Aperiodic EEG activity tracks 1/f stimulus characteristics and the allocation of cognitive resources

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The statistics of many natural phenomena including the human electrophysiological response follow a power law, that is, they share a $1/f^x$ distribution. The reduction in signal magnitude with increasing frequency is aptly captured by the slope, or exponent (χ) of the power spectral density. The spectral exponent of electrophysiological recordings recently has been hypothesized to reflect the balance of excitatory and inhibitory activity (E:I ratio) in populations of cortical neurons. It is unclear, however, to which degree exogenous stimulus characteristics or endogenous processes such as the selective allocation of cognitive resources alter the electrophysiological spectral exponent. We here present evidence from an experiment, during which we recorded electroencephalography (EEG) while participants (N = 25) detected faint target stimuli in streams of auditory or visual noise. Importantly, all noise stimuli were generated to exhibit different χ values in their modulation spectra. Spectral exponents over auditory and visual sensory cortices tracked χ values of the respective stimulus domain on the single trial level. Furthermore, attention reduced spectral exponents, which suggests increased E:I ratio (E>I) in sensory regions of the attended domain.

Keywords: electrophysiology; sensory; attention;

Background

Electrophysiological recordings of brain activity represent the pooled activity from large ensembles of neurons. The spectra of such recordings are characterized by initial peaks and a decrease in power with increasing frequency. Hence, the shape of electrophysiological spectra in log/log space can be described by a function of the form $P(f) = a + 1/f^x$ where $P(f)$ represents the power at frequency f, *a* an intercept term and χ the exponent of the spectrum.

Recently, a tight relation between changes in the balance of excitatory and inhibitory activity (E:I ratio) in populations of cortical neurons and the spectral exponent has been described (Gao, Peterson, & Voytek, 2017): A reduced spectral exponent, i.e. a flatter spectrum, is linked to an increased E:I balance (Excitation>Inhibition).

Importantly, spectral exponents of human electrophysiology do not only decrease with age (Voytek et al.,

2015; Waschke, Wöstmann, & Obleser, 2017) but are also positively related to cognitive performance within individuals (Sheehan, Sreekumar, Inati, & Zaghloul, 2018). On the one hand, an age-related flattening of the power spectrum might represent a reduction in inhibitory activity that comes with age. On the other hand, a momentary relative increase of excitation could foster sensory processing and cognitive performance.

Although it has been hypothesized that such a behaviorally relevant change in E:I balance might result from the selective allocation of cognitive resources to a specific task, direct evidence in favor of this mechanism is missing. Furthermore, it is unclear if and how the spectral profile of sensory stimuli influences population activity of sensory neurons and thus the spectral exponent of electrophysiological recordings.

To test and compare the influence of exogenous stimuli and endogenous modality-specific attention on the spectral exponent of human electrophysiological recordings, we chose a twofold approach: First, we validate in an open data set the spectral exponent of non-invasive electroencephalogram (EEG) recordings in humans as a proxy of E:I balance by comparing the impact of propofol and ketamine which are known to have opposing effects on the E:I balance. Second, we present evidence from an experiment during which participants (N = 25) were concurrently presented with auditory as well as visual noise and detected target sounds within one of both modalities while we recorded EEG. Importantly, both auditory and visual noise stimuli were designed to exhibit different spectral exponents in their amplitude modulation (AM) spectra ($1/f^0$, $1/f^1$, $1/f^2$, $1/f^3$) while keeping their frequency spectra identical ($1/f^0$).

Methods

EEG activity under different anesthetics

We analyzed data from a previously published study (Sarasso et al., 2015) where the EEG of healthy participants was recorded during quiet wakefulness and after the administration of several commonly used anesthetics. We here focused on the comparison between

propofol and ketamine. Thus, data from eight different participants (four per anesthetic) were used. We down-sampled EEG data to 1000 Hz and applied an acausal finite impulse response bandpass filter (.3–100 Hz, order 127) before data were split up into 5 second epochs. As recordings varied in duration, this resulted in different numbers of epochs per anesthetic and participant (propofol: 108 ±96 trials; ketamine: 76 ± 27 trials). The power spectrum of each trial and electrode between 1 and 100 Hz was estimated using the Welch method. Single trial spectral exponents were obtained with help of a novel algorithm for the parameterization of neural power spectra (Haller et al., 2018) and fitted to frequencies between 2 and 60 Hz.

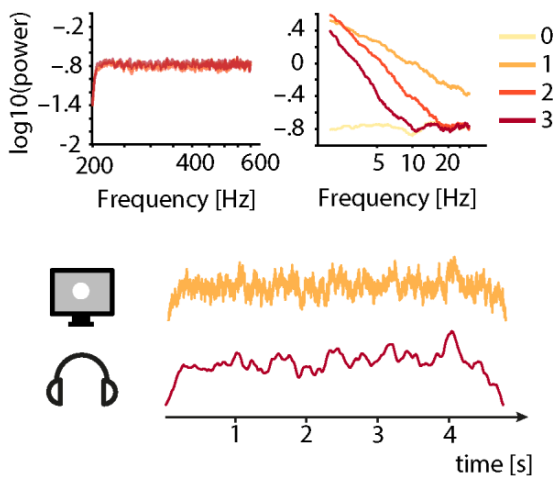## EEG during a multisensory detection task

Figure 1: Frequency spectra of used stimuli (upper left) and amplitude-modulation spectra (upper right). While frequency content was constant across conditions, AM spectra varied. Bottom: Participants watched a central disk fluctuate in luminance (orange) and listened to noise over headphones (red).

General procedure 25 undergraduate students (21 ± 3 years old, 10 male) took part in the experiment and received course credit for their participation. All participants gave written informed consent, reported normal hearing and had normal or corrected to normal vision. All experimental procedures were approved by the institutional review board of the University of California, San Diego, Human Research Protections Program.

Participants were seated in a quiet room in front of a computer screen. Auditory stimuli were presented over headphones (Sennheiser®) using a low-latency audio soundcard (Native Instruments). 64-channel EEG was recorded using the brainamp and the actichamp extension box (Brainproducts).

Auditory and visual stimuli of different AM spectra were built in three steps: First, 30 seconds of white noise (sampling frequency 44.1 kHz) were high-pass filtered at 200 Hz. Second, four random time-series of same duration but differing $1/f^\chi$ exponent ($\chi = 0$, 1, 2, or 3) were generated using an inverse Fourier transform and low-pass filtered at 100 Hz. Finally, separate multiplication of the white noise carrier with the modulators of different spectral shape resulted in four signals that only vary in their AM but not in their frequency spectra (see Fig. 1). The same noise was used for auditory and visual stimulati after root mean square normalization (auditory) or down-sampling to 85 Hz and scaling between 0.5 and 1 (visual). Noise stimuli presented during the experiment were cut out from the 30 s long time-series. All stimuli were generated using custom Matlab® code. Participants were concurrently presented with auditory and visual noise and were instructed to detect faint regular amplitude modulations in one of both modalities. While auditory noise was presented via headphones, visual noise was displayed as a disk in the center of the screen which fluctuated in luminance across time. The experiments essentially represented a balanced 4 (AM spectral exponent: 0, 1, 2, 3) x 2 (Modality-specific attention: auditory vs. visual) design and consisted of 54 trials per condition, resulting in a total of 432 trials. Trials were presented in 12 blocks of 36 trials each. The modality participants were instructed to attend alternated between blocks and was randomized for the first block. Importantly, AM exponents were uncorrelated between modalities across trials. Participants pressed the space bar whenever a target sound occurred in the attended modality. Targets consisted of short sinusoidal amplitude modulations (6–7.5 Hz, 400 ms) and modulation depth was varied throughout the experiment to keep performance around 70 % correct.

Prior to each trial, the central white fixation cross changed its color to green and back to white. After 500 ms the presentation of noise in both modalities started simultaneously. Trials ended with the central fixation cross re-appearing on the screen, lasted between 4 and 4.5 seconds and were separated by silent inter-trial intervals (2–3.25 s). After each experimental block, participants received feedback in form of a percentage correct score and were asked to take a break of at least one minute before continuing.

EEG pre-processing and analyses Artifacts representing heartbeat, movement, eye blinks or saccades and channel noise were removed using independent component analysis based on functions from the fieldtrip and EEGlab toolboxes (Delorme & Makeig, 2004; Oostenveld, Fries, Maris, & Schoffelen, 2011). Continuous EEG signals were referenced to the average of all 64 channels and filtered between 0.3 and 100 Hz. Data was segmented into trials between -1 and 5 seconds peri-stimulus. Trials containing artifacts were removed based on visual inspection. Single trial power spectra between 1 and 100 Hz were calculated based on the EEG signal between 600 ms after noise onset and the appearance of a target sound. The FOOOF

package (Haller et al., 2018) was used to estimate single trial spectral exponents fitted between 2 and 60 Hz. We used linear mixed models to analyze both the tracking of spectral exponents in sensory stimuli as well as the impact of modality-specific attention on the trial level. This approach allowed us to model the spectral exponent of the EEG at one electrode as a function of stimulus spectral exponents and attention while at the same time controlling for a number of covariates such as trial number or the number of samples used to estimate spectra in a given trial. We fitted one model per electrode and used FDR correction to control for multiple comparisons (Benjamini & Hochberg, 1995).

Results

The spectral exponent of human EEG captures changes in E:I balance

First, we contrasted spectral components of human EEG recordings between quiet wakefulness and anesthesia for two different anesthetics: propofol and ketamine. While propofol is known to result in a net increase of inhibition, ketamine results in a relative increase of excitation (Sarasso et al., 2015). In accordance with modelling work and invasive recordings (Gao et al., 2017), propofol anesthesia should thus lead to an increase in the spectral exponent and Ketamine anesthesia to a decrease. As can be discerned from Figure 1, spectral exponents of the human EEG indeed were sensitive to the effect of different anesthetics: Exponents increased under propofol and decreased under ketamine anesthesia in all participants.
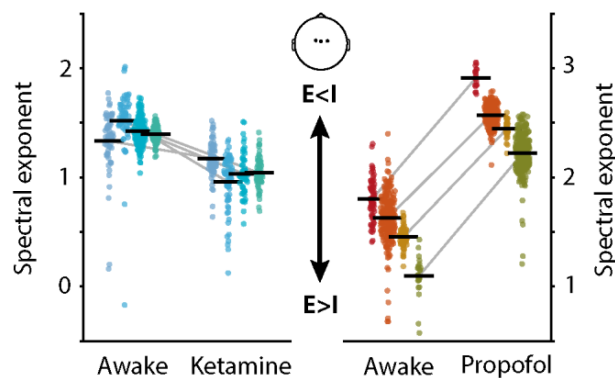

Figure 2: Spectral exponents averaged over 3 central EEG channels (inset) decrease during ketamine anesthesia (left panel) but increase under propofol. Single dots represent 5 second snippets, vertical bars the average within a participant.

The EEG spectral exponent tracks 1/f stimulus characteristics and modality-specific attention

Second, we modeled the spectral exponent during each trial of the detection task as a function of modality-specific attention and the spectral exponents of the auditory and visual stimuli presented during the respective trial. EEG spectral exponents were positively related to the exponents of sensory stimuli and hence tracked stimulus characteristics on the level of single trials (Fig. 3).
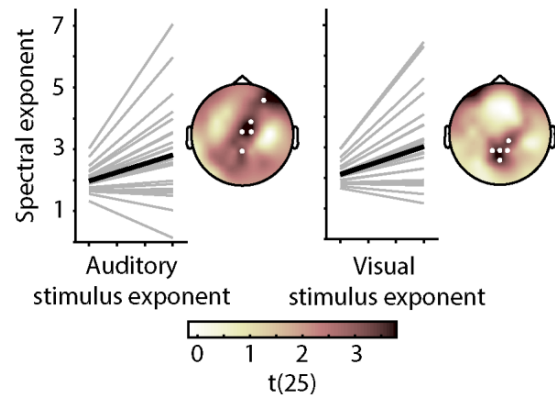

Figure 3: EEG spectral exponents track auditory stimulus exponents at fronto-central channels (left panel) and visual stimulus exponents at occipital channels (right panel). White dots mark electrodes where $p < .05$, FDR corrected. Thin lines represent single participants, black line the average.

Furthermore, the topography of the tracking effect appears reminiscent of brain activity from different sensory regions: while the tracking of auditory stimuli peaks over fronto-central electrodes, pointing to generators in auditory cortices, the tracking of visual stimuli is located over occipital channels. Importantly, our analyses revealed no meaningful interaction of attentional focus and stimulus tracking (all $p > .1$). Thus, auditory and visual stimulus characteristics were tracked regardless of the current attended modality.
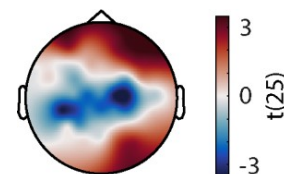

Figure 4: Average EEG spectral exponents contrasting auditory versus visual attention trials (auditory – visual). Exponents over central channels were reduced during auditory attention trials, and over frontal and occipital channels during visual attention trials, respectively.

Modality-specific attention itself, however, led to a reduction in the EEG spectral component over sensory

specific regions (Fig 4). The subtraction of average EEG spectral exponents during trials of visual attention from trials of auditory attention resulted in a clear negative cluster over central regions and a positive cluster over frontal and occipital channels.

Discussion & Conclusion

Here, we investigated the potency of the EEG spectral exponent to track exogenous stimulus features on the one hand and endogenous processes like selective attention on the other hand.

Importantly, the spectral exponent of openly available EEG data showed a tight negative relationship with E:I balance: Exponents were elevated during propofol-induced relative increases in inhibition but reduced during relative excitation increases through ketamine anesthesia (Fig. 2). Those findings do not only replicate but also clarify earlier results regarding the impact of ketamine (Colombo et al., 2019) and establish the EEG spectral exponent as a non-invasive marker of E:I balance.

Furthermore, EEG spectral exponents tracked the spectral shape of sensory stimuli in a modality-specific manner. EEG-channels informative of stimulus spectral exponents varied between modalities and were reminiscent of sources in auditory or visual cortices, respectively. Those results speak to a tracking of stimulus features which is not realized through the rhythmic entrainment of neural activity but rather through the pooled activity of rate-sensitive neurons as previously proposed for audition (Garcia-Lazaro, Ahmed, & Schnupp, 2006). Although stimulus features were tracked regardless of the currently attended modality, modality-specific attention led to a reduction of EEG spectral exponents over channels linked to signals from sensory-cortical regions of the attended domain. This suggests an increase in excitatory activity via feedback connections following the selective allocation of cognitive resources to a sensory modality, as previously proposed by modeling work (Chance, Abbott, & Reyes, 2002).

In sum, the spectral exponent of the human EEG depicts pronounced changes in E:I balance inuced by different anesthetics. More importantly, the EEG spectral exponent does not only track stimulus characteristics but also depicts more subtle changes in E:I balance that follow the selective allocation of attentional resources.

Acknowledgements

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