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Neural responses to perturbations in visual and auditory metronomes during sensorimotor synchronization

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ABSTRACT

Tapping in synchrony to an isochronous rhythm involves several key functions of the sensorimotor system including timing, prediction and error correction. While auditory sensorimotor synchronization (SMS) has been well studied, much less is known about mechanisms involved in visual SMS. By comparing error correction in auditory and visual SMS, it can be determined if the neural mechanisms for detection and correction of synchronization errors are generalized or domain specific. To study this problem, we measured EEG while subjects tapped in synchrony to separate visual and auditory metronomes that both contained small temporal perturbations to induce errors. The metronomes had inter-onset intervals of 600 ms and the perturbations where of 4 kinds: ± 66 ms to induce period corrections, and ± 16 ms to induce phase corrections. We hypothesize that given the less precise nature of visual SMS, error correction to perturbed visual flashing rhythms will be more gradual than with the equivalent auditory perturbations. Additionally, we expect this more gradual error correction will be reflected in the visual evoked potentials. Our findings indicate that the visual system is only capable of more gradual phase corrections to even the larger induced errors. This is opposed to the swifter period correction of the auditory system to large induced errors. EEG data found the peak N1 auditory evoked potential is modulated by the size and direction of an induced error in line with previous research, while the P1 visual evoked potential was only effected by the large late-coming perturbations resulting in reduced peak latency. Looking at the error response EEG data, an Error Related Negativity (ERN) and related Error Positivity (pE) was found only in the auditory + 66 condition, while no ERN or pE were found in any of the visual perturbation conditions. In addition to the ERPs, we performed a dipole source localization and clustering analysis indicating that the anterior cingulate was active in the error detection of the perturbed stimulus for both auditory and visual conditions in addition to being involved in producing the ERN and pE induced by the auditory + 66 perturbation. Taken together, these results confirm that the visual system is less developed for synchronizing and error correction with flashing rhythms by its more gradual error correction. The reduced latency of the P1 to the visual + 66 suggests that the visual system can detect these errors, but that detection does not translate into any meaningful improvement in error correction. This indicates that the visual system is not as tightly coupled to the motor system as the auditory system is for SMS, suggesting the mechanisms of SMS are not completely domain general.

1. Introduction

Tapping in synchrony to a rhythmic stimulus like a metronome involves the use of several key components of the sensorimotor system including time, prediction, and error correction. Finger tapping has been widely used to study sensorimotor functions and abilities, especially with auditory sensorimotor synchronization (Repp, 2005). Behavioral studies of finger tapping have contributed to our understanding of how movement trajectories contribute to error correction in motor timing (Balasubramaniam et al., 2004; Hove et al., 2014). Recently, neuroimaging techniques have also been used to build understanding of the neural basis of error correction in sensorimotor synchronization (SMS) using EEG (Praamstra et al., 2003; Jang et al., 2016) By studying the neural processes involved in visual and auditory SMS, the two modalities can be compared, and thus tested to see to what extent the neural mechanisms of SMS are modality specific or generalized.

To understand the differences between auditory and visual SMS we must first understand the differing capabilities between the two. One of the largest differences is the greater variability of the timing of taps

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with visual SMS (Repp, 2005). In addition to the differences in tapping variability, there are different limits to the tempo at which a stimulus can be entrained to; an auditory metronome can be synchronized to an interonset interval (IOI) as low as 100 ms, while the lower IOI limit for accurate visual synchronization to a flashing stimulus is around 500 ms (Repp, 2005). Even though there are clear differences in synchronization ability between the visual and auditory domains, it remains to be seen exactly why those differences exist.

Another important aspect of synchronizing movements to rhythmic stimulus is error detection and correction. Monitoring of the timing of each stimulus and of the synchronized movements is necessary to ensure continued synchronization. Since any movement action takes time from initiation to completion, the timing of each stimulus must be predicted in advance (Chen et al., 1998). The prediction of the onset of each oncoming event then allows for a comparison of the predicted timing with the actual timing for error detection in the stimulus. Errors of synchronization must be monitored for in addition to errors in the stimulus before error correction can occur. To study the nature of error correction in SMS, occasional temporal perturbations in an otherwise isochronous stimulus have been used to induce errors (Thaut et al., 1998; Repp, 2000, 2001), and a two-level system of error correction has been put forward (Vorberg and Wing, 1996). The models posit that error correction falls into two types: Period correction and Phase correction. A period correction occurs in response to a large, noticeable error in timing, and involves updating a central time keeper. A phase correction takes place in response to a small error in timing that is below the conscious threshold and is thought to involve a more peripheral adaptive process (Repp, 2001; Repp and Keller, 2004).

To understand the neural mechanisms involved in error correction in SMS, previous work on auditory error correction has shown a modulation of the auditory-evoked potentials believed to modulate attention in response to errors in the timing of an otherwise isochronous auditory rhythm (Tecchio et al., 2000; Praamstra et al., 2003). The auditory evoked potentials, in this case the auditory P1 and N1, have shown that both the direction of the induced error, and the magnitude of the error modulate the components (Praamstra et al., 2003). In addition to the sensory evoked potentials, error induced potentials have been found in response to synchronization errors caused by perturbing the timing of a metronome (Praamstra et al., 2003). The error related components, the Error Related Negativity (ERN) and associated Error Related Positivity (Pe) have been shown to be indicative of detection of response errors, allowing for another measure of the error response (Yeung et al., 2004).

This study explores the differences in auditory and visual SMS error correction, as well as the correlating neural substrates. By measuring EEG while synchronizing finger taps with separate auditory and visual flashing metronomes, both with occasional timing errors, we can measure behavioral and neural differences between the two sense modalities. We hypothesize that since the visual system does not facilitate the same temporal precision in synchronizing to a visual flashing metronomes as the auditory system facilitates with an auditory metronome that error correction in the visual system will be a more gradual phase correction, even for larger perturbations. We further expect this reduced error correction ability to be reflected in a diminished modulation of the visual evoked components compared to the auditory evoked components, as well as reduced error response components.

2. Materials and methods

2.1. Participants

Ten subjects participated in the experiment (6 females; ages 18–34). All participants were right handed. Data from 4 additional subjects were collected but not included in analysis because they were unable to synchronize with the visual stimulus. All participants had normal hearing and normal or corrected vision. Participants gave informed consent after the experimental procedures where explained. This study was approved by the Institutional review board (IRB) for research ethics and human subjects. To estimate sample size, we used power computations for an analysis of variance using G*Power (Faul et al., 2009). Sample size estimation showed a minimum sample of 8 subjects would be necessary for a large effect size (.4), as seen in previous experiments by Praamstra et al. (2003). In this study, all analyses were performed to detect a significant effect at the $\alpha = .05$ level, thus indicating that our sample size of 10 to be more than adequate.

2.2. Task

Participants were asked to tap in synchrony to separate auditory and visual metronomes with an inter-onset interval (IOI) of 600 ms. The 600 ms interval (standard IOI) was chosen because a faster visual metronome is difficult for most people to synchronize to (Repp and Su, 2013). In both sequences, there were occasional perturbations of the duration of the IOI. There were four types of perturbations; increasing the standard IOI by 16 ms, or by 66 ms; and decreasing the standard IOI by 16 ms, or by 66 ms. The intervals were chosen based on the Praamstra et al. (2003) protocol and increased to scale with the larger IOI (600 ms compared to 500 ms), and due to the limitations of the 60 Hz monitor used in the study.

The experiment was split into the auditory condition and the visual condition, with a counterbalanced design so half of the subjects did the auditory condition first, and half did the visual condition first, but never on the same day. Each half of the experiment consisted of 120 blocks, with each block consisting of sequences of 50 stimuli with a minimum of 3 s between each block. Each sequence contained 4 perturbations, with the perturbation in a given sequence always of one type. The temporal location of the perturbations was varied to avoid being predictable, with a minimum of 9 non-perturbed stimuli between perturbations. Subjects were given a 10-min break at the halfway point of each condition. The experiment began with applying the EEG cap after written consent was obtained. Subjects were then given written instructions for the experiment, and performed one practice block that contained shifts of each type before starting.

The auditory stimuli consisted of 50 ms 1000-Hz pure tones with a 10 ms rise time and 30 ms fall time presented through headphones at a comfortable volume. The visual stimuli consisted of a 50 ms gray flash on a black screen. Subjects faced a monitor while seated with the screen 65 cm away from the participants' head. For both conditions, the screen was black with a gray fixation cross consisting of two lines approximately 3 mm wide and each 4 cm long arranged perpendicular to each other in a cross fashion, that remained constant. The flashes in the visual condition where a shade of gray lighter than the fixation cross and 3 cm x 3 cm square (as measured on screen) in the center of the screen. The flashes appeared behind the fixation cross so that the fixation cross was always visible. Gray was chosen instead of a brighter color to help reduce the after-image effect. Tapping was performed with the index finger of the right hand on a metal plate attached to a Makey Makey input device that records tapping by sending a small electrical signal to an output lead that the subject holds on their left hand. An input lead for the Makey Makey was then attached to a metal plate that the subject tapped. When the subject touched the metal plate, it completed a circuit in the Makey Makey which sends the signal to the computer to indicate a tap (Collective and Shaw, 2012). Subjects performed the task while seated in a comfortable chair.

2.3. EEG data acquisition and processing

EEG was continuously recorded with an ANT-Neuro 32 electrode cap with electrodes placed according to the 10–20 International electrode system and recorded at 1024 Hz. The EEG data were uploaded and processed with EEGLAB (Delorme and Makeig, 2004), and the ERP