

# Cortical excitability shapes somatosensory perception with spatiotemporally structured dynamics

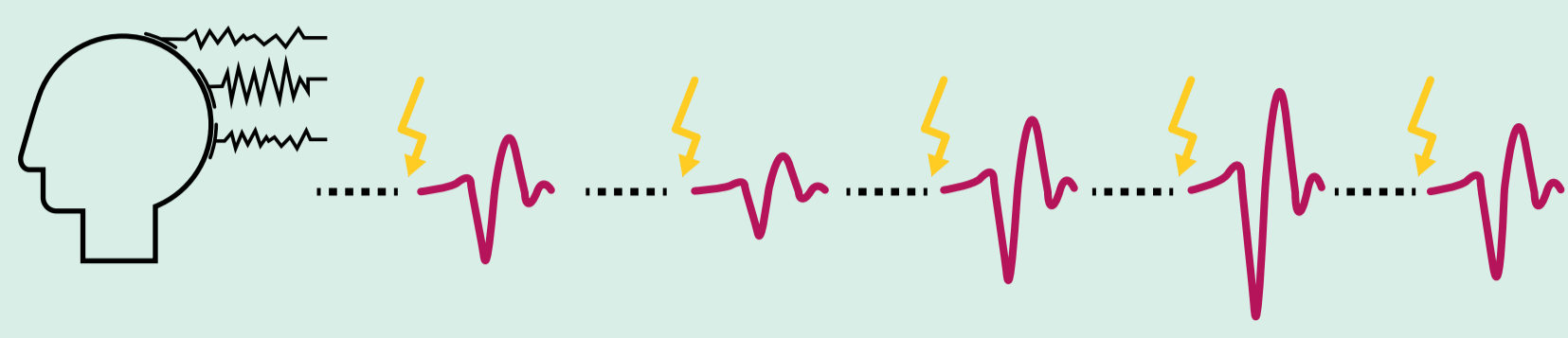
T. Stephani<sup>1,2</sup>, A. Hodapp<sup>1</sup>, M. Jamshidi Idaji<sup>1,2,3</sup>, B. Nierula<sup>4</sup>, F. Eippert<sup>4</sup>, A. Villringer<sup>1,5,6</sup> & V. V. Nikulin<sup>1,7,8</sup>

<sup>1</sup>Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany | <sup>2</sup>International Max Planck Research School NeuroCom, Leipzig, Germany | <sup>3</sup>Machine Learning Group, Technical University of Berlin, Berlin, Germany | <sup>4</sup>Max Planck Research Group Pain Perception, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany | <sup>5</sup>MindBrainBody Institute, Berlin School of Mind and Brain, Humboldt University Berlin, Berlin, Germany | <sup>6</sup>Clinic for Cognitive Neurology, University Hospital Leipzig, Leipzig, Germany | <sup>7</sup>Neurophysics Group, Department of Neurology, Charité - Universitätsmedizin Berlin, Berlin, Germany | <sup>8</sup>Bernstein Center for Computational Neuroscience, Berlin, Germany

contact: stephani@cbs.mpg.de | @TilmanStephani



## Introduction



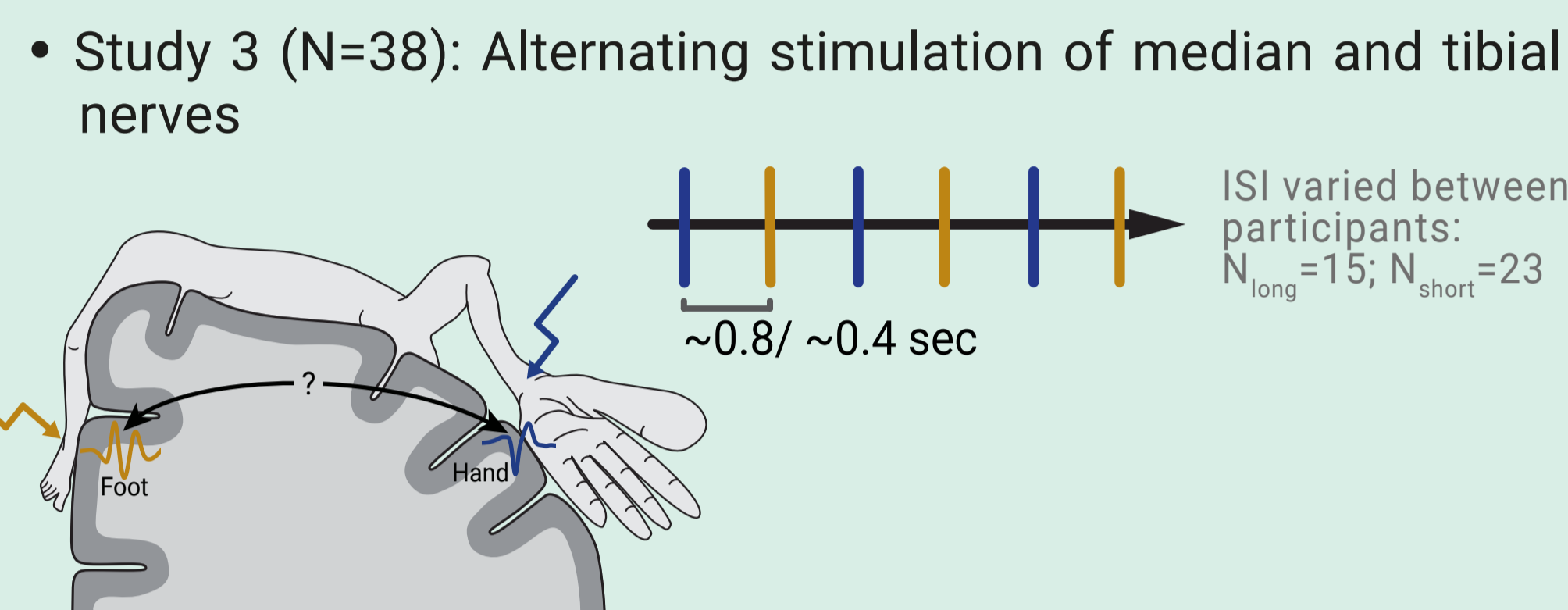
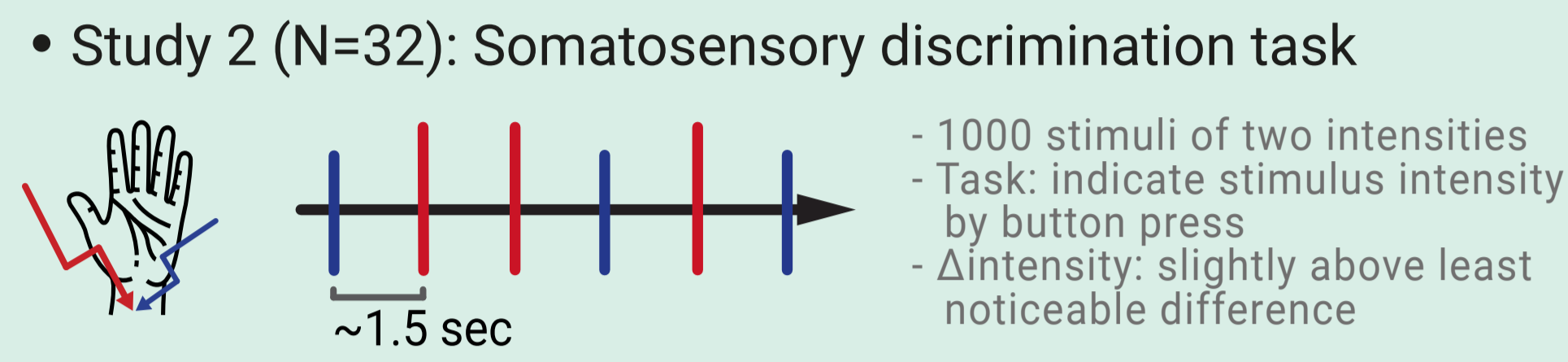
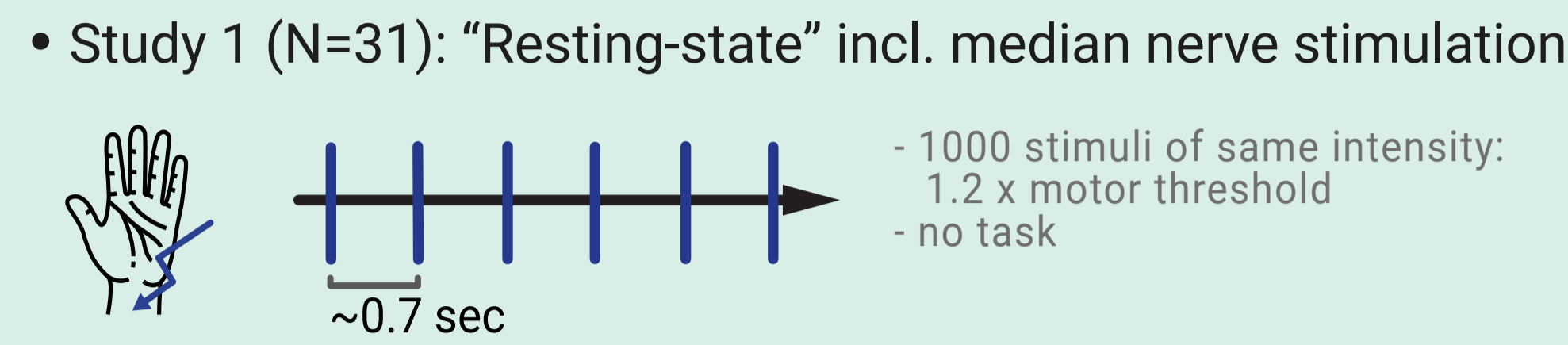
In perception, no neural response is exactly the same, even to identical sensory stimuli – why?

- Moment-to-moment variability of sensory processing is associated with instantaneous changes of cortical excitability. [1-4]
- Yet it is unclear how these dynamics are organized and on which level the modulation of perception takes place.

1. What is the temporal structure of spontaneous fluctuations of cortical excitability?
2. How do excitability changes relate to the intensity perception of sensory stimuli?
3. Do these fluctuations reflect local or global dynamics?

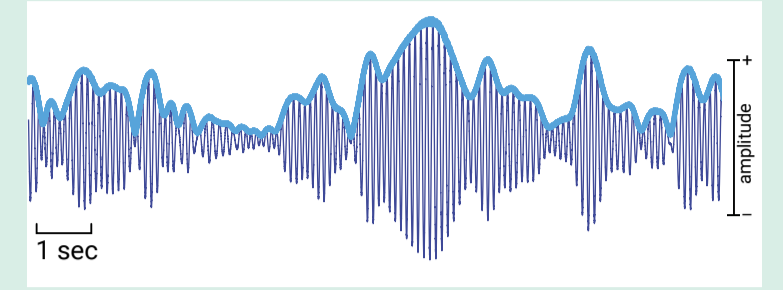
## Methods

- Three somatosensory stimulation paradigms in humans

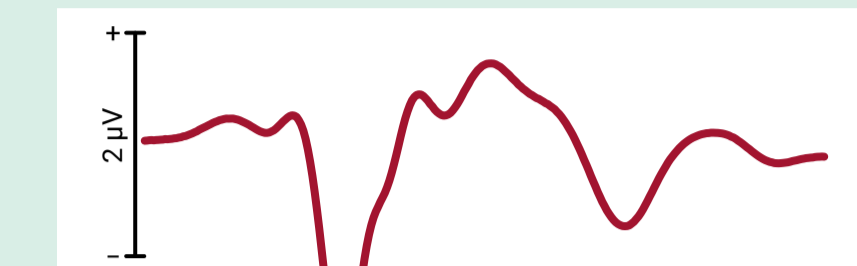


- EEG measures of cortical excitability

a) Pre-stimulus oscillatory activity in the alpha band (8-13 Hz) of the EEG [4-7]



b) N20 component of the somatosensory evoked potential (SEP)

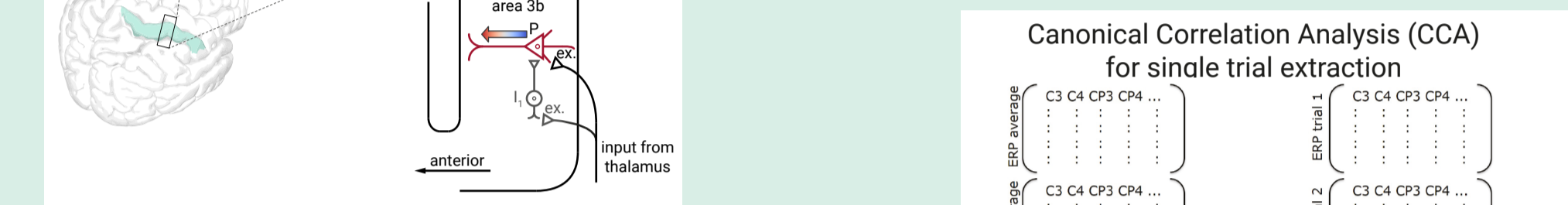


- reflects initial excitatory post-synaptic potentials (EPSP) in Brodmann area 3b [8-10]

- direct measure of cortical excitability in response to median nerve stimulation

- Single-trial SEPs extracted using Canonical Correlation Analysis (CCA) [11]

- homologous component in tibial nerve stimulation: P40 component

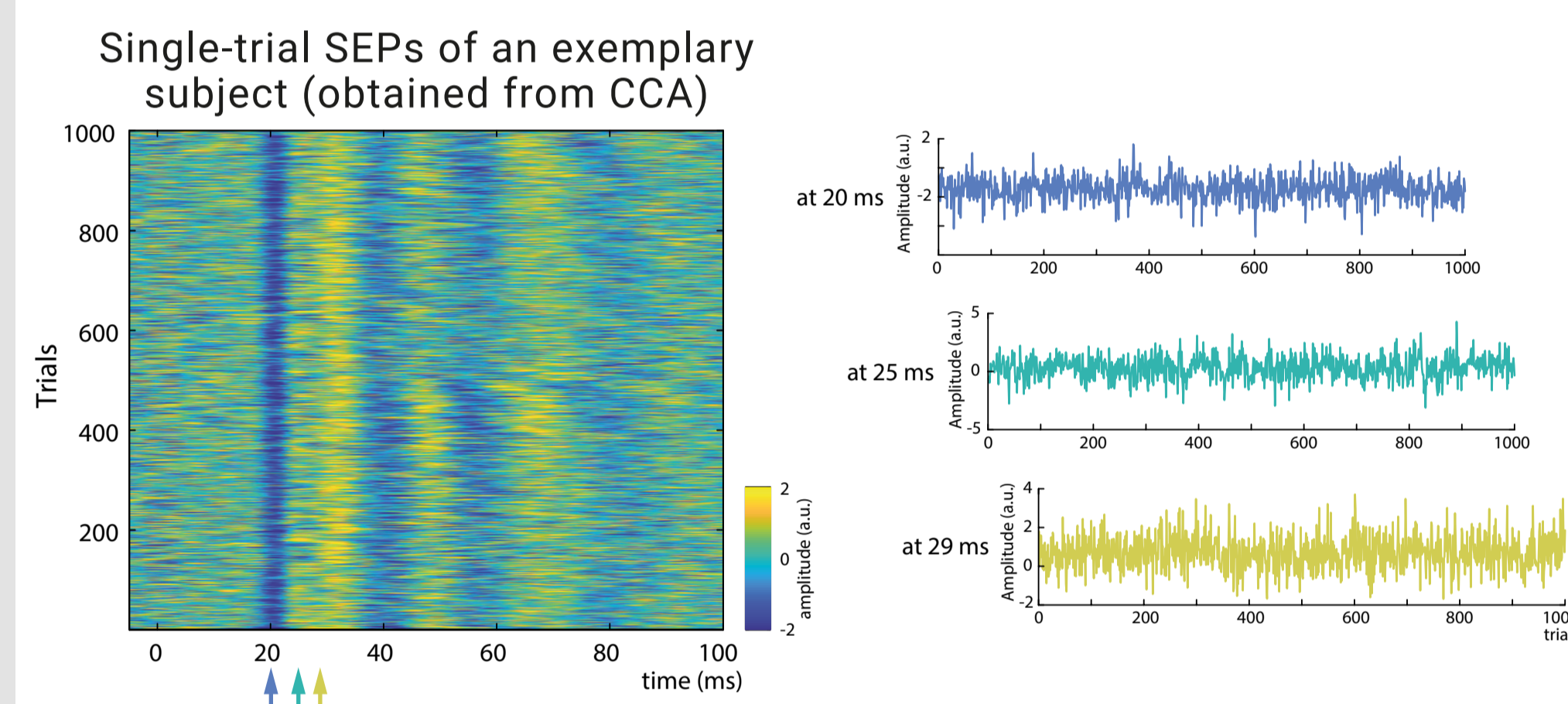


- Additional peripheral measures:

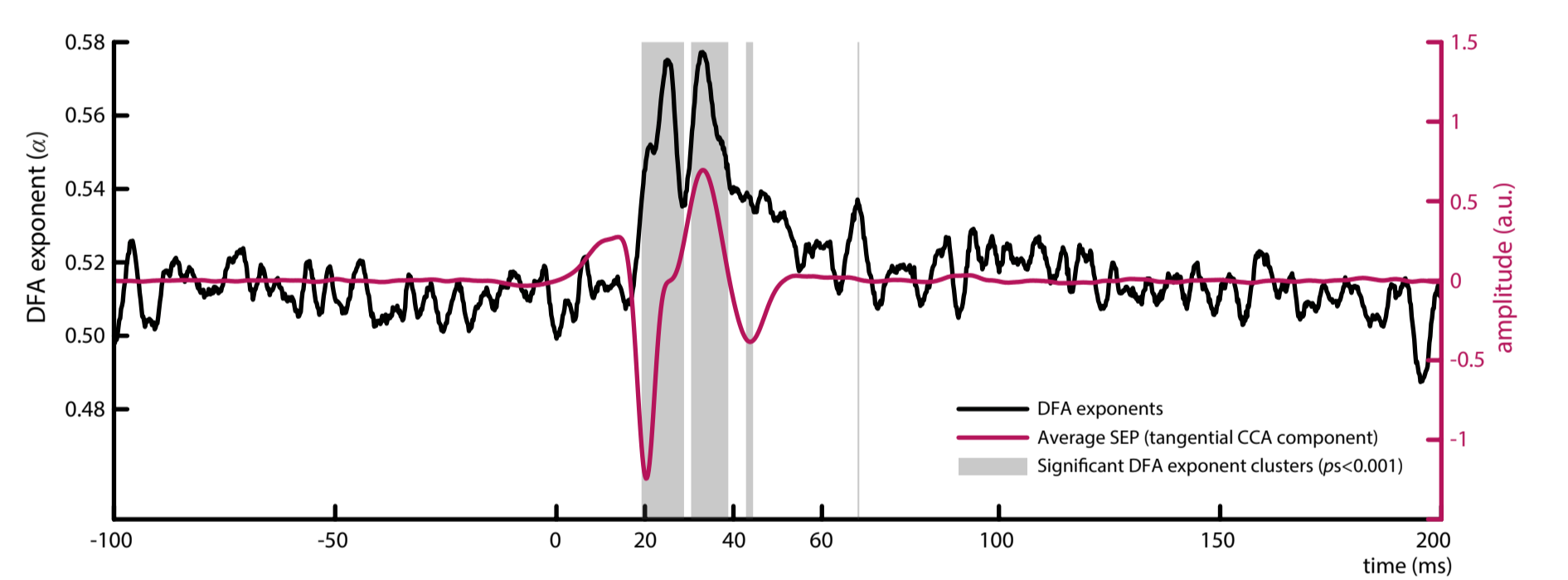
- CNAP (compound nerve action potential)
- CMAP (compound muscle action potential)

## Results

### Study 1 Signatures of criticality in excitability fluctuations



### Grand average of DFA exponents and SEP



- Variability in cortical excitability is of a special type: power-law dynamics in early SEP amplitudes over trials ("scale-freeness"), quantified using Detrended Fluctuation Analysis (DFA) [12]:

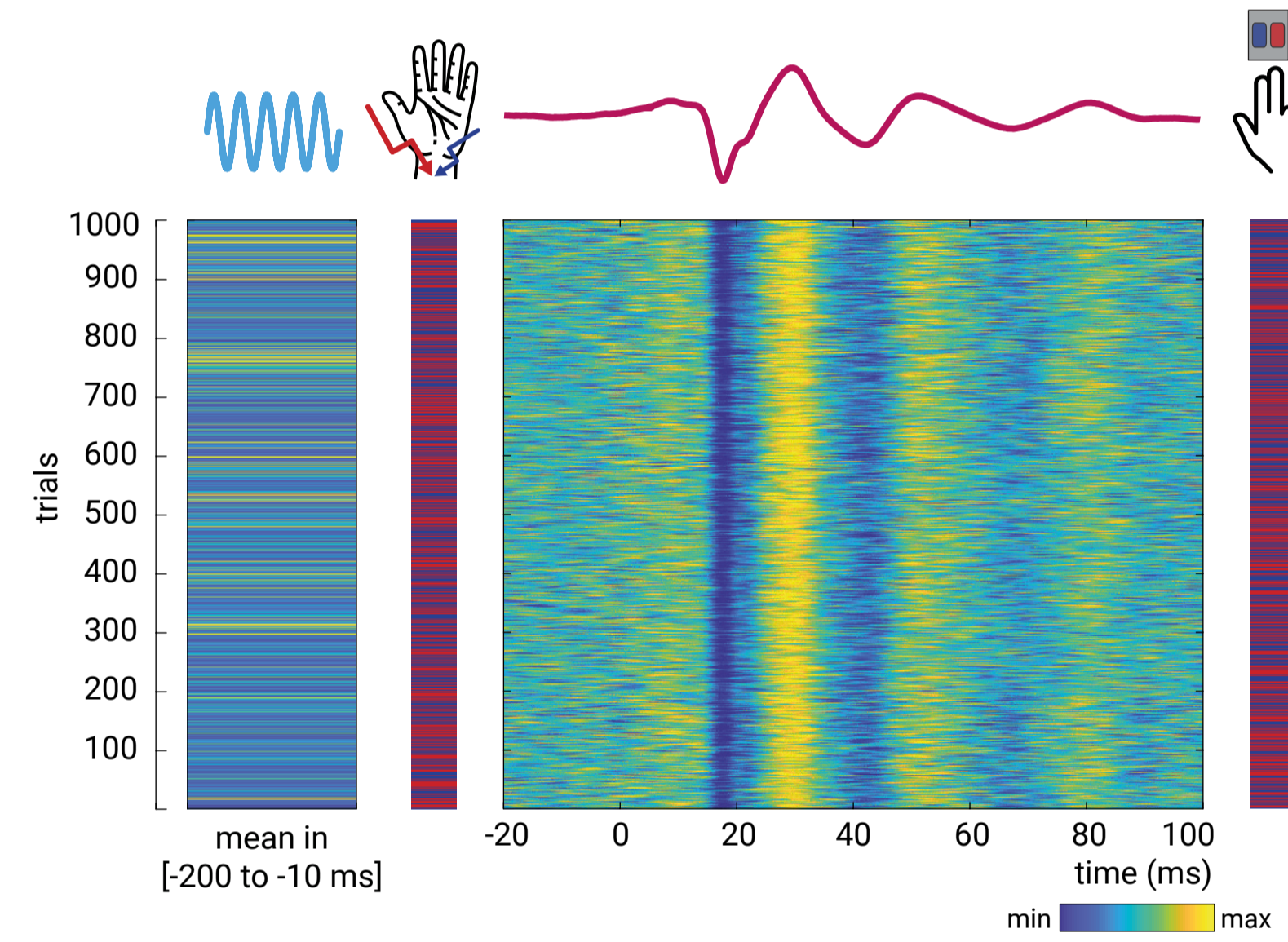
$$F(\tau) \sim \tau^\alpha$$

- Signature of (self-)organization of a system at a so-called critical state [13-15]

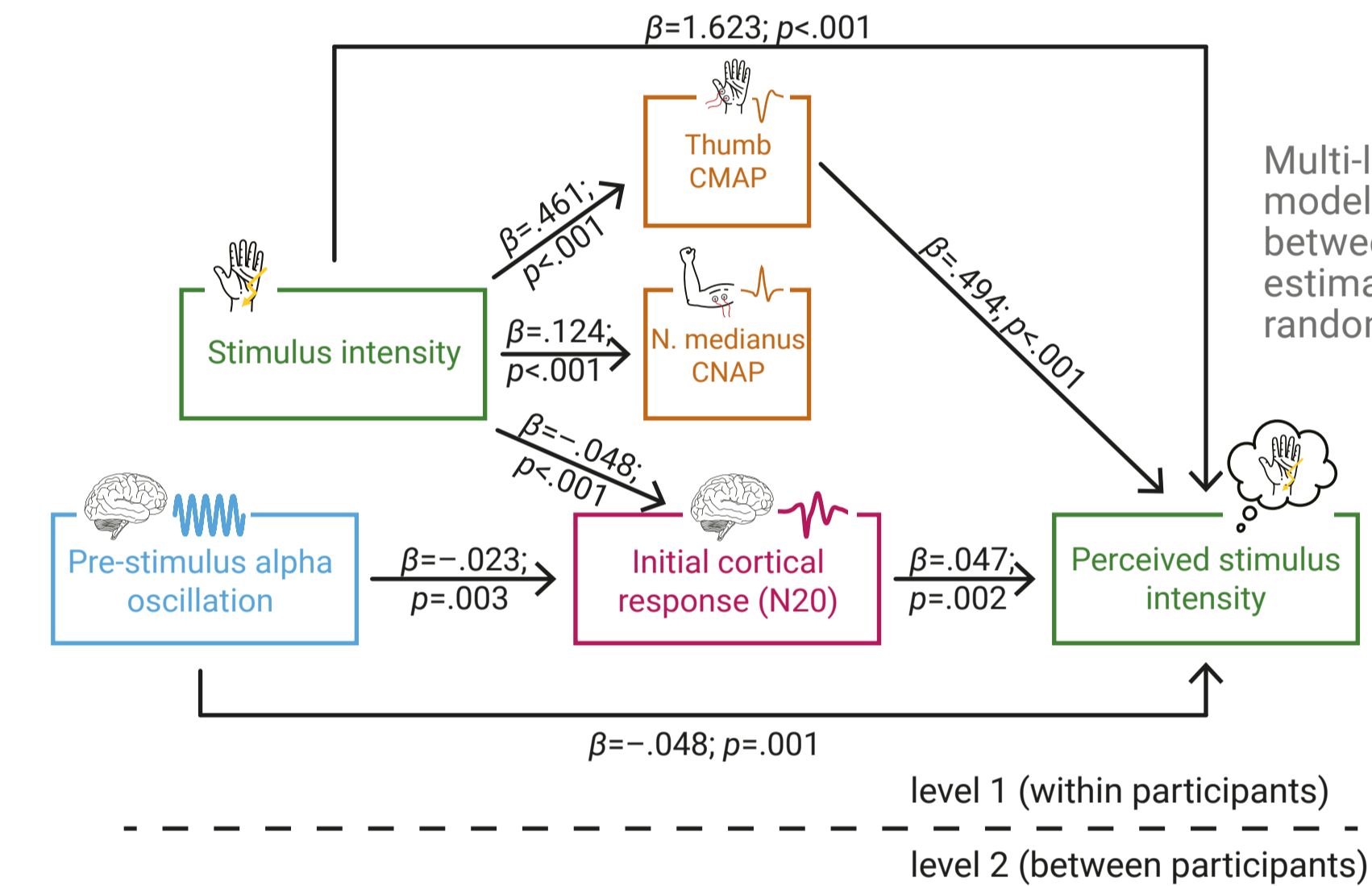
Stephani, Waterstraat, Haufe, Curio, Villringer & Nikulin, 2020, JNeurosci

### Study 2

### Relation between instantaneous excitability and perceived stimulus intensity



- Neural excitability shapes the perceived stimulus intensity already during the very first cortical response (~20 ms)
- Reflected both in fluctuations of pre-stimulus alpha oscillatory activity (8-13 Hz) and single-trial SEPs

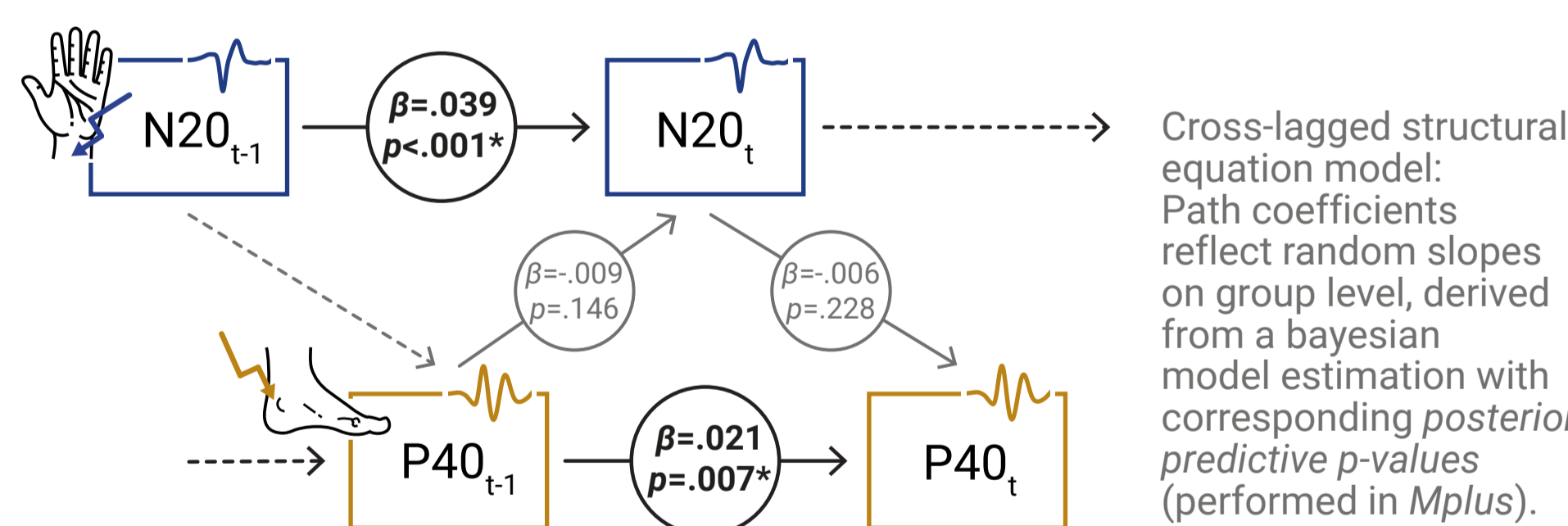


Multi-level structural equation model (SEM) with effect paths between manifest variables estimated on level 1 and random intercepts on level 2.

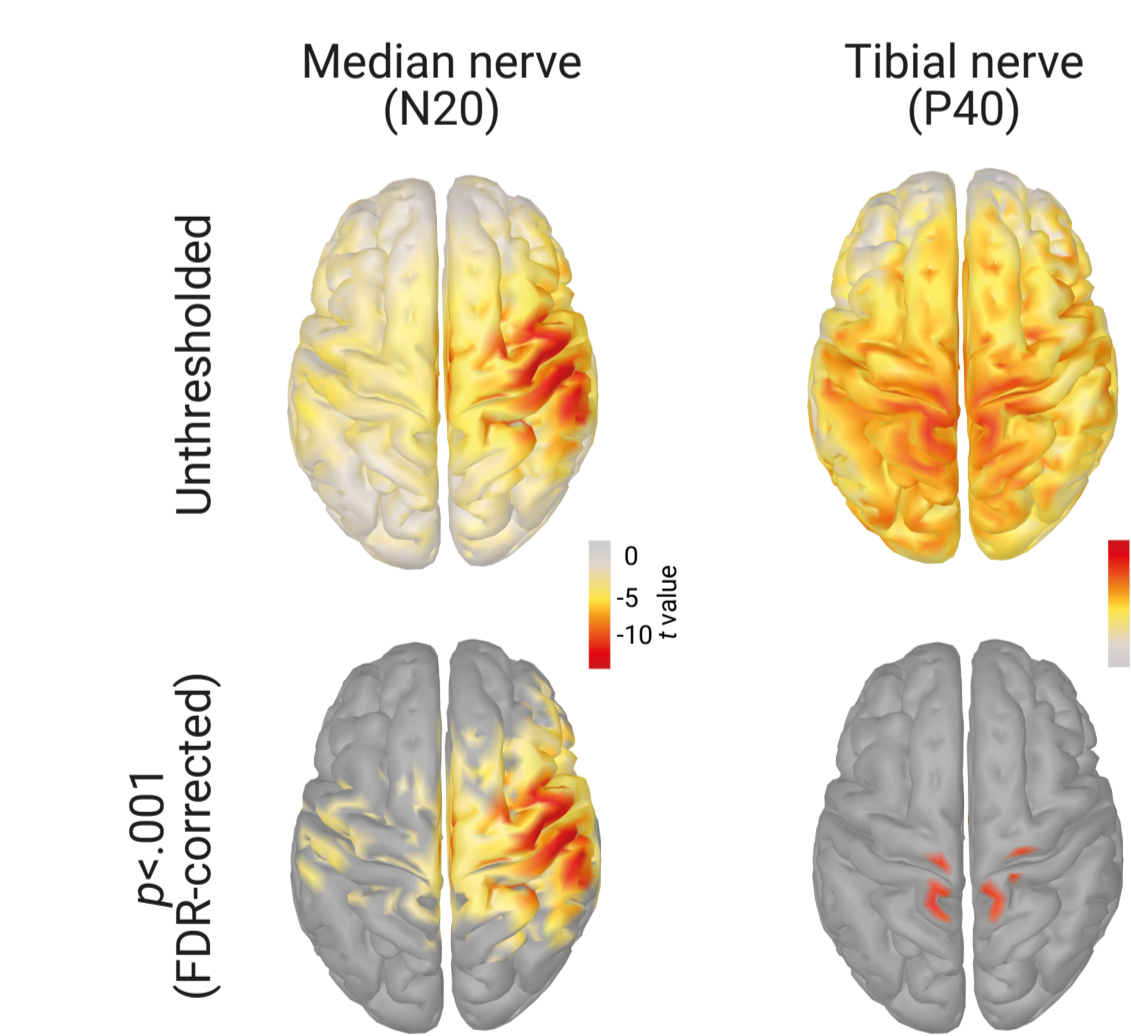
Stephani, Hodapp, Jamshidi Idaji, Villringer & Nikulin, 2021, eLife

### Study 3

### Local dynamics of cortical excitability with somatotopic organization



- Temporal dependencies within but not between stimulation sites
- No influence on effects by ISI and by peripheral nerve activity (not shown here)



Linear mixed effects models in source space:  
 $N20 \sim 1 + \text{prestimulus alpha}_{\text{vertex } i} + (1|\text{subject})$   
 $P40 \sim 1 + \text{prestimulus alpha}_{\text{vertex } i} + (1|\text{subject})$

Analysis pooled across long and short ISIs (N=38).

- Effects show a somatotopic organization (spatial specificity)

Stephani, Nierula, Villringer, Eippert & Nikulin, 2022, NeuroImage

## Discussion

1. Cortical excitability fluctuates over time with a temporal structure that is characteristic for dynamics near a critical state.

→ Possible benefits: dynamic range, information processing and capacity are maximized [16,17]

2. Changes of cortical excitability influence how strong stimuli are perceived from earliest cortical processing onwards.

→ In line with previous findings on alpha oscillations [18,19] and extending to supra-threshold stimuli

→ Opposing signatures of stimulus intensity and excitability in initial cortical responses (may reflect the EEG's sensitivity to post-synaptic currents not potentials)

3. Spatially confined neural state-response dynamics: Excitability fluctuations are organized somatotopically.

## Conclusion:

**Spontaneous fluctuations of cortical excitability do not occur stochastically independently (=random noise) but reflect structured system dynamics (=functional signals) with behaviorally relevant consequences for perception.**

## References

- [1] Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: Gating by inhibition. *Frontiers in human neuroscience*, 4, 186.
- [2] Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain research reviews*, 53, 82-98.
- [3] Samaha, J., Iemi, L., Haegens, S., & Busch, N. A. (2020). Spontaneous Brain Oscillations and Perceptual Decision-Making. *Trends in cognitive sciences*, 24, 639-653.
- [4] Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., & Thut, G. (2008). Spontaneous fluctuations in posterior alpha-band EEG activity reflect variability in excitability of human visual areas. *Cerebral Cortex*, 18, 2010-2018.
- [5] Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *The Journal of Neuroscience*, 29, 7869-7876.
- [6] Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus alpha phase predicts visual awareness. *The Journal of Neuroscience*, 29, 2723-2732.
- [7] Forschack, N., Nierhaus, T., Müller, M. M., & Villringer, A. (2017). Alpha-Band Brain Oscillations Shape the Processing of Perceptible as well as Imperceptible Somatosensory Stimuli during Selective Attention. *The Journal of Neuroscience*, 37, 6983-6994.
- [8] Allison, T., McCarthy, G., Wood, C. C., & Jones, S. J. (1991). Potentials Evoked in Human and Monkey Cerebral Cortex by Stimulation of the Median Nerve. *Brain*, 114, 2465-2503.
- [9] Wikström, H., Huttunen, J., Korvenoja, A., Virtanen, J., Salonen, O., Aronen, H., & Ilmoniemi, R. J. (1996). Effects of interstimulus interval on somatosensory evoked magnetic fields (SEFs): A hypothesis concerning SEF generation at the primary sensorimotor cortex. *Electroencephalography and Clinical Neurophysiology/ Evoked Potentials Section*, 100, 479-487.
- [10] Brynäs-Haylett, M., Luo, J., Kennerly, A. J., Harris, S., Boorman, L., Milne, E., Vautrelle, N., Hayashi, Y., Whalley, B. J., Jones, M., Berwick, J., Riera, J., & Zheng, Y. (2017). The neurogenesis of P1 and N1: A concurrent EEG/LFP study. *NeuroImage*, 146, 575-588.
- [11] Waterstraat, G., Fedele, T., Burghoff, M., Scheer, H.-J., & Curio, G. (2015). Recording human cortical population spikes non-invasively—An EEG tutorial. *Journal of Neuroscience Methods*, 250, 74-94.
- [12] Kantelhardt, J. W., Koscielny-Bunde, E., Rego, H. H., Havlin, S., & Bunde, A. (2007). Detecting long-range correlations with detrended fluctuation analysis. *Physica A: Statistical Mechanics and its Applications*, 295, 441-454.
- [13] Begg, J. M., & Plenz, D. (2003). Neuronal Avalanches in Neocortical Circuits. *The Journal of Neuroscience*, 23, 11167-11177.
- [14] Linkenkaer-Hansen, K., Nikouline, V. V., Palva, J. M., & Ilmoniemi, R. J. (2001). Long-Range Temporal Correlations and Scaling Behavior in Human Brain Oscillations. *The Journal of Neuroscience*, 21, 1370-1377.
- [15] Palva, J. M., Zhigalov, A., Hirvonen, J., Korhonen, O., Linkenkaer-Hansen, K., & Palva, S. (2013). Neuronal long-range temporal correlations and avalanche dynamics are correlated with behavioral scaling laws. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 3585-3590.
- [16] Kinouchi, O., & Copelli, M. (2006). Optimal dynamical range of excitable networks at criticality. *Nature Physics*, 2, 348-351.
- [17] Sheu, W. L., & Plenz, D. (2013). The functional benefits of criticality in the cortex. *The Neuroscientist*, 19, 88-100.
- [18] Limbach, K., & Corballis, P. M. (2016). Prestimulus alpha power influences response criterion in a detection task. *Psychophysiology*, 53(8), 1154-1164.
- [19] Orabona, M., Poliakoff, E., Eidsdreyer, W., Klapouschik, E., S. Lloyd, D. M. (2017). Pre-stimulus alpha oscillations over somatosensory cortex predict tactile misperceptions. *Neuropsychologia*, 96, 9-18.

