

A common representation of time across visual and auditory modalities

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ARTICLE INFO

Keywords:

Time perception
Multivariate pattern analysis
EEG
Vision
Audition

ABSTRACT

Humans' and non-human animals' ability to process time on the scale of milliseconds and seconds is essential for adaptive behaviour. A central question of how brains keep track of time is how specific temporal information across different sensory modalities is. In the present study, we show that encoding of temporal intervals in auditory and visual modalities are qualitatively similar. Human participants were instructed to reproduce intervals in the range from 750 ms to 1500 ms marked by auditory or visual stimuli. Our behavioural results suggest that, although participants were more accurate in reproducing intervals marked by auditory stimuli, there was a strong correlation in performance between modalities. Using multivariate pattern analysis in scalp EEG, we show that activity during late periods of the intervals was similar within and between modalities. Critically, we show that a multivariate pattern classifier was able to accurately predict the elapsed interval, even when trained on an interval marked by a stimulus of a different sensory modality. Taken together, our results suggest that, while there are differences in the processing of intervals marked by auditory and visual stimuli, they also share a common neural representation.

Introduction

The ability to estimate time is essential for humans and non-human animals to interact with their environment (Buhusi and Meck, 2005; Mauk and Buonomano, 2004; Merchant et al., 2013a). Intervals in the range of hundreds of milliseconds to seconds are critical for sensory and motor processing, learning, and cognition (Buhusi and Meck, 2005; Mauk and Buonomano, 2004; Merchant et al., 2013a). However, the mechanisms underlying temporal processing in this range are still largely discussed. A central unanswered question is whether temporal processing depends on dedicated or intrinsic circuits (Ivry and Schlerf, 2008). Dedicated models propose that temporal perception depends on central specialised mechanisms, as an internal clock, that create a unified perception of time (Ivry and Schlerf, 2008). This class of models can account for behavioural findings such as correlations in performance for some temporal tasks (Keele et al., 1985) and the observation that learning to discriminate a temporal interval in one sensory modality can sometimes be transferred to other modalities (Bueti and Buonomano, 2014).

Intrinsic models of time propose that a variety of neural circuits distributed across the brain are capable of temporal processing. One of the most known examples is the state-dependent network - SDN (Mauk

and Buonomano, 2004). Within this framework, neural circuits can take advantage of the natural temporal evolution of its states to keep track of time (Mauk and Buonomano, 2004). One of the main advantages of such models is that they can explain the known differences of temporal processing across sensory modalities (van Wassenhove, 2009) and that learning a specific interval does not commonly improve temporal performance in other intervals (Bueti and Buonomano, 2014).

Given that both dedicated and intrinsic views can account for some results while not explaining others, there has been an increase in interest in hybrid models, according to which local task-dependent areas interact with a higher central timing system (Merchant et al., 2013a; Wiener et al., 2011). The main advantage of hybrid models is that they can explain why performance in some timing tasks seems to be correlated across participants, while still exhibiting modality and task-related differences (Merchant et al., 2008b, 2008a).

In humans, studies that investigate these different models employ a variety of methods, such as behavioural, neuroimaging and neuropharmacological manipulations, on healthy participants and neurological patients (Coull et al., 2011; Ivry and Schlerf, 2008; Kononowicz et al., 2016; Merchant et al., 2013a; Wiener et al., 2011). Although the high temporal resolution of EEG should in principle be optimal to track neural processing during temporal tasks, the contribution of these

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methods has been controversial. One of the main difficulties is the absence of a clear electrophysiological correlate of temporal processing (for a recent review see (Kononowicz et al., 2016)). This lack of electrophysiological markers makes it hard to judge, for example, whether temporal processing in different modalities share a common representation (N'Diaye et al., 2004).

In a recent study, we have shown that multivariate pattern analysis (MVPA) can reveal spatiotemporal dynamics of brain activity related to temporal processing (Bueno et al., 2017). Multivariate approaches can take advantage of small differences in the signal across electrodes that might not be detectable using classical EEG methods. These pattern recognition methods allow the assessment of whether brain states evoked by different tasks, stimuli and sensory modalities are qualitatively similar.

In the present study, we investigated whether encoding of temporal intervals in different sensory modalities is qualitatively similar. Our behavioural results suggest that, although participants are more accurate in reproducing intervals marked by auditory stimuli, there is a strong correlation over observers in performance between modalities. Critically, we show that a multivariate pattern classifier based on EEG activity can predict the elapsed interval, even when trained on an interval marked by a different sensory modality. Taken together, our results suggest that, while there are differences in the processing of intervals marked by auditory and visual stimuli, they also share a common neural representation.

Materials and methods

Participants

Twenty volunteers (age range, 18–30 years; 11 female) gave informed consent to participate in this study. All of them had normal or corrected-to-normal vision and were free from psychological or neurological diseases. The experimental protocol was approved by The Research Ethics Committee of the Federal University of ABC. All experiments were performed in accordance with the approved guidelines and regulations.

Experimental design

The experiment consisted of a temporal reproduction task. The stimuli were presented using the Psychtoolbox v.3.0 package (Brainard, 1997) on a 20-in. CRT monitor with a vertical refresh rate of 60 Hz, placed 50 cm in front of the participant.

Each trial started with a fixation point that participants fixated throughout the trial. After a delay (1.5 s), two flashes or tones were presented, separated by a sample interval (measured between tone or flash onsets). After a random delay (1.5–2.5 s), volunteers were re-exposed to the same interval. After another random delay (1.5–2.5 s), a ready stimulus was presented to the participant, indicating the beginning of the reproduction task 1. Volunteers had to reproduce the exposed interval, initiated by the ready stimulus (RS) and ended by a

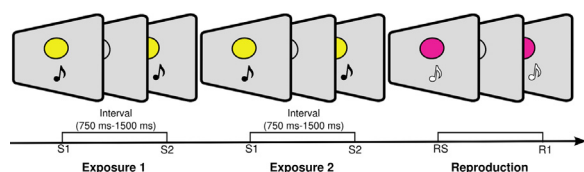


Fig. 1. Temporal reproduction task. (A) Sequence of events during a trial. Each trial consisted of two equal empty intervals (between 750 ms and 1500 ms), marked by two stimuli. In auditory blocks, the interval was marked by two brief tones (1000 Hz, 100 ms), while in visual blocks the interval was marked by two flashes (0.5° of visual angle, 100 ms). Participants were instructed to reproduce the interval at the end of each trial.

stimulus caused by a button press (R1).

In auditory blocks, the tones consisted of 1000 Hz tones (100 ms duration), while the ready and end stimuli consisted of 500 Hz tones. In visual blocks, the flashes that marked the interval consisted of yellow 0.5° of visual angle discs (100 ms duration), while the ready and end stimuli consisted of magenta flashes of the same size. No direct feedback was given.

The sample intervals ranged between 750 ms and 1500 ms and were uniformly distributed. Each block (visual or auditory) consisted of 120 trials. Half of the participants performed the visual block first, while the other half performed the auditory block first.

Behavioural analysis

Events in which intervals were reproduced as longer than double the sample interval or shorter than half the sample interval were considered errors and excluded from further analyses. The proportion of errors was low for both modalities (auditory: 0.0042 ± 0.0011 ; maximum proportion of rejected trials per participant = 0.0167; visual: 0.0092 ± 0.0031 ; maximum proportion of rejected trials per participant = 0.0583).

Similarly to previous studies (Cicchini et al., 2012; Jazayeri and Shadlen, 2010), the total error in the reproduction task was partitioned into two components: the average bias (BIAS) and the average variance (VAR). These two metrics are directly related to the overall mean squared error (MSE). To calculate these components, sample intervals were first binned into six equally sized bins and, for each bin, an estimate of both measures were calculated. The BIAS for each bin was calculated as the average difference between the reproduced interval and the sample intervals. The VAR for each bin was calculated as the variance of the difference between reproduced and real intervals. The final estimate of the BIAS was calculated as the root mean square of the BIAS across bins and of the VAR as the average VAR across bins (Jazayeri and Shadlen, 2010). For ease of interpretation and comparison with previous studies, the VAR values were plotted using its square root $\sqrt{\text{VAR}}$.

We further calculated a regression index (RI) to index the tendency of reproduced intervals to regress towards the mean sample. This index was calculated as the difference in slope between the best linear fit on the reproduced interval and perfect performance (Cicchini et al., 2012). This measure varies from 0 (perfect performance) to 1 (complete regression to the mean, after allowing for a constant bias). The same linear fit between real and reproduced intervals was used to calculate the indifference points for both modalities. This point refers to the physical interval where durations are reproduced veridically.

To analyse the scalar property of time, we computed the slope of the generalised Weber function (García-Garibay et al., 2016; Getty, 1975; Ivry and Hazeltine, 1995). A linear regression between the variance of the reproduced intervals and the mean subjective duration squared was performed as follows:

$$\sigma^2 = k^2 T^2 + \sigma_{indep}^2 \quad (1)$$

where k is the slope that approximates the Weber fraction and σ_{indep}^2 is a constant representing the time-independent component of the variability. To account for the systematic bias found in the reproduced intervals, we used an approach similar to García-Garibay et al. (2016) in which T^2 was computed based on the linear fit between real and reproduced intervals.

All measures were calculated separately for each participant and condition (auditory and visual). At the group level, comparisons between the calculated parameters were done using paired t -tests (two-sided). To investigate correlations across participants for all three measures, Pearson correlations were calculated between the values of each measure in visual and auditory conditions.

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