Association between resting-state oscillatory activity and EEG markers of temporal processing

Baojun Tang

Department of Cognitive Science

University of California, San Diego

2021-2022

Committee

Dr. Andrea Chiba

Dr. Lara Rangel

Gina M. D'Andrea-Penna

Introduction

Temporal processing (timing) is a crucial aspect of human cognition due to the inherently temporal nature of the environment with which we consciously and unconsciously interact (Lashley, 1951). Dynamic events--such as speech, movement, and social interaction--would become incomprehensible if one were to lack the ability to process the temporal sequence, spacing, and duration of sensory stimuli. It is therefore of particular interest for scientists to investigate temporal processing in the brain. Prior efforts have attempted to quantify temporal processing ability through either behavioral or neural indices. For example, Duzcu et al., 2019 examined brain evoked potentials in response to periodic stimuli, while Thompson et al., 2015 investigated sensorimotor synchronization (SMS) ability through finger-tapping tasks.

However, neural indices elicited by perception of temporal information lack behavioral representation and cannot support ecological interpretations of individual timing ability; behavioral indices like SMS better represent individual timing ability, but intrinsically involve both a neural and a motor component; accordingly, individual differences in individual timing ability need to be disentangled from individual differences in motor ability.

Therefore, it could be enlightening to explore temporal processing ability incorporating both behavioral and neural responses. A study completed by graduate student D'Andrea-Penna and colleagues (2020) suggested a new paradigm that probed timing ability, correlating behavioral and neural indices acquired from separate tasks involving rhythmic stimuli and/or behavior.

Specifically, D'Andrea-Penna and colleagues examined the N1-P2 complex, an emitted P300 ("omission-evoked potential,") and a possible "metric negativity," which are demonstrated by previous research to be modulated by temporal expectancy (Besson et al., 1997; Besson and Faita, 1995; Duzcu, 2019; Duzcu et al., 2019; Jongsma et al., 2004; Kononowicz and van Rijn, 2014; Lange, 2009; Menceloglu et al., 2020; Picton and Hillyard, 1974; Rothermich et al., 2010; Rothermich et al., 2012; Ruchkin et al., 1980; Ruchkin and Sutton, 1978; Schafer et al., 1981; Stekelenburg and Vroomen, 2015; Todorovic and de Lange, 2012) and, therefore, are treated as candidates for electrophysiological markers of timing ability. They found that subjects who generated larger N1-P2 amplitudes in response to inserted irregular beats in a sequence of periodic beats, during passive listening, performed better in a sensorimotor synchronization task in which they tried to synchronize their finger tapping with externally played isochronous beats.

This particular paper reports a follow-up study based on the above-mentioned findings by D'Andrea-Penna and colleagues. The new study investigates the relationship between baseline brain activation state, which we hypothesize may affect the efficacy with which auditory stimuli are processed, and, correspondingly, the N1-P2 amplitude in response to unexpected stimuli, which appears to predict performance on a solo-tapping task. To evaluate this hypothesis, we will use electroencephalography (EEG) to examine the resting-state oscillatory activity along with the N1-P2 component generated during a passive listening task.

Background

Electroencephalographic (EEG) experiments that examined timing and rhythmic ability found that the N1-P2 complex is modulated by temporal expectancy (Schafer et al., 1981; Lange, 2009; Todorovic and de Lange, 2012; Kononowicz and van Rijn, 2014; Duzcu, 2019; Duzcu et al., 2019; Menceloglu et al., 2020). The N1-P2 complex is an auditory evoked potential elicited by stimulus onsets, offsets, and changes in quality that objectively reflect the conscious detection of any discrete change in the auditory environment and indicates early sensory processing (Näätänen, 1990; Remijn et al., 2014; Hyde, 1997). It has been used as an objective predictor of auditory threshold in adults and older children since the late 1960s (Lightfoot, 2016). It is also possibly modulated by top-down attention-related mechanisms (Hillyard et al., 1973; Parasuraman, 1978). In addition, Näätänen, 1990 reports that N1 amplitude may correlate with the subjective perception of stimulus obtrusiveness with larger amplitudes suggesting greater obtrusiveness, indicating a possible relationship between N1 amplitude and conscious evaluation of stimulus quality.

The activation state of the cortex is proposed to influence the fidelity of sensory inputs and resolution of perceptual processing (Harris & Thiele, 2011). For example, modulating the cortex through stimulating cholinergic projections has been shown to desynchronize the cortex, presumably inducing activity that is of lower amplitude and higher-frequency; this “activated” cortical state leads to improved processing of visual information (Minces et al, 2017, Bauer et al, 2012). Typically, this shift in cortical state also accompanies the emergence of more gamma frequency oscillations (40-150 Hz). Even a single gamma cycle has been proposed to be a computational mechanism for temporal coding (Fries et al, 2007).

Temporally coordinated neural activity in one brain region could influence activity in downstream regions due to the temporal summation of neural inputs. Assume multiple upstream neurons project their axons to one single downstream neuron: if all upstream neurons release neurotransmitters and stimulate the downstream neuron in close temporal proximity, the presynaptic inputs are likely to summate at the soma, generating a larger excitatory postsynaptic potential (EPSP) and increasing the probability of the postsynaptic neuron firing an action potential.

From a neural oscillation perspective, the gamma rhythm is a “narrow” rhythm in the sense that it is characterized by high-frequency oscillations, short wavelengths, and narrow oscillatory cycles. If a group of neurons demonstrates synchronized firing activity in a gamma pattern, they would be exhibiting action potentials within small gamma rhythmic windows. On the other hand, the alpha rhythm, characterized by lower-frequency oscillations, demonstrates longer wavelengths and wider oscillatory cycles. A group of neurons synchronized in an alpha pattern would exhibit action potentials within wider temporal windows. Considering that the effect of temporal summation increases as the interval between inputs decreases, neural activity synchronized in higher-frequency oscillations and nested in narrower temporal windows should have a higher probability of eliciting downstream firing activity (Jensen et al., 2007).

Previous studies proposed that gamma synchronization could underlie neurons in downstream brain regions selectively responding to attended stimuli (Jensen et al., 2007). It was also found that increases in gamma-synchronized activity correlate with faster reaction time (Womelsdorf et al., 2006). Benasich and colleagues (2008) found a significant positive correlation between language/cognitive skills levels, self-control/attentional shift abilities, and resting frontal gamma power in young children. Through optogenetically inducing gamma oscillations in the mouse neocortex, Siegle and colleagues (2014) were able to enhance the animals’ ability to detect sub-salient vibrissal stimuli. Thus, across different species and task demands, the presence of gamma oscillatory activity has consistently been associated with increases in sensation, perception, attention, and even the development of academic skills.

Consequently, this project aims to evaluate the potential association of resting-state oscillatory activity recorded during resting or stimulus-free periods of the passive-listening task to the amplitude of the N1-P2 component generated during active periods of the tasks. We specifically hypothesize that high-frequency resting-state oscillatory activity in the gamma-band contributes to the generation of larger N1-P2 amplitude to unexpected stimuli.

Methods - majority adopted from D'Andrea-Penna et al. (2020)

Participants

A total of 4 participants between ages 18 and 24 were recruited from the University of California, San Diego, CA. One participant was excluded from the analysis due to excessive noise and artifacts in their EEG data. For efficiency, all sessions were conducted in groups of 2, but the tasks relevant to this study did not involve interaction between participants.

Stimuli and Procedure - cited from D'Andrea-Penna et al. (2020)

> For both the tapping task and passive listening session, participants heard rhythmic streams of tone bursts from a speaker (~75 dB, sound pressure level). Each burst consisted of an 800-Hz sine pulse, 50 ms in duration with a 10-ms ramp up and ramp down to avoid clicks at onsets and offsets. All auditory stimuli and analog triggers were presented—and tapping recorded—using Adobe Audition with a Focusrite Scarlett 18i20

audio/digital interface with a sampling rate of 44.1 kHz. Stimulus presentation with a powered JBL studio monitor introduced a 3-ms latency. The auditory stimuli were sent to the speaker through one of the output channels of the audio digital interface. On another output channel, we sent a simultaneous analog trigger. The analog trigger was collected through one input channel of the audio digital interface, together with the activity from the piezoelectric elements that were glued to the tapping boards. With this configuration, the triggers and participants' actions were collected simultaneously. Thus, the signals that we used for analysis were synchronized with a precision of one sample (i.e., less than a millisecond)

Tapping - modified from D'Andrea-Penna et al. (2020)

Participants tapped individually for 1 min to isochronous beats. For the tapping task, beats were separated by a 600-ms IOI, a relatively comfortable pace for SMS (Repp, 2005). Beats were occasionally omitted (15% probability); however, participants were instructed to maintain the basic rhythm while tapping and to tap where the beat "should be," despite the omissions. Participants tapped onto wood blocks affixed to drums at approximately lap height, under which piezoelectric sensors were placed to record their taps as digital audio files into Adobe Audition.

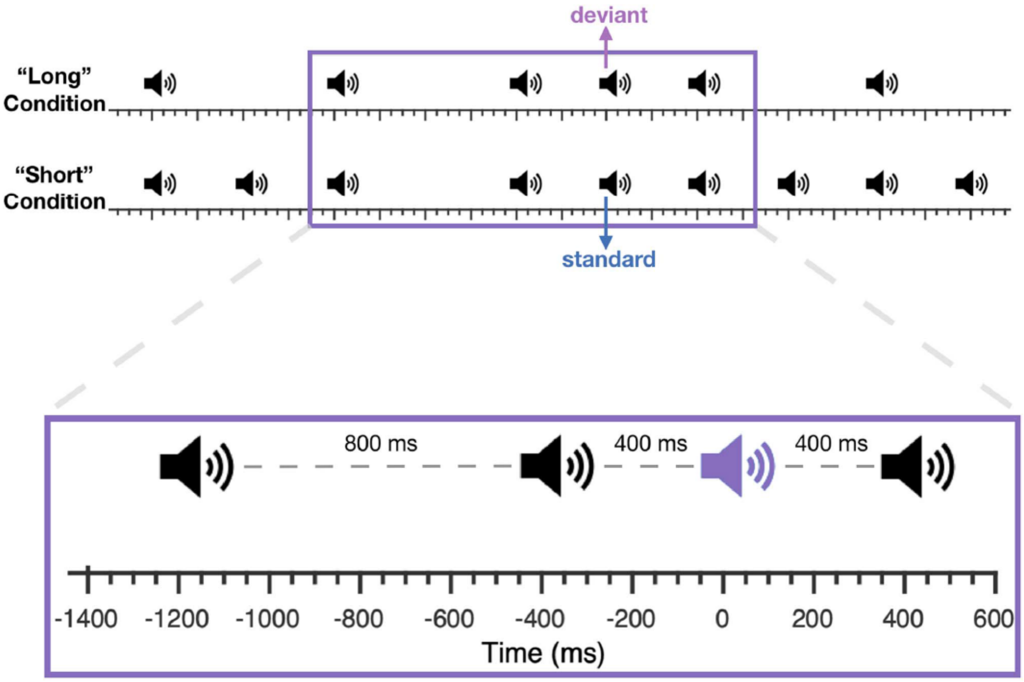


Figure 1. Passive listening temporal oddball paradigm. Participants passively listen to streams of sounds in 2 conditions. The "long" condition includes isochronous beats that are sometimes interrupted by an unexpected beat ("deviant"). The "short" condition is twice as fast as the long condition and contains occasional omissions. This arrangement allows us to compare brain responses with deviants and standards, which are physically the same sequence of stimuli to control for neural adaptation but vary in temporal expectancy.

Passive Listening - modified from D'Andrea-Penna et al. (2020)

A 30-min passive listening session followed the tapping task. To avoid the confound of sensory adaptation, in which EP amplitude decreases with shorter IOI's (Rothman et al., 1970), we developed a two-condition paradigm consisting of 2 trial types that were presented alternately 8 times (for a total of 16 trials). The "long condition" used a 800-ms IOI, with rare extra beats occurring at a 400-ms IOI (halfway between surrounding 800-ms IOI beats, 15% probability). The "short condition" used a 400-ms IOI, with rare omissions (15% probability). These 2 conditions strategically allowed for identical stimulus sequences in which the same 2 IOI’s preceded the key sound to which the evoked brain response was measured (either an extra beat in the long condition or a standard in the short condition), controlling for adaptation such that only their expectancy differed. Henceforth, the extra beats in the long condition will be referred to as “deviants” and the sequence-matched, expected beats in the short condition will be called “standards.” Between each super-block (containing one block of the long condition followed by one block of the short condition - active periods) we inserted 60 s of silence (resting periods) for baseline EEG data collection.

EEG Acquisition - modified from D'Andrea-Penna et al. (2020)

During passive listening, participants wore custom, 5-channel dry EEG headsets containing electrodes at Fp1, Fp2, Cz, O1, and O2 (Cognionics; Chi et al., 2013). Two frontal electrodes served as ground, and EEG data was referenced to the left earlobe. The headsets employ flexible plastic sensors with tines that penetrate hair to contact the scalp and active Ag/AgCl electrodes. Each headset was connected to a laptop using a USB isolator and running Cognionics Data Acquisition software. Cz was positioned approximately at vertex, and alcohol pads were used to clean participants’ foreheads and other electrode sites when necessary. Signal quality was inspected prior to recording. Square-wave triggers, with variable amplitude serving as event codes, were sent into the headset as analog input and recorded as an additional channel. Data were recorded at 4000 Hz to preserve the onsets of the triggers.

Analysis - majority adapted from D'Andrea-Penna et al. (2020)

Tapping - modified from D'Andrea-Penna et al. (2020)

Tapping time series underwent a vector strength (VS) analysis, which provided a measure of each participant's ability to synchronize with the external rhythm—particularly of their ability to tap with a consistent phase relative to the driving beat. VS is defined as:

$$VS = \frac{1}{N} \left| \sum_{j=1}^{N} e^{i\,\phi j} \right|$$

where N is the total number of taps by one participant, ϕj is the tap phase relative to the driving rhythm for tap number j, and i is the imaginary unit. Accordingly, VS is one if a tapper is perfectly consistent, maintaining the same phase across taps, and zero if the participant taps randomly (Khalil et al., 2013).

EEG Preprocessing - modified from D'Andrea-Penna et al. (2020)

EEG data from the passive listening was processed and analyzed using EEGLAB (Delorme and Makeig, 2004). We used data from Cz, consistent with previous studies examining the N1-P2 complex (Hillyard et al., 1973; Parasuraman, 1978; Schafer et al., 1981). After identifying the different types of events (standard and deviant beats) using the amplitude-coded square waves from the trigger channel, data were downsampled to 500 Hz. A low-pass Hamming windowed sinc finite impulse response (FIR) filter with a cutoff frequency of 30 Hz was applied to the data prior to event selection and epoching. The deviant and standard beats (Fig. 1) were selected, epoched, and baseline corrected to the 50-ms period preceding the beat.

EEG Artifact Rejection

Automatic artifact rejection with extreme values removed signals with voltages beyond ∓50 µV in event epochs. Manual artifact rejection (visual inspection) removed major artifacts including eye blinks, mechanical disruptions, and irregular high-amplitude noise in the baseline EEG data (Using the EEG Lab software, Delorme & Makeig, 2004).

N1-P2 Identification

By averaging across epochs, time-locked to the same type of event (in this case, a sound), random noise that obscures the ERPs in raw data is smoothed out and the ERPs can be revealed. . The N1 was then identified as the first prominent negative deflection that occurred around 100ms post-stimulus and the P2 was identified as the positive deflection that followed the N1.

Spectral Analysis

EEG signals are also comprised of neural oscillations at a variety of frequencies. To study this oscillatory activity, we employed a power spectral density analysis on baseline EEG data using the channel spectra and maps tool in EEGLAB (Delorme and Makeig, 2004). EEGLAB's channel spectra function estimates the spectral density of data with Welch's method (Welch, 1967). Welch's method basically estimates the power spectral density curve from the EEG by taking a sliding window of time bins and generating the average of the fast Fourier Transforms (FFTs) across all windows.

Statistics

Statistical analysis was not performed to test significance due to the small sample size. If we had collected data from more subjects, we would correlate the deviant-standard N1-P2 magnitude difference with solo tapping performance using Spearman's correlation coefficient to account for non-normally distributed and skewed VS scores. We would also correlate participants' individual gamma power (in two different bins, 30-50 and 50-80) with deviant-standard N1-P2 magnitude difference to address our hypothesis that high-frequency resting-state oscillatory activity in the gamma-band contributes to the generation of larger N1-P2 amplitude to unexpected stimuli. In addition, we would address our hypothesis regarding the activational state of the cortex by examining the power of slow-wave activity with respect to the N1-P2. Specifically, we would window the alpha power surrounding the alpha power peak (typically at 10 Hz) in each subject and correlate that window with deviant-standard N1-P2 magnitude difference.

Expected Results

We expect that participants who generated a larger deviant-standard N1-P2 magnitude difference would perform better in the solo tapping task, which was found in our previous experiment (D'Andrea-Penna et al., 2020). We also expect that participants who generated a larger deviant-standard N1-P2 magnitude difference would exhibit more high-frequency oscillatory activity during the resting periods of the passive listening task because more concentrated attention, more activated brain states, and improved ability to process sensory stimuli are characterized by lower amplitude, higher-frequency oscillatory activity (Moruzzi and Magoun, 1949). We would, additionally, predict a negative correlation between deviant-standard N1-P2 magnitude difference and alpha power, indicating that a desynchronized cortical state leads to higher fidelity sensory coding.

Results

N1-P2 to Deviant and Standard Beats

To test if deviant beats elicit larger N1-P2 than standard beats, we analyzed the N1-P2 amplitude of the two types of beats. Consistent with dynamic attending theory (Jones and Boltz, 1989) and the concept of neural adaptability (Schafer, 1982), the N1-P2 magnitude to deviant beats was larger than the N1-P2 to standard beats in both subjects. Statistical analysis was not performed to test significance due to the small sample size.

VS

VS was used to quantify the participants' ability to tap with a consistent phase relative to the driving beat. The participant that generated a larger deviant-standard N1-P2 magnitude difference had a higher VS score of 0.96. The participant that generated a smaller deviant-standard N1-P2 magnitude difference had a lower VS score of 0.79. Statistical analysis was not performed to test significance due to the small sample size.

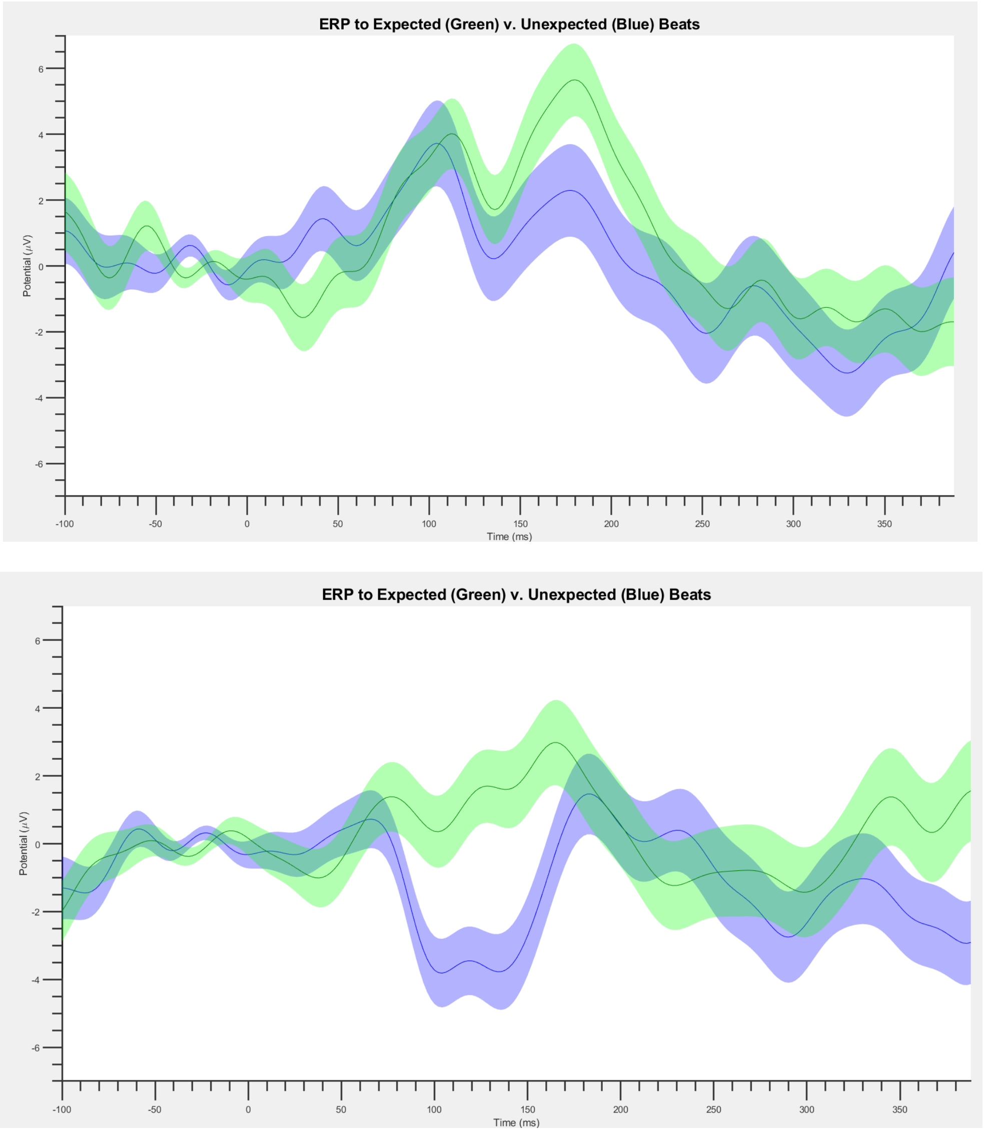
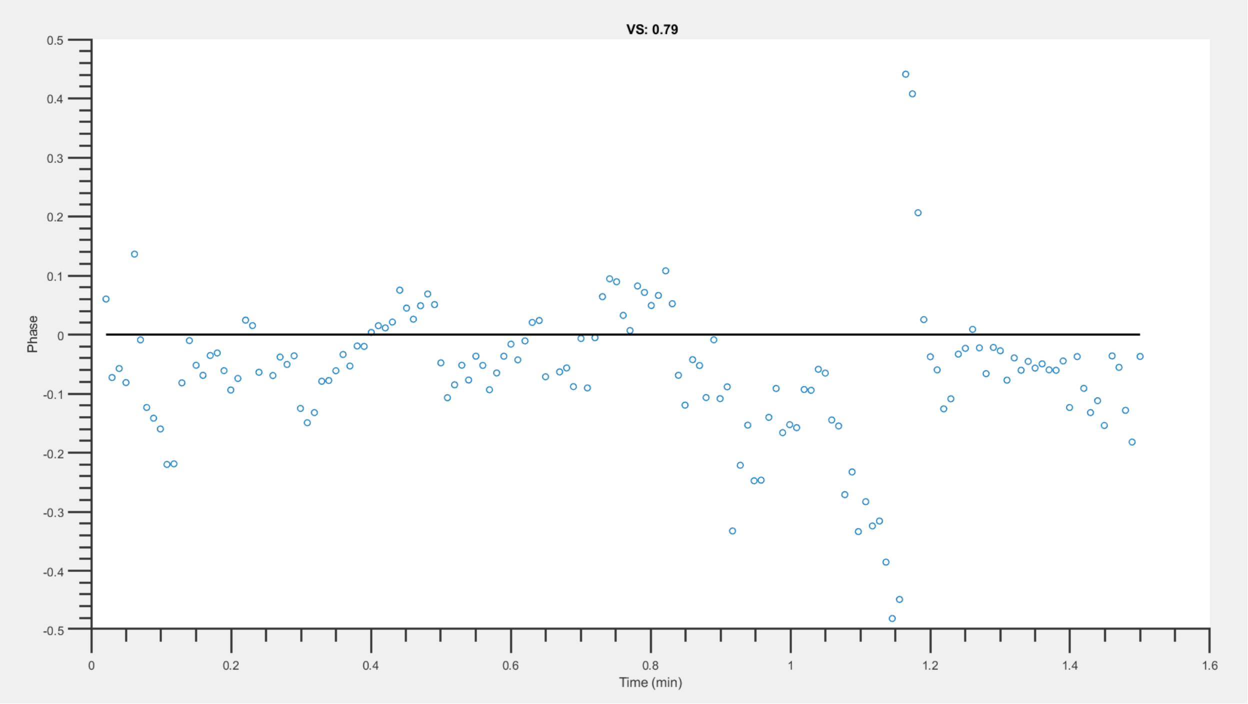


Figure 2. N1-P2 complex (a negative deflection that occurs at around 100ms after the stimulus and the following positive deflection) to expected (standard, shown in green) and unexpected (deviant, shown in blue) beats in two of the three participants. The N1-P2 to unexpected beats is larger than that to expected beats in both participants. The second participant generated a larger deviant-standard N1-P2 magnitude difference than the first participant.



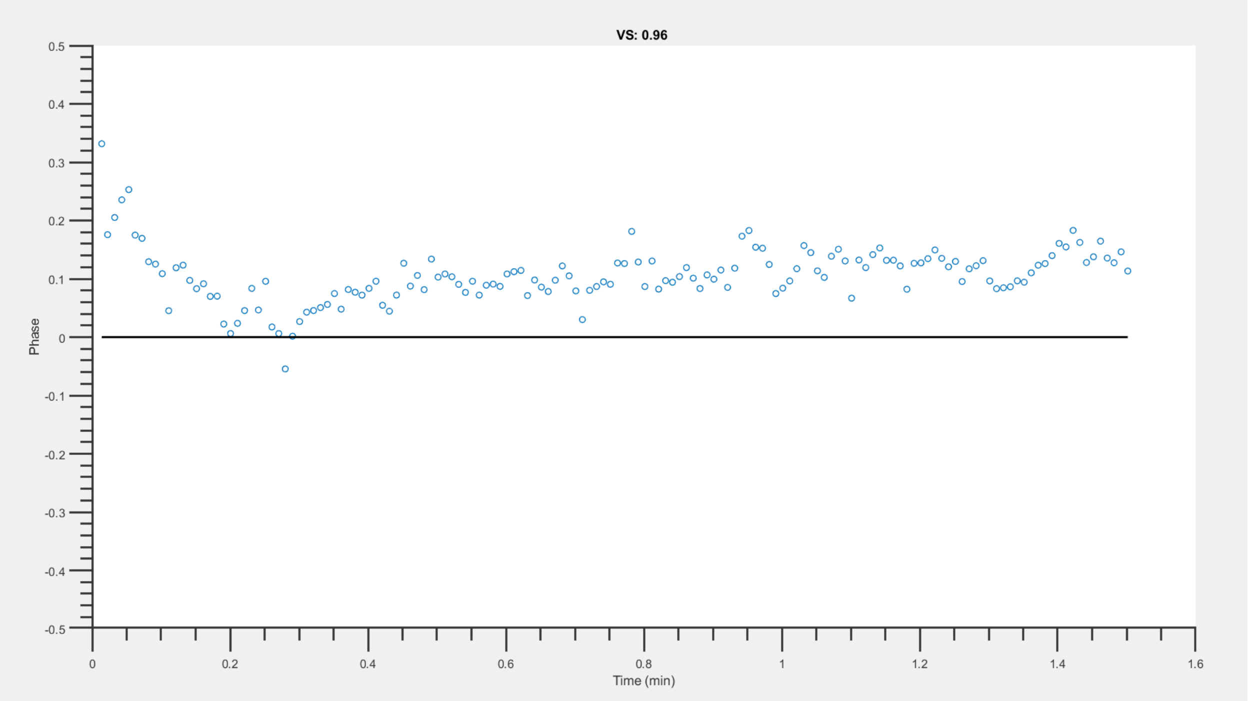


Figure 3. VS scores of the two participants. The first participant had a VS score of 0.79. The second participant had a VS score of 0.96. While the first participant showed a lot of variation in their tapping time relative to the beats, the second participant consistently tapped in a constrained period before the beats.

Spectral analysis

Without a large enough sample size, we were unable to find convincing evidence to support our hypothesis that better synchronizers would exhibit more high-frequency oscillatory activity during resting periods of the passive listening task. However, we found that the best synchronizer among the three participants exhibited a distinctive lack of alpha frequency activity, unlike the other two participants. This is consistent with a previous finding that alpha-band activity negatively correlates with stimulus-specific information fidelity such that decreases in alpha power are coupled with increases in stimulus-specific information (Griffiths et al., 2019).

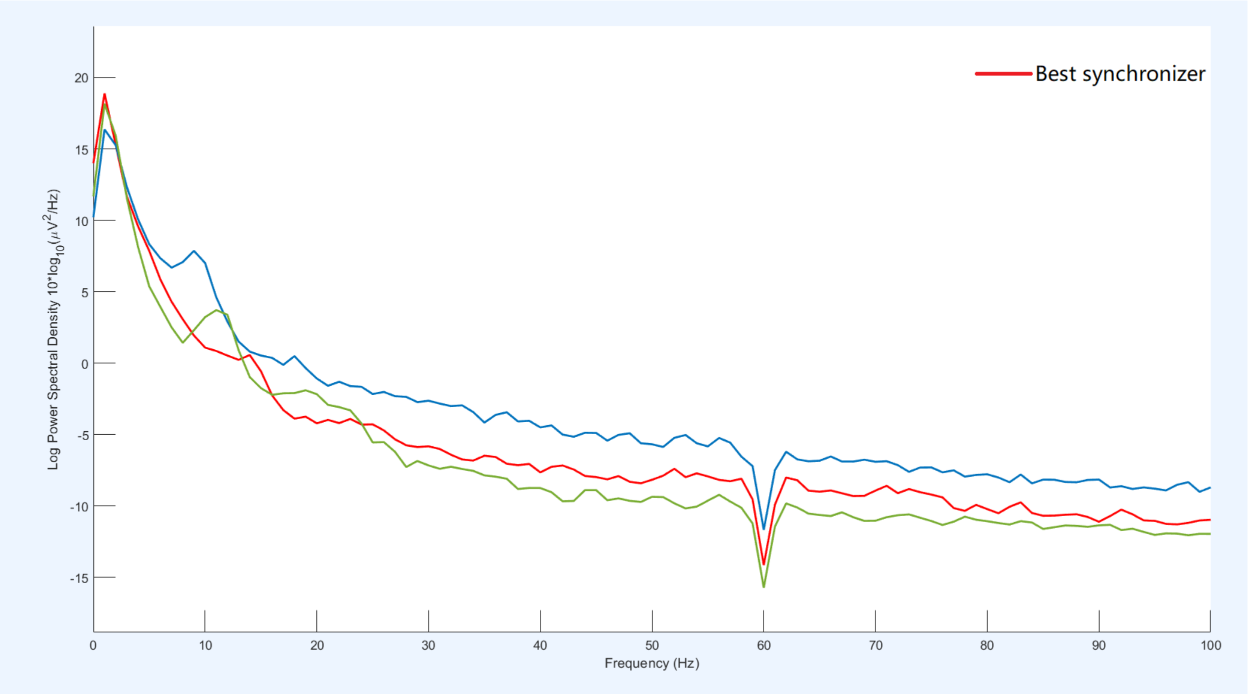


Figure 4. Spectral density plot of baseline EEG data (Cz). Red trace represents the best synchronizer. A peak that shows up at ~10Hz for the other two participants is distinctively not present in the red trace.

Discussion

Our results show that the N1-P2 complex to deviant beats is generally larger than that to standard beats and that a participant who generated a larger deviant-standard N1-P2 magnitude difference performed better in the solo-tapping task than a participant who generated a smaller deviant-standard N1-P2 magnitude difference. These are consistent with results from D'Andrea-Penna et al. (2020), which report a significant positive correlation between deviant-standard N1-P2 magnitude difference and performance in a solo-tapping task. Interestingly, the best synchronizer among the three participants demonstrated a distinct lack of an alpha peak that was noticeably present in the other two participants' power spectral density traces.

It is well-accepted among neuroscientists that oscillatory activity in the cortex is desynchronized during wakefulness and REM sleep and is synchronized during idleness and non-REM sleep. However, several recent studies on rodents and humans demonstrated that the brain alternates frequently between smaller fluctuations of synchronized and desynchronized states during the already "desynchronized" wakefulness. Researchers proposed that these changes underlie mechanisms that provide a balance of external sensory information processing and internal maintenance states during wakefulness (Harris and Thiele, 2011). It was also found that selectively stimulating cortical cholinergic projections in wakeful mice led to further desynchronization of cortical activity, more precise and rapid visual information encoding, and changes in visual signal-to-noise ratio (Minces et al., 2017). In human subjects, pharmacologically increasing acetylcholine in the cortex reduced oscillatory activity in the alpha-band and improved subjects' performance on a visual attention task (Bauer et al. 2012). In addition, it was found that the effect of decreased alpha activity also manifests in the auditory system, as it led to an improved ability to ignore auditory distractors (Weisz et al., 2020). Lastly, Griffiths et al. (2019) found that alpha-band activity negatively correlates with stimulus-specific information fidelity, and decreases in alpha power are coupled with increases in stimulus-specific information.

The lack of alpha peak that we found in the best synchronizer, who also exhibited the largest deviant-standard N1-P2 difference, is consistent with the abovementioned findings and the N1-P2 amplitude-performance correlation discovered in our previous experiment (D'Andrea-Penna et al., 2020) in that a better performing (in a solo tapping task) cortex is characterized by more desynchronized oscillatory activity and more exaggerated response to unexpected stimuli (in simple passive listening) relative to cortices that perform more poorly. However, due to the limited sample size, it would be inappropriate to infer that such a feature would also be present in other good synchronizers. Therefore, the most obvious extension of this project would be the collection of more data. This would enable us to correlate the deviant-standard N1-P2 magnitude difference with solo tapping performance to further support our previous findings and would also enable us to correlate participants' individual gamma power with the deviant-standard N1-P2 magnitude difference to properly address our hypothesis that high-frequency resting-state oscillatory activity in the gamma-band contributes to the generation of larger N1-P2 amplitude to unexpected stimuli. Our findings in this experiment pointed us toward other potential features of a desynchronized/aroused cortex such as reduced alpha power (Bauer et al., 2012; Griffiths et al., 2019; Weisz et al., 2020) and 1/f power spectral density slope in the range from 30 to 45 Hz (Lendner et al., 2020). We expect to incorporate analyses of these elements into future experiments. We might also want to test the same subjects on multiple occasions to see whether their cortical state and synchronization abilities are transient or whether they represent a stable temporal phenotype.

If we do find that higher-frequency resting-state activity correlates with the generation of higher amplitude N1-P2 complex, which is linked to better performance in the solo-tapping task, we may be able to suggest that brain activational state is related to individual performance in tasks that assess timing ability and that we may be able to improve timing ability by manipulating brain state. We might also consider behavioral training regimens for fluidly transitioning the cortex into an activated state to see whether it is possible to augment the temporal phenotype of those who have both poorer detection of temporal features of the auditory stream and the ability to rhythmically synchronize with a temporal pattern.

Acknowledgment

I would like to thank Dr. Andrea Chiba for guiding me through the entire process with expertise and patience. Taking your Cognitive Neuroscience class in the process of this project has been a great experience: the concepts in 107C served as great theoretical background for this honors project and working on this project furthered my understanding of class messages. I would like to thank Gina M. D’Andrea-Penna for letting me participate in this follow-up study of hers and for guiding me through the technical difficulties in this process. I would like to thank Dr. Marta Kutas for helping me greatly in the process of presentation revision. I would also like to thank Dr. Lara Rangel for introducing me to concepts that prepared me for this project.

Finally, I would like to thank the entire Cognitive Science community for providing me with this opportunity.

Reference

Bauer, M., Kluge, C., Bach, D., Bradbury, D., Heinze, H. J., Dolan, R. J., & Driver, J. (2012). Cholinergic enhancement of visual attention and neural oscillations in the human brain. Current biology : CB, 22(5), 397–402. https://doi.org/10.1016/j.cub.2012.01.022

Benasich, A. A., Gou, Z., Choudhury, N., & Harris, K. D. (2008). Early cognitive and language skills are linked to resting frontal gamma power across the first 3 years. Behavioral brain research, 195(2), 215–222. https://doi.org/10.1016/j.bbr.2008.08.049

Besson, M., & Faïta, F. (1995). An event-related potential (ERP) study of musical expectancy: Comparison of musicians with nonmusicians. Journal of Experimental Psychology: Human Perception and Performance, 21(6), 1278–1296. https://doi.org/10.1037/0096-1523.21.6.1278 Brandeis, D., Naylor, H., Halliday, R., Callaway, E., & Yano, L. (1992). Scopolamine effects on visual

Besson, M., Faita, F., Czternasty, C., & Kutas, M. (1997). What's in a pause: Event-related potential analysis of temporal disruptions in written and spoken sentences. Biological Psychology, 46(1), 3–23. https://doi.org/10.1016/S0301-0511(96)05215-5

Cantero, J. L., Atienza, M., Gómez, C., & Salas, R. M. (1999). Spectral structure and brain mapping of human alpha activities in different arousal states. Neuropsychobiology, 39(2), 110–116. https://doi.org/10.1159/000026569

Chi, Y. M., Wang, Y., Wang, Y.-T., Jung, T.-P., Kerth, T., & Cao, Y. (2013). A Practical Mobile Dry EEG System for Human Computer Interfaces. In D. D. Schmorrow & C. M.

Fidopiastis (Eds.), Foundations of Augmented Cognition(pp. 649–655). Springer Berlin Heidelberg.

D'Andrea-Penna, G. M., Iversen, J. R., Chiba, A. A., Khalil, A. K., & Minces, V. H. (2020). One Tap at a Time: Correlating Sensorimotor Synchronization with Brain Signatures of Temporal Processing. Cerebral cortex communications, 1(1), tgaa036. https://doi.org/10.1093/texcom/tgaa036

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Duzcu H. (2019). A neural marker of the start-gun in interval timing: Onset N1P2. Behavioral Neuroscience. 133(4), 414–427.https://doi.org/10.1037/bne0000325

Duzcu, H., Özkurt, T. E., Mapelli, I., & Hohenberger, A. (2019). N1-P2: Neural markers of temporal expectation and response discrimination in interval timing. Acta Neurobiologiae Experimentalis, 79(2), 193–204. https://doi.org/10.21307/ane-2019-017

Fries, P., Nikolić, D., & Singer, W. (2007). The gamma cycle. Trends in neurosciences, 30(7), 309–316. https://doi.org/10.1016/j.tins.2007.05.005

Griffiths, B. J., Mayhew, S. D., Mullinger, K. J., Jorge, J., Charest, I., Wimber, M., & Hanslmayr, S. (2019). Alpha/beta power decreases track the fidelity of stimulus-specific information. eLife, 8, e49562. https://doi.org/10.7554/eLife.49562

Harris, K. D., & Thiele, A. (2011). Cortical state and attention. *Nature reviews. Neuroscience*, *12*(9), 509–523. https://doi.org/10.1038/nrn3084

Hillyard, S. A., Hink, R. F., Schwent, V. L., & Picton, T. W. (1973). Electrical Signs of Selective Attention in the Human Brain. Science, 182(4108), 177. https://doi.org/10.1126/science.182.4108.177

Hyde M. (1997). The N1 response and its applications. Audiology & neuro-otology, 2(5), 281–307. https://doi.org/10.1159/000259253

Jensen, O., Kaiser, J., & Lachaux, J. P. (2007). Human gamma-frequency oscillations associated with attention and memory. Trends in neurosciences, 30(7), 317–324. https://doi.org/10.1016/j.tins.2007.05.001

Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. Psychological review, 96(3), 459–491. https://doi.org/10.1037/0033-295x.96.3.459

Jongsma, M. L. A., Quiroga, R. Q., & van Rijn, C. M. (2004). Rhythmic training decreases latency-jitter of omission evoked potentials (OEPs) in humans. Neuroscience Letters, 355(3), 189–192. https://doi.org/10.1016/j.neulet.2003.10.070

Khalil, A. K., Minces, V., McLoughlin, G., & Chiba, A. (2013). Group rhythmic synchrony and attention in children. Frontiers in Psychology, 4. https://doi.org/10.3389/fpsyg.2013.00564

Kononowicz, T. W., & van Rijn, H. (2014). Decoupling Interval Timing and Climbing Neural Activity: A Dissociation between CNV and N1P2 Amplitudes. Journal of Neuroscience, 34(8), 2931– 2939. https://doi.org/10.1523/JNEUROSCI.2523-13.2014

Lange, K. (2009). Brain correlates of early auditory processing are attenuated by expectations for time and pitch. Brain and Cognition, 69(1), 127–137. https://doi.org/10.1016/j.bandc.2008.06.004

Lashley, K. S. (1951). The problem of serial order in behavior. In L. A. Jeffress (Ed.), Cerebral Mechanisms in Behavior, pp. 112–146. New York: Wiley.

Lendner, J. D., Helfrich, R. F., Mander, B. A., Romundstad, L., Lin, J. J., Walker, M. P., Larsson, P. G., & Knight, R. T. (2020). An electrophysiological marker of arousal level in humans. eLife, 9, e55092. https://doi.org/10.7554/eLife.55092

Lightfoot G. (2016). Summary of the N1-P2 Cortical Auditory Evoked Potential to Estimate the Auditory Threshold in Adults. Seminars in hearing, 37(1), 1–8. https://doi.org/10.1055/s-0035-1570334

Menceloglu, M., Grabowecky, M., & Suzuki, S. (2020). Rhythm Violation Enhances Auditory-Evoked Responses to the Extent of Overriding Sensory Adaptation in Passive Listening. Journal of Cognitive Neuroscience, 1–18. https://doi.org/10.1162/jocn_a_01578

Minces, V., Pinto, L., Dan, Y., & Chiba, A. A. (2017). Cholinergic shaping of neural correlations. Proceedings of the National Academy of Sciences of the United States of America, 114(22), 5725-5730. https://doi.org/10.1073/pnas.1621493114

Moruzzi, G., & Magoun, H. W. (1949). Brain stem reticular formation and activation of the EEG. Electroencephalography and clinical neurophysiology, 1(1-4), 455-473.

Näätänen, R. (1990). The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. Behavioral and Brain Sciences, 13(2), 201–233. https://doi.org/10.1017/S0140525X00078407

Parasuraman, R. (1978). Auditory evoked potentials and divided attention. Psychophysiology, 15(5), 460-465.

Picton, T. W., & Hillyard, S. A. (1974). Human auditory evoked potentials. II: Effects of attention. Electroencephalography and Clinical Neurophysiology, 36, 191–200. https://doi.org/10.1016/0013-4694(74)90156-4

Remijn, G. B., Hasuo, E., Fujihira, H., & Morimoto, S. (2014). An introduction to the measurement of auditory event-related potentials (ERPs). Acoustical Science and Technology, 35(5), 229–242. https://doi.org/10.1250/ast.35.229

Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. Psychonomic Bulletin & Review, 12(6), 969–992. https://doi.org/10.3758/BF03206433

Rothermich, K., Schmidt-Kassow, M., & Kotz, S. A. (2012). Rhythm’s gonna get you: Regular meter facilitates semantic sentence processing. Neuropsychologia, 50(2), 232–244. https://doi.org/10.1016/j.neuropsychologia.2011.10.025

Rothermich, K., Schmidt-Kassow, M., Schwartze, M., & Kotz, S. A. (2010). Event-related potential responses to metric violations: Rules versus meaning: NeuroReport, 21(8), 580–584. https://doi.org/10.1097/WNR.0b013e32833a7da7

Rothman, H. H., Davis, H., & Hay, I. S. (1970). Slow evoked cortical potentials and temporal features of stimulation. Electroencephalography and Clinical Neurophysiology, 29(3), 225–232. https://doi.org/10.1016/0013-4694(70)90135-5

Ruchkin, D. S., & Sutton, S. (1978). Emitted P300 potentials and temporal uncertainty. Electroencephalography & Clinical Neurophysiology, 45(2), 268–277. https://doi.org/10.1016/0013-4694(78)90010-X

Ruchkin, D. S., Sutton, S., & Stega, M. (1980). Emitted P300 and slow wave event-related potentials in guessing and detection tasks. Electroencephalography and clinical neurophysiology, 49(1-2), 1– 14. https://doi.org/10.1016/0013-4694(80)90346-6

Schafer, E. W. P. (1982). Neural Adaptability: A Biological Determinant of Behavioral Intelligence. International Journal of Neuroscience, 17(3), 183–191.

Schafer, E. W. P., Amochaev, A., & Russell, M. J. (1981). Knowledge of stimulus timing attenuates human evoked cortical potentials. Electroencephalography and Clinical Neurophysiology, 52(1), 9–17. https://doi.org/10.1016/0013-4694(81)90183-8

Siegle, J. H., Pritchett, D. L., & Moore, C. I. (2014). Gamma-range synchronization of fast-spiking interneurons can enhance detection of tactile stimuli. Nature Neuroscience, 17(10), 1371–1379. https://doi.org/10.1038/nn.3797

Stekelenburg, J. J., & Vroomen, J. (2015). Predictive coding of visual–auditory and motor-auditory events: An electrophysiological study. Brain Research, 1626, 88–96. https://doi.org/10.1016/j.brainres.2015.01.036

Thompson, E. C., White-Schwoch, T., Tierney, A., & Kraus, N. (2015). Beat synchronization across the lifespan: intersection of development and musical experience. PloS one, 10(6), e0128839.

Todorovic, A., & de Lange, F. P. (2012). Repetition Suppression and Expectation Suppression Are Dissociable in Time in Early Auditory Evoked Fields. Journal of Neuroscience, 32(39), 13389– 13395. https://doi.org/10.1523/JNEUROSCI.2227-12.2012

Veit, J., Hakim, R., Jadi, M. P., Sejnowski, T. J., & Adesnik, H. (2017). Cortical gamma band synchronization through somatostatin interneurons. Nature neuroscience, 20(7), 951–959. https://doi.org/10.1038/nn.4562

Weisz, N., Kraft, N. G., & Demarchi, G. (2020). Auditory cortical alpha/beta desynchronization prioritizes the representation of memory items during a retention period. eLife, 9, e55508. https://doi.org/10.7554/eLife.55508

Welch, P. (1967). The use of fast Fourier transform for the estimation of power spectra: a method based on time averaging over short, modified periodograms. IEEE Transactions on Audio and Electroacoustics, 15(2), 70–73.

Womelsdorf, T., Fries, P., Mitra, P. P., & Desimone, R. (2006). Gamma-band synchronization in visual cortex predicts speed of change detection. Nature, 439(7077), 733–736. https://doi.org/10.1038/nature04258