceived rather than physical duration. In line with the suggested role of neural entrainment in improved processing of temporally predictable stimuli, as well as previous experimental findings supporting a relationship between neural response magnitudes and perceived duration, we interpret the present results within a neural response magnitude framework: Neural entrainment in regular sequences leads to an increased neural response toward each individual stimulus in the sequence, and therefore to higher average neural responses in isochronous intervals, which in turn increases duration estimates.

An alternative explanation for the connection between PPC and duration judgments may be along the lines of attentional mechanisms. As noted above, entrainment itself can be considered a mechanism of attentional selection (e.g., Lakatos et al., 2008), attentional markers like the P3b are influenced by regular stimulation (Schmidt-Kassow et al., 2009), and attention, in turn, is related to perceived duration (e.g., Grondin, 2010). In this respect, the idea that attention (as interconnected with entrainment and respective changes in neural response magnitudes) is related to the overestimation of isochrony is well in line with our interpretation of the data in a neural response magnitude framework of perceived duration. To minimize the possible concern that the PPC difference between intervals perceived as longer and intervals perceived as shorter is due to random fluctuations in attention (e.g., Kashiwase et al., 2012; Kim et al., 2007), we checked for differences in pre- and poststimulus alpha power over entrainment channels. Phases of low alpha power have been related to states of high responsiveness toward external stimulation while high alpha power is associated with low excitability phases (e.g., Hanslmayr et al., 2011; Klimesch et al., 2007; Mathewson et al., 2009). As shown in Fig. S2, for anisochronous intervals, an increase in alpha power over entrainment channels during intervals perceived as longer was found between 350 and 500 ms. This finding is surprising, as one would assume decreased alpha power being related to a state of higher attention toward external stimulation (e.g., Hanslmayr et al., 2011) and thereby longer perceived duration. Independent of how the difference in anisochronous intervals can be interpreted, the PPC effect for isochronous intervals perceived as longer versus those perceived as shorter is not paralleled by a significant difference in alpha power and alpha power. There is a non-significant tendency of decreased prestimulus alpha power for isochronous intervals perceived as longer; however, this tendency is not correlated with either the subject-wise PPC effect for isochronous intervals nor the subject-wise PSE. The present analysis of alpha power therefore makes an interpretation of the PPC effect solely based on random attentional fluctuations unlikely. Although beyond the scope of the present article, the observed poststimulus alpha effect in anisochronous sequences and the non-significant tendency for isochronous sequences may speak toward a role of attentional states in the current task and could be an interesting subject for future exploration.

Going back to the initial interpretation of the PPC increase being related to an increase in neural response magnitude and therefore increased perceived duration, it must be kept in mind that the present work does not provide a direct measure of neuronal firing. It can therefore only hint at neural response magnitudes being the modulating factor that leads to an influence of entrainment on temporal estimates. Future research should aim at clarifying the proposed relationship between neural response magnitudes, entrainment, and perceived duration, for example, by investigating the interaction between entrained (and non-entrained) stimulus presentation and other ways of modifying neural response magnitudes (e.g., stimulus intensity) regarding their effect on perceived duration. Future experiments should also attempt to establish a trial-to-trial relationship between entrainment and perceived duration, for which the present study did not have sufficient power, and take a closer look at how inter-individual differences in entrainment strength predict different perceived duration distortions. Furthermore, clarification is needed regarding entrained channels and frequency bands that are crucially influencing duration estimates. In the present data, when comparing isochronous versus anisochronous sequences, we found the expected increase of PPC around the stimulation frequency, 4 Hz, but even more channels showed an increase at the harmonic frequency, around 8 Hz (see Fig. 2B). An increase in the PPC, but no changes in power, around 8 Hz for isochronous as compared to anisochronous intervals, hints at the 8 Hz PPC effect also reflecting stimulus-driven entrainment rather than, for example, resonance with participants' intrinsic alpha rhythm. However, the difference in PPC between isochronous intervals judged as longer and those judged as shorter was present only at 3.5 to 4.5 Hz, but not 7.5 to 8.5 Hz, suggesting that entrainment at the fundamental frequency but not the second harmonic drives the behavioral overestimation of isochrony. Similarly, the correlation of the PPC difference due to perceived duration with the amount of behavioral overestimation of isochronous sequences was only present at 3.5 to 4.5 Hz over 3.5 to 4.5 Hz entrainment channels. The absence of a similar relationship between 7.5 and 8.5 Hz phase consistency and perceived duration may hint at a different functional role of the PPC increase in the harmonic frequency of isochronous stimulation (see, e.g., Campbell and Maffei, 1970; Di Russo et al., 2001; Kim et al., 2007 for a functional differentiation between fundamental and harmonic frequency in visual stimulation) and may put into question whether the latter is genuinely related to entrainment, or a different physiological mechanism. Future studies varying the stimulation frequency and testing whether entrained channels as well as the link with perceived duration differ between different frequency bands, and potentially interact with an individual's dominant theta and alpha frequencies, may be able to shed further light on this issue.

In sum, the present experiment is the first to show a direct link between neural entrainment and duration judgments. It thereby demonstrates that the overestimation of isochronous as compared to anisochronous auditory stimulation (Grimm, 1934; Horr and Di Luca, 2015b; Thomas and Brown, 1974) may be explained based on neural response magnitudes. We believe that the present approach is a good starting point for future research investigating how, and to which extent, the link between entrainment strength, neural response magnitude, and duration perception may explain different experimental findings regarding the influence of interval structure and temporal predictability on perceived duration.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2016.02.011.

## Acknowledgments

This research was funded by the Marie Curie Grant CIG 304235 "TICS."

## References

Adams, R.D., 1977. Intervening stimulus effects on category judgments of duration. Percept. Psychophys. 21, 527–534.

Berglund, B., Berglund, U., Ekman, G., Frankenhaeuser, M., 1969. The influence of auditory stimulus intensity on apparent duration. Scand. J. Psychol. 10, 21–26.

Birngruber, T., Schröter, H., Ulrich, R., 2014. Duration perception of visual and auditory oddball stimuli: does judgment task modulate the temporal oddball effect? Atten. Percept. Psychophys. 76, 814–828.

Brandt, M.E., 1997. Visual and auditory evoked phase resetting of alpha EEG. Int. J. Psychophysiol. 26, 285–289.

Brown, S.W., 1995. Time, change, and motion: the effects of stimulus movement on temporal perception. *Percept. Psychophys.* 57, 105–116.

Buffardi, L., 1971. Factors affecting the filled-duration illusion in the auditory, tactual, and visual modalities. *Percept. Psychophys.* 10, 292–294.

Campbell, F.W., Maffei, L., 1970. Electrophysiological evidence for the existence of orientation and size detectors in the human visual system. J. Physiol. 207, 635–652.

Canolty, R.T., Knight, R.T., 2010. The functional role of cross-frequency coupling. Trends Cogn. Sci. 14, 506–515.

Chen, K.M., Yeh, S.L., 2009. Asymmetric cross-modal effects in time perception. Acta Psychol. 130, 225–234.

Cohen, M.X., 2014. Analyzing neural time series data: theory and practice. MIT Press, Cambridge, Massachusetts.

Cravo, A.M., Rohenkohl, G., Wyart, V., Nobre, A.C., 2013. Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex. J. Neurosci. 33, 4002–4010.

Di Russo, F., Spinelli, D., Morrone, M.C., 2001. Automatic gain control contrast mechanisms are modulated by attention in humans: evidence from visual evoked potentials. Vis. Res. 41, 2435–2447.

Ding, J., Sperling, G., Srinivasan, R., 2006. Attentional modulation of SSVEP power depends on the network tagged by the flicker frequency. Cereb. Cortex 16, 1016–1029.

Dupont, P., Orban, G.A., De Bruyn, B., Verbruggen, A., Mortelmans, L., 1994. Many areas in the human brain respond to visual motion. J. Neurophysiol. 72, 1420–1424.

Eagleman, D.M., Pariyadath, V., 2009. Is subjective duration a signature of coding efficiency? Philos. Trans. R. Soc. Lond. B Biol. Sci. 364, 1841–1851.

Efron, R., 1970. The minimum duration of a perception. Neurophysiologia 8, 57–63.

Fahy, F.L., Riches, I.P., Brown, M.W., 1993. Neuronal activity related to visual recognition memory: long-term memory and the encoding of recency and familiarity information in the primate anterior and medial inferior temporal and rhinal cortex. Exp. Brain Res. 96, 457–472.

Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn. Sci. 10, 14–23.

Grimm, K., 1934. Der Einfluß der zeitform auf die wahrnehmung der zeitdauer. Z. Psychol. 132, 104–132.

Grondin, S., 2010. Timing and time perception : A review of recent behavioral and neuroscience findings. Atten. Percept. Psychophys. 72, 561–582.

Hanslmayr, S., Gross, J., Klimesch, W., Shapiro, K.L., 2011. The role of $\alpha$ oscillations in temporal attention. Brain Res. Rev. 67, 331–343.

Hasuo, E., Nakajima, Y., Tomimatsu, E., Grondin, S., Ueda, K., 2014. The occurrence of the filled duration illusion: A comparison of the method of adjustment with the method of magnitude estimation. Acta Psychol. 147, 111–121.

Horr, N.K., Di Luca, M., 2015a. Filling the blanks in temporal intervals: the type of filling influences perceived duration and discrimination performance. Front. Psychol. 6, 1–8.

Horr, N.K., Di Luca, M., 2015b. Taking a long look at isochrony: perceived duration increases with temporal, but not stimulus regularity. Atten. Percept. Psychophys. 77, 592–602.

Horr, N.K., Di Luca, M., 2015c. Timing rhythms: perceived duration increases with a predictable temporal structure of short interval fillers. PLoS One 10, e0141018.

Jansen, B.H., Agarwal, G., Hedge, A., Boutros, N.N., 2003. Phase synchronization of the ongoing EEG and auditory EP generation. Clin. Neurophysiol. 114, 79–85.

Jervis, B.W., Nichols, M.J., Johnson, T.E., Allen, E., Hudson, N.R., 1983. A fundamental investigation of the composition of auditory evoked potentials. IEEE Trans. Biomed. Eng. 30, 43–50.

Kashiwase, Y., Matsumiya, K., Kuriki, I., Shioiri, S., 2012. Time courses of attentional modulation in neural amplification and synchronization measured with steady-state visual-evoked potentials. J. Cogn. Neurosci. 24, 1779–1793.

Kim, E., McAuley, J.D., 2013. Effects of pitch distance and likelihood on the perceived duration of deviant auditory events. Atten. Percept. Psychophys. 75, 1547–1558.

Kim, Y.J., Grabowecky, M., Paller, K.,.A., Muthu, K., Suzuki, S., 2007. Attention induces synchronization-based response gain in steady-state visual evoked potentials. Nat. Neurosci. 10, 117–125.

Klimesch, W., Sauseng, P., Hanslmayr, S., Gruper, W., Freunberger, R., 2007. Event-related phase reorganization may explain evoked neural dynamics. Neurosci. Biobehav. Rev. 31, 1003–1016.

Kononowicz, T.W., van Rijn, H., 2014. Decoupling interval timing and climbing neural activity: A dissociation between CNV and N1P2 amplitudes. J. Neurosci. 34, 2931–2939.

Lakatos, P., Chen, C.-M., O'Connell, M.N., Mills, A., Schroeder, C.E., 2007. Neuronal oscillations and multisensory interaction in primary auditory cortex. Neuron 53, 279–292.

Lakatos, P., Karmos, G., Mehta, A.D., Ulbert, I., Schroeder, C.E., 2008. Entrainment of neuronal oscillations as a mechanism of attentional selection. Science 320, 110–113.

Linden, D.E., Prvulovic, D., Formisano, E., Vollinger, M., Zanella, F.E., Goebel, R., Dierks, T., 1999. The functional neuroanatomy of target detection: an fMRI study of visual and auditory oddball tasks. Cereb. Cortex 9, 815–823.

Makeig, S., Bell, A.J., Jung, T.-P., Sejnowski, T.J., 1996. Independent component analysis of electroencephalographic data. In: Touretzky, D., Mozer, M., Hasselmo, M. (Eds.), Advances in Neural Information Processing Systems, 8. MIT Press, Cambridge, MA, pp. 145–151.

Makeig, S., Westerfield, M., Jung, T.P., Enghoff, S., Courchesne, E., Sejnowski, T.J., 2002. Dynamic brain sources of visual evoked reponses. Trends Cogn. Sci. 8, 204–210.

Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164, 177–190.

Mathewson, K.E., Gratton, G., Fabiani, M., Beck, D.M., Ro, T., 2009. To see or not to see: prestimulus alpha phase predicts visual awareness. J. Neurosci. 29, 2725–2732.

Matthews, W.J., 2013. How does sequence structure affect the judgment of time? exploring a weighted sum of segments model. Cogn. Psychol. 66, 259–282.

Matthews, W.J., Terhune, D.B., Van Rijn, H., Eagleman, D.M., Sommer, M.A., Meck, W.H., 2014. Subjective duration as a signature of coding efficiency: emerging links among stimulus repetition, predictive coding and cortical GABA levels. Timing Time Percept. Rev. 1, 1–11.

Mayo, J.P., Sommer, M.A., 2013. Neuronal Correlates of Visual Time Perception at Brief Timescales. 110. PANAS, pp. 1506–1511.

McAuley, J.D., Fromboluti, E.K., 2014. Attentional entrainment and perceived event duration. Philos. Trans. R. Soc., B 369, 1–10.

Miller, J., Ulrich, R., 2001. On the analysis of psychometric functions: the Spearman–Kärber method. *Percept. Psychophys.* 63, 1399–1420.

Min, B.-K., Busch, N.A., Debener, S., Kranczioch, C., Hanslmayr, S., Engel, A.K., Herrmann, C.S., 2007. The best of both worlds: Phase-reset of human EEG alpha activity and additive power contribute to ERP generation. Int. J. Psychophysiol 65, 58–68.

Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell. Neurosci. 2011, 1–9.

Pariyadath, V., Eagleman, D.M., 2008. Brief subjective durations contract with repetition. J. Vis. 8, 1–6.

Rainer, G., Miller, E.K., 2000. Effects of visual experience on the representation of objects in the prefrontal cortex. Neuron 27, 179–189.

Rammsayer, T.H., Lima, S.D., 1991. Duration discrimination of filled and empty auditory intervals: cognitive and perceptual factors. *Percept. Psychophys.* 50, 565–574.

Ranganath, C., Rainer, G., 2003. Neural mechanisms for detecting and remembering novel events. Nat. Rev. Neurosci. 4, 193–204.

Roelofs, C.O., Zeeman, W.P., 1951. Influence of different sequences of optical stimuli on the estimation of duration of a given interval of time. Acta Psychol. 8, 89–128.

Sadeghi, N.G., Pariyadath, V., Apte, S., Eagleman, D.M., Cook, E.P., 2011. Neural correlates of subsecond time distortion in the middle temporal area of visual cortex. J. Cogn. Neurosci. 23, 3829–3840.

Schiffman, H.R., Bobko, D.J., 1974. Effects of stimulus complexity on the perception of brief temporal intervals. J. Exp. Psychol. 103, 156–159.

Schmidt-Kassow, M., Schubotz, R.I., Kotz, S., 2009. Attention and entrainment: P3b varies as a function of temporal predictability. Cogn. Neurosci. Neuropsychol. 20, 31–36.

Schneider, T.R., Debener, S., Oostenveld, R., Engel, A.,.K., 2008. Enhanced EEG gamma-band activity reflects multisensory semantic matching in visual-to-auditory object priming. NeuroImage 42, 1244–1254.

Schroeder, C.E., Lakatos, P., 2009. Low-frequency neuronal oscillations as instruments of sensory selection. Trends Neurosci. 32, 9–18.

Schroeder, C.E., Lakatos, P., Kajikawa, Y., Partan, S., Puce, A., 2008. Neuronal oscillations and visual amplification of speech. Trends Cogn. Sci. 12, 106–113.

Schroeder, C.E., Steinschneider, M., Javitt, D.C., Tenke, C.E., Givre, S.J., ... Vaughan Jr., H.G., 1995. Localization of ERP generators and identification of underlying neural processes. Electroencephalogr. Clin. Neurophysiol. 44, 55–75.

Tallon-Baudry, C., Bertrand, O., Delpuech, C., Pernier, J., 1996. Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. J. Neurosci. 16, 4240–4249.

Thomas, E.C., Brown, I., 1974. Time perception and the filled-duration illusion. Percept. Psychophys. 16, 449–458.

Tse, P.U., Intriligator, J., Rivest, J., Cavanagh, P., 2004. Attention and the subjective expansion of time. *Percept. Psychophys.* 66, 1171–1189.

Van Diepen, R.M., Cohen, M.X., Denys, D., Mazaheri, A., 2013. Attention and temporal expectations modulate power, not phase, of ongoing alpha oscillations. J. Cogn. Neurosci. 27, 1573–1586.

Vinck, M., Van Wingerden, M., Womelsdorf, T., Fries, P., Pennartz, C.M.A., 2010. The pairwise phase consistency: a bias-free measure of rhythmic neuronal synchronization. NeuroImage 51, 112–122.

Ng, B.S.W., Schroeder, T., Kayser, C., 2012. A precluding but not ensuring role of entrained low-frequency oscillations for auditory perception. J. Neurosci. 32, 12268–12276.

Wiggs, C.L., Martin, A., 1998. Properties and mechanisms of perceptual priming. Curr. Opin. Neurobiol. 8, 227–233.

Wimber, M., Maaß, A., Staudigl, T., Richardson-Klavehn, A., Hanslmayr, S., 2012. Rapid memory reactivation revealed by oscillatory entrainment. Curr. Biol. 22, 1482–1486.

Xuan, B., Zhang, D., He, S., Chen, X., 2007. Larger stimuli are judged to last longer. J. Vis. 7, 1–5.