Encoding of event timing in the phase of neural oscillations

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ABSTRACT

Time perception is a critical component of conscious experience. To be in synchrony with the environment, the brain must deal not only with differences in the speed of light and sound but also with its computational and neural transmission delays. Here, we asked whether the brain could actively compensate for temporal delays by changing its processing time. Specifically, can changes in neural timing or in the phase of neural oscillation index perceived timing? For this, a lag-adaptation paradigm was used to manipulate participants' perceived audiovisual (AV) simultaneity of events while they were recorded with magnetoencephalography (MEG). Desynchronized AV stimuli were presented rhythmically to elicit a robust 1 Hz frequency-tagging of auditory and visual cortical responses. As participants' perception of AV simultaneity shifted, systematic changes in the phase of entrained neural oscillations were observed. This suggests that neural entrainment is not a passive response and that the entrained neural oscillation shifts in time. Crucially, our results indicate that shifts in neural timing in auditory cortices linearly map participants' perceived AV simultaneity. To our knowledge, these results provide the first mechanistic evidence for active neural compensation in the encoding of sensory event timing in support of the emergence of time awareness.

Introduction

While dedicated neural structures for time perception have been described (Buhusi and Meck, 2005; Coull et al., 2004; Harrington et al., 1998; Ivry and Schlerf, 2008; Morillon et al., 2009; Treisman et al., 1990; van Wassenhove, 2009; Wittmann, 2009, 2013), the encoding of sensory event timing has been proposed to result from the intrinsic dynamics of neural populations not necessarily dedicated to temporal processing (Johnston and Nishida, 2001; Karmarkar and Buonomano, 2007; van Wassenhove, 2009). For instance, the timing of a colored visual patch could be encoded in the dynamics of the neural population dedicated to the analysis of color (Karmarkar and Buonomano, 2007; Moutoussis and Zeki, 1997). In this non-dedicated view, the latency of neural responses could provide an index for event timing (Johnston and Nishida, 2001; Zeki and Bartels, 1998). Under this latency code hypothesis, timing mechanisms are based on the changes of neural routing delays in sensory areas coding for a specific sensory attribute (Moutoussis and Zeki, 1997; Zeki and Bartels, 1998). To date however, electroencephalographic (EEG) studies have reported little-to-no

correspondence between neural latencies and participants' perceived timing (McDonald et al., 2005; Vibell et al., 2007), and rather suggest that it is the phase of neural oscillations that plays a crucial role in the encoding of visual event timing (Chakravarthi and Vanrullen, 2012; Gho and Varela, 1988).

We here provide further evidence that the encoding of event timing is realized in the phase of neural oscillations (in auditory cortex). It is well known that distinct phases of low-frequency neural oscillations are associated with periods of high and low neural excitability (Buzsáki, 2010; Lakatos et al., 2008). These fluctuations have been shown to impose temporal constraints on the "what" of perception by modulating the perceptual detection threshold of various stimuli (Busch et al., 2009; Fiebelkorn et al., 2013; Henry and Obleser, 2012; Monto et al., 2008; Neuling et al., 2012). They have also been proposed to serve parsing and informational chunking of sensory information over time (VanRullen and Koch, 2003) notably for complex temporal structures such as speech (Giraud and Poeppel, 2012). Indeed, neural oscillations are known to be entrained to external rhythms (Rees et al., 1986; Regan, 1966) and this entrainment may allow the alignment of cortical processing to the timing of sensory events (Giraud and Poeppel, 2012; Schroeder and Lakatos, 2009). As such, this mechanism naturally provides a means for the brain to internalize external temporal regularities (Schroeder and Lakatos, 2009). In line with this proposal, the phase of low-frequency neural oscillations has been

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shown to reflect temporal expectancy or predictability of event timing (Stefanics et al., 2010). Here, we hypothesize that the brain could use oscillatory entrainment to establish a temporal reference frame and we thus ask whether the phase of entrained neural oscillations actually encodes the "when" of perception. Specifically, the preferred phase of oscillatory entrainment is known to be context-dependent (Besle et al., 2011; Gomez-Ramirez et al., 2011; Lakatos et al., 2008; Rees et al., 1986), suggesting that neural entrainment may not be a passive neural response. Additionally, preferential phases of entrained neural oscillations are subject-specific (Besle et al., 2011), making this neural index particularly well-suited for investigating the highly subjective and variable nature of time perception.

To test the specific hypothesis that the phase of an entrained neural oscillation directly informs on the variability of conscious timing, we transiently shifted participants' perceived timing using a lag-adaptation paradigm (Fujisaki et al., 2004; Miyazaki et al., 2006; Vroomen et al., 2004). Fig. 1 provides an overview of the experimental paradigm. During the induced changes of perceived timing, participants' brain activity was recorded with magnetoencephalography (MEG). During a given lag-adaptation block, audiovisual stimuli were presented rhythmically to induce an entrainment of oscillatory activity in sensory cortices. Analysis of MEG data showed that the preferential phase of entrained neural oscillations shifted during adaptation. Crucially, phase shifts of neural oscillatory entrainment in auditory cortex mirrored individuals' perceived simultaneity.

Fig. 1. Experimental design. (A) Three different audiovisual (AV) lag-adaptations were tested: simultaneous AV presentation (S, black), sound leading visual by 200 ms (A200V, red) and visual leading sound by 200 ms (V200A, green). Each lag-adaptation block was followed by a temporal order judgment (TOJ) block during which participants reported which of the auditory or visual event occurred first. One MEG session comprised eight blocks of each lag-adaptation (S, V200A and A200V). S blocks were run at the beginning and at the end of the MEG session; A200V and V200A alternated within the session. (B) In all lag-adaptation blocks, 65 AV stimuli were presented at an average rate of 1 Hz with a random jitter of +/−100 ms. This experimental manipulation was designed to elicit neural entrainment at 1 Hz in sensory cortices.

Materials and methods

Participants

Nineteen participants (7 females, mean age: 24 years old) took part in the study. All had normal or corrected-to-normal vision, normal color vision and normal hearing, and were naive as to the purpose of the study. Each participant provided a written informed consent in accordance with the Declaration of Helsinki (2008) and the Ethics Committee on Human Research at NeuroSpin (Gif-sur-Yvette, France). Three subjects were excluded from the study: one subject did not finish the experiment, and two were unable to perform the temporal order judgment task properly. A total of sixteen participants were thus considered for MEG analyses.

Stimuli

The experiment was written in Matlab using the Psychophysics toolbox (Brainard, 1997). Visual stimuli consisted of disks lasting 16.7 ms (1 frame). A visual annulus (9.5° of visual angle) consisted in the superposition of circles with different shades of gray. Visual stimuli were projected at a 60 Hz refresh rate onto a screen placed 90 cm away from participants seated under the MEG dewar. Auditory stimuli consisted of 16 ms duration white noise (incl. 5 ms fade-in and fade-out). Auditory stimuli were presented via Etymotic earphones (Etymotic Research Inc., USA).

Procedure

Two types of blocks were used in this experiment namely, lag-adaptation (3 conditions: S, A200V or V200A) and temporal order judgment (TOJ) blocks. In the lag-adaptation blocks (Fig. 1B), a series of simultaneous (S) or desynchronized audiovisual events were displayed (A200V: audition leading vision by 200 ms or V200A: vision leading audition by 200 ms). During the lag-adaptation block, a stream of 65 AV stimuli was presented. The stream of AV events was displayed at an average rate of 1 Hz; the stimulus onset asynchrony (SOA) between two successive auditory or visual stimuli was randomly chosen from a normal distribution with a mean of 1 s and a standard deviation of 100 ms: thus, each SOA has 95% probability to fall between 804 ms and 1196 ms. The first 20 AV events and the last 15 AV events in the stream were made up of stimuli with a constant temporal lag. Three lags were tested: in the S condition, AV stimuli were synchronously displayed (lag = 0 ms); in the A200V condition, the sound preceded the visual stimulus by 200 ms and in the V200A condition, the visual stimulus preceded the sound by 200 ms. During the lag-adaptation block, participants were asked to count the number of temporal deviants that were introduced in the middle part of the lag-adaptation block. Temporal AV deviants consisted of desynchronized AV stimuli that deviated from the constant lag introduced at the beginning of the block. This task was introduced to insure that participants attended the temporal dimension of the AV stream which was reported to enhance temporal recalibration effects (Heron et al., 2010). Crucially however, only the first 20 and last 15 AV stimuli are reported here namely the periods during which no temporal deviants were introduced. Each lag-adaptation block was systematically followed by a TOJ in which participants' subjective simultaneity of AV events was evaluated. In the TOJ blocks, AV stimuli were displayed with delays ranging from +/−317, +/−217, +/−133, +/−67, to 0 (a negative delay corresponds to the auditory leads and a positive delay corresponds to the visual leads). After each presentation of an AV pair, participants had to judge which of the sound or the visual event appeared first in a two alternative forced choice (2-AFC). Each condition was tested four times leading to a total of 36 trials in the TOJ blocks. The experiment started and ended with 4S blocks (i.e. 4 times 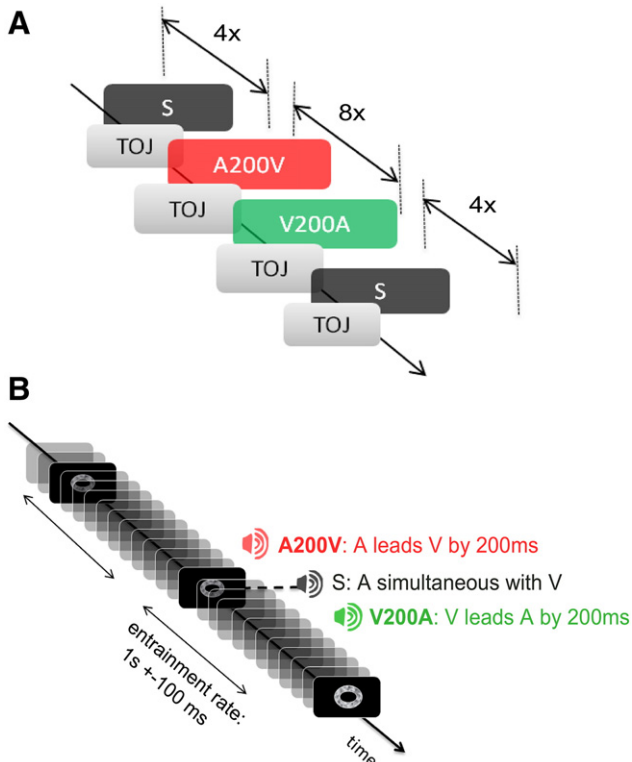S + TOJ). Other blocks were alternated between