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Supplemental Information

Phase-Coded Oscillatory Ordering Promotes the Separation of Closely Matched Representations to Optimize Perceptual Discrimination

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Supplemental Data Items

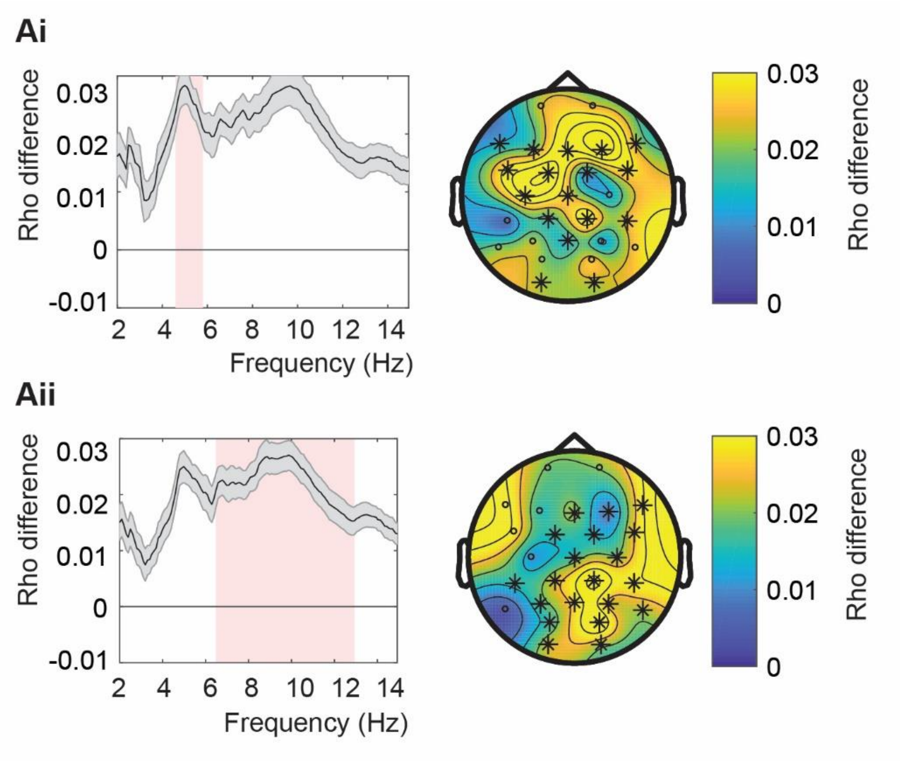

Figure S1. Phase opposition analysis, related to Figure 3. The theta (A) and alpha (Aii) clusters are displayed. The left panels display the correlation difference relative to the permuted correlation for the channels included in the cluster. Shaded grey areas indicate the standard error of the mean. Pink areas include the frequencies belonging to the cluster. The right panels display the topographies for the respective significant frequency bins. Asterisks indicate the channels included in the cluster.

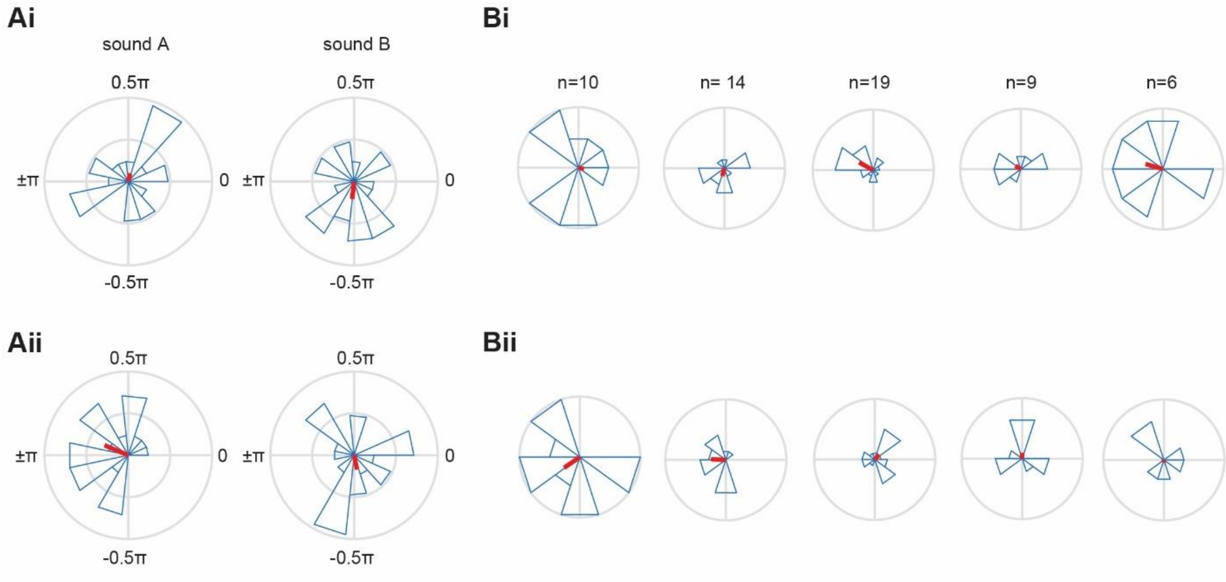

Figure S2. Phase specific effects, related to Figure 3. A) For the maximum t-value in the cluster the phase histograms of sound A and sound B are presented (over subjects) for the theta (Ai) and alpha (Aii) cluster. B) Phase difference between sound A and B split up for different sound types (sound 5-9) for the theta (Bi) and alpha (Bii) cluster.

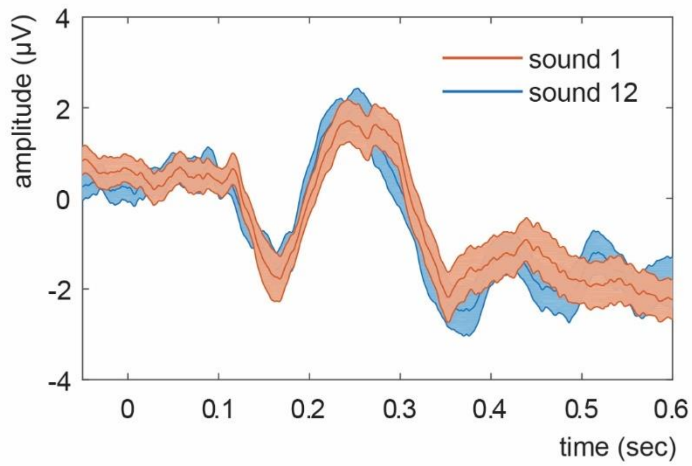

Figure S3. ERPs of the two extremes sounds, related to Figure 4. Shaded area indicates the standard error of the mean.

Transparent Methods

Experimental model and subject details

Participants

Twenty-one participants completed the experiment (participants' demographics were not recorded). All were informed about the experiment after given informed consent. The study was approved by the local ethical committee at the Faculty of Psychology and Neuroscience at Maastricht University (ethical approval number: ECP-127 14_04_2013). Participants received course credits or monetary compensation for their time.

Method details

Stimuli and procedure

Ripple sounds were presented to the participants consisting of 50 logarithmically spaced sinusoids spanning 5 octaves. Sounds had varying velocities (six velocities linearly spaced between 1 and 1.63 cycles/second) and densities (0.25 and 0.125 cycles/octave). The fundamental frequency determined the category boundary, which was arbitrarily set at 200 Hz. Six sounds were created in each category and were logarithmically spaced 7.2 until 26.1 Hz away from the category boundary. Modulation was set to 100 percent and sounds lasted for 500 ms.

First, participants were provided with some examples of extremes of both categories to familiarize them with the sounds. Subsequently, they performed one block of baseline categorization to which they did not get any feedback (not reported here). During the main experiment sounds were randomly presented and participants had to identify the sounds as either belonging to category A or B. Which sound was categorized as A or B was counterbalanced over participants. Participants were required to close their eyes during the whole sessions and received auditory feedback to their performance. The interval after the participant's response and the next sounds was jittered between 1.5 and 2.5 sec. In total there were four blocks in which 576 sounds were presented in total, lasting approximately 35 minutes. EventIDE was used for stimulus presentation (OkazoLab Ltd, The Netherlands) and sound were presented via ER-30 insert earphones (Etymotic Research) at a comfortable sound level.

EEG recordings and pre-processing

32 channels EEG data was recorded with Brain-Vision Recorder (Brain Products; BrainCap MR). Channels included: Fp1, Fp2, F2, F3, C4, C4, P3, P4, O1, O2, F7, F8, PO3, PO4, P7, P8, Fz, Cz, Pz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, CP6, Oz, and A1. A2 was used as online reference, and Afz as ground. Three additional channels were included to measure eye movements (left and right from outer cantus and below the left eye). Data was recorded at a 5000 Hz sampling rate using hardware filters

with a bandpass of 0.01-1000 Hz and an additional 100 Hz low-pass software filter. A BrainAmp MR Plus EEG amplifier was used. Impedance was kept below 10 kiloOhm.

For the pre-processing we cut the data from -3 to 2 around sound onset. Data was re-referenced to the average of all channels, demeaned, and resampled to 1000 Hz. Bad trials were removed via visual inspection and bad channels were interpolated. ICA was performed to remove remaining eye movements and muscle artefacts.

Quantification and statistical analysis

Behavioural analysis: We fitted a psychometric curve to the data assessing the proportion that the participant identified the sounds as sound A (for the participants with reversed categorization, we recoded the sound identities). A psychometric function was fitted to this data using a probit function (guessing and lapsing rate at 0, using the frequency as independent variable, and proportion sound A as dependent variable; Modelfree fitting toolbox version 1.1. (Zchaluk and Foster, 2009)). For later analysis we extracted the 20 and 80 percentile for each participant.

EEG phase-categorization correlation: for frequencies ranging from 2 to 15 Hz (in steps of 0.1 Hz) we extracted the phase at stimulus onset. We did this by cutting the data 3 cycles prior to sound onset until sound onset and performing a fast Fourier analysis with Hanning tapers. Thus, for each frequency another window was chosen. All analyses were restricted to sounds that were identified below 80% correct to avoid ceiling effects. Still, to ensure that the effects were not due to physical differences in the stimuli, we performed a GLM with a binomial distribution on the response choice data (sound A or sound B) per participant with stimulus type as factor to remove any effects of stimulus type. The residuals of this analysis were used in a circular-linear correlation with pre-stimulus phase. The same correlation was repeated for 1000 times using permuted labels of the categorization, thereby creating a null distribution for the correlation. Dependent samples t-tests were performed between the actual correlation and the median of each individual's null distribution. Cluster statistics was used to correct for multiple comparisons ('nonparametric_individual' cluster threshold, with 'maxsum' clusterstatistics. We tested one-sided as circular-linear correlations are only positive;(Maris and Oostenveld, 2007)). The same analysis was repeated but using the phase opposition index as proposed in (VanRullen, 2016).

Positive clusters were further investigated by extracting for the maximum t-value within the cluster the phase angles per participant. We performed a Rayleigh test of the mean phases for sound A and sound B categorization over participants to test for phase consistency over participants. To test for any systematic phase clustering the phase opposition index (VanRullen, 2016) was calculated per participant. Group statistics was performed by inversing the p-values of the permutations of individual participants to z-values and performing a z-test.

EEG phase-accuracy correlation: Instead of modulating the response of the participants, phase could modulate the behavioural performance of the participant, as previously found for detection studies(Mathewson, Gratton, Fabiani, Beck and Ro, 2009; Ten Oever, Van Atteveldt and Sack, 2015; Busch, Dubois and VanRullen, 2009; Hanslmayr, Volberg, Wimber, Dalal and Greenlee, 2013). To test this hypothesis, we repeated the same analysis was performed as described above in *"EEG phase-categorization correlation"*, but instead the correlation was based on phase with residuals of the accuracy instead of categorization.

Phase dependent TRF: For the significant *EEG phase-categorization correlation* frequency bins we investigated whether the evoked responses' similarity to either one of the two sound categories was also modulated by phase. To do so, we estimated the temporal response function (TRF) for each trial with the sound envelope of pitch 1 sounds and the envelope of pitch 12 sounds. The TRF is an encoding model and is calculated via the linear convolution of a specific input (here, the sound envelope) with a measured output (here, EEG), thereby providing an estimation over time how well the systems output can be estimated with a particular input property (Crosse, Di Liberto, Bednar and Lalor, 2016; Lalor, Power, Reilly and Foxe, 2009). The envelope was estimated by zero padding the sounds with 100 ms on either side, extracting the absolute of the Hilbert transform and resampling the sounds to 1000 Hz (matching the sampling rate of the EEG). EEG was epoched for -0.1 – 0.6 seconds around sound onset. Trials with sound pitches that were identified under 80% accuracy were extracted and for each trial we estimated the TRF with sound envelope of pitch 1 and pitch 12 sounds (using envelopes of sounds matching the velocity and density of the original sounds) using the mTRF toolbox (Crosse, Di Liberto, Bednar and Lalor, 2016). The lambda of the estimation was set to a 1000, based on fitting the TRF of the trials containing the extreme sounds (independent trials).

To estimate phase dependency of the estimated TRF we subtracted for each trial the TRF estimated with pitch 12 sound envelopes from the TRF estimated with pitch 1 sound envelopes (TRF1-TRF12). This TRF difference was used in a circular correlation with pre-stimulus phase (at frequencies determined by the *EEG phase-categorization correlation* analysis, using the same pre-stimulus estimates).

Estimating the circular correlation on the TRF difference allowed us to control for baseline TRF amplitude shifts caused by a different phase at stimulus onset: the baseline shift would be subtracted out from the TRF12-TRF1 calculation. Thereby, we could investigate whether the amplitude of the TRF1 vs TRF12 was modulated by the phase at stimulus onset, that is, whether the EEG response resembled sound 1 or sound 12 more dependent on the phase of the sound presentation. The TRF difference estimates were statistically compared to an estimated chance correlation calculated with permuted TRF difference – pre-stimulus phase comparisons (n = 500; using the median of the null distribution for each participant per time-frequency point). Dependent samples t-tests were performed between the actual correlation and the median of each individual's null distribution. Cluster statistics were used to correct for multiple comparisons ('nonparametric_individual' cluster threshold, with 'maxsum' clusterstatistics. One-sided alpha).

The same analysis was repeated but subtracting the TRF of the correct sound category of the TRF from the incorrect sound category at frequency ranges identified in the "*EEG phase-accuracy* *correlation".* If phase modulates the accuracy of the participants, it is expected that the difference between TRF for correct and incorrect sound categories is bigger for specific phase ranges.

Behavioral and TRF phase comparison: The phase of the behavioral and TRF results were compared by calculating the phase difference per participants. The phase of the behavior was estimated from the frequency and channel of the maximum t-value within the cluster. The phase of the TRF was estimated at the time point of the maximum t-value within any cluster at the channel of the behavioral effect. The non-uniformity of the phase difference around zero was tested using the v-statistics.

Performance- phase-modulation correlation: In the final analysis we investigated whether the strength of this phase modulation had an influence on their overall discrimination performance. As such we extracted for each participant the phase modulation index: the difference between the observed correlation from the median of the null distribution divided by the median of the null distribution. This was extracted for all frequency ranges previously identified to influence behavioural responses, for the phase modulation of discrimination and accuracy. This phase modulation index was correlated with the slope of the psychometric curve, an index of how well participants could discriminate the sounds. A positive correlation would indicate that participants with stronger phase modulation had a higher discriminative performance.

Supplemental References

Busch, N.A., Dubois, J. and VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. The Journal of Neuroscience 29, 7869-7876.

Crosse, M.J., Di Liberto, G.M., Bednar, A. and Lalor, E.C. (2016). The multivariate temporal response function (mTRF) toolbox: a MATLAB toolbox for relating neural signals to continuous stimuli. Front. Hum. Neurosci. 10, 604.

Hanslmayr, S., Volberg, G., Wimber, M., Dalal, S.S. and Greenlee, M.W. (2013). Prestimulus oscillatory phase at 7 Hz gates cortical information flow and visual perception. Curr. Biol. 23, 2273-2278.

Lalor, E.C., Power, A.J., Reilly, R.B. and Foxe, J.J. (2009). Resolving precise temporal processing properties of the auditory system using continuous stimuli. J. Neurophysiol. 102, 349-359.

Maris, E. and Oostenveld, R. (2007). Nonparametric statistical testing of EEG-and MEG-data. Journal of neuroscience methods 164, 177-190.

Mathewson, K.E., Gratton, G., Fabiani, M., Beck, D.M. and Ro, T. (2009). To see or not to see: prestimulus α phase predicts visual awareness. J. Neurosci. 29, 2725-2732.

Ten Oever, S., Van Atteveldt, N. and Sack, A.T. (2015). Increased stimulus expectancy triggers low-frequency phase reset during restricted vigilance. J. Cognit. Neurosci. 27, 1811-1822.

VanRullen, R. (2016). How to evaluate phase differences between trial groups in ongoing electrophysiological signals. Front. Neurosci. 10, 426.

Zchaluk, K. and Foster, D.H. (2009). Model-free estimation of the psychometric function. Attention, Perception, & Psychophysics 71, 1414-1425.