





Words and pseudowords elicit distinct patterns of 30-Hz EEG responses in humans

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Abstract

Meaningful words, such as *moon*, and physically similar but meaningless pseudowords, such as *moom*, were presented visually in a lexical decision task. The EEG was recorded from 17 scalp electrodes. Significant differences between both stimulus classes were observed in evoked spectral responses of the ' γ -band' ~30 Hz. A hemisphere by wordness interaction demonstrated that 30-Hz spectral power over the left hemisphere was reduced after pseudowords only. These results indicate that γ -band responses reflect the different cognitive processes induced by words and pseudowords. A possible explanation is the following. Synchronous activation of large cortical cell assemblies takes place after word presentation but not after presentation of pseudowords.

Key words: 30 Hz; Cell assembly; Cognitive; EEG; Evoked spectral response; Lexical processing; γ -Band; Language

Recent neurophysiological research has provided strong evidence that coherent oscillations of large groups of neurons are of utmost significance for neuronal processing. This evidence comes from single- and multi-unit recordings in animals' brains. When moving bars are presented, neurons of primary and higher-order visual cortices get simultaneously active at a rate that may vary within the ' γ -band' (20–100 Hz) [6]. This led researchers to speculate that γ -band oscillations reflect a fundamental mechanism of cortical information processing, namely of binding of neurons that process sensory information into cell assemblies. Such cell assemblies are candidate devices for the representation of 'gestalt' and 'meaning'.

While it is obvious *that* synchronous oscillations play a role in perception and in neuronal processing in general, it is not yet clear *what* specific role they play. Whenever a cybernetic system is forced to deviate from its stable state, it may exhibit some oscillatory activity before reaching another stable state. Thus, periodic activity

On the cortical level, word presentation most likely leads to activation of neuronal cell assemblies. When humans produce and perceive words, neuron ensembles in the perisylvian cortex become frequently active at the same time and, therefore, strengthen their connections (Hebb's law) so that they develop into strongly coupled cell assemblies [3,5]. Since pseudowords are rarely perceived or produced, it is quite unlikely that cell assemblies develop that correspond to them. Therefore, word presentation should lead to cell assembly activation

in the brain could be a trivial by-product of sensory stimulation. However, it may well be that periodic activity indeed 'means' higher-order cortical (and/or subcortical) processing. In this case, distinct patterns of periodic activity should correlate with specific modes of cognitive processing. It is possible to test this prediction by using two classes of stimuli that invoke different higher-order processes, while having the same perceptual complexity, for example words and meaningless combinations of letters, i.e. pseudowords, such as *surm*, *harf* or *fasp*. If words and pseudowords are equally long and made up by the same letters, it is guaranteed that both stimulus classes are of equal perceptual complexity but, nevertheless, trigger distinct cognitive processes.

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(ignition) while pseudoword presentation should not cause such an ignition. If assembly ignition is followed by fast inhibitory processes, coherent periodic activity in the γ -range can be explained as a consequence of the ignition process. This predicts that word presentation followed by cell assembly ignition should lead to stronger γ -band responses compared with pseudoword presentation. Such differences may be visible on large-scale measures, such as the EEG. When thousands of neurons become active simultaneously, they cause potential changes which can be detected in the EEG [4,11]. In this paper, we report an experiment investigating spectral EEG responses following word and pseudoword presentation.

15 right-handed native-speakers of German with at least 14 years of formal education were paid for their participation. None of the subjects had left-handed family members. 128 stimuli, 64 German words and 64 pseudowords, were selected. All items consisted of two syllables and were matched for length (four to eight letters). All words had high frequencies of occurrence (>50/ Mio.). Stimuli appeared in pseudo-random order on a computer screen 2.5 m away from the subjects. Stimulus presentation time was 100 ms; stimulus onset asynchrony varied randomly between 3.5 and 4.5 s. Subjects had to decide as fast and accurately as possible whether the stimuli presented were meaningful words of German or not. Yes/no responses were carried out with the left hand by pressing a switch to the left or right. Switch direction and word/pseudoword decisions were counterbalanced between subjects. The EEG was recorded using a cap carrying 17 tin electrodes. To monitor activity over the perisylvian language cortex, the following recording sites were selected. P3/P4 of the 10/20 system were moved one-tenth of the nasion-inion distance away from P_z ('angular electrodes') and T3/T4 were moved the same distance towards Cz ('Sylvian electrodes'). Two additional pairs of electrodes were placed half-way between the Sylvian electrodes and F7/F8 ('Broca electrodes') and between the Sylvian electrodes and the angular electrodes ('Wernicke electrodes'). Furthermore, F3, F4, F7, F8, C₂, C3, C4, O1 and O2 were chosen. Note that over each hemisphere, a lateral row of electrodes was placed over the perisylvian cortex and its vicinity (frontal (F7/8) Broca – sylvian – Wernicke – angular – occipital (O1/ 2)). Six Ag/AgCl electrodes were used for reference and for monitoring eye movements. These were placed on the mastoids, above and below both eyes. All impedances were kept below 3 k Ω . All channels were recorded with a C₂ reference and converted off-line to linked mastoids. Signals were recorded in the 0.0796-70-Hz band and sampled with 200 Hz. Trials, including artifacts >100 μ V caused by blinks or eye movements, were excluded. The EEG was recorded for 1.28 s/trial (256 data points), starting 0.1 s before word onset (100 ms baseline). Only trials with correct lexical decisions were analysed.

All recording sites were projected on a sphere approximating the standard head shape. Average spherical coordinates of electrodes were taken or calculated from Lagerlund et al. [9]. Potential distributions were interpolated on the sphere using spherical splines [14]. The interpolation between two adjacent projections of recording sites was based on the angle between them and the weighted sum of Legendre polynomials. Next, 2-D spherical Laplacians were calculated and current source densities (CSDs) were estimated for the 17 recording sites [14]. CSDs were obtained for each time point of each trial. Compared with raw EEG data, CSD analysis makes it possible to calculate activity at critical electrodes independently of the activity at the reference electrode. In addition, this procedure enhances the contribution of local brain activity to the signal, while global contributions of distant sources are minimized [7,10]. Note that using raw EEG data would make it impossible to determine whether spectral responses are generated at the critical electrode or at the reference, and whether they are influenced by generators distant from the electrodes. Normalized average evoked spectral responses were calculated in the following way. CSDs (256 data points corresponding to 1.28 s of recording) were first padded to zeros by using cosines, and then submitted to FFT. Amplitudes of the FFT transformed signal were multiplied by cosine-shaped windows (25-35, 35-45 and 55-65 Hz). Subsequently, the filtered signals were restored by inverse FFTs and rectified by calculating root mean squares (RMSs). These spectral power values were averaged over trials. Finally, all data points were normalized, i.e. divided by the respective baseline value. All further analyses were based on the logarithm of these normalized spectral power values. Logarithms were calculated to approximate a Gaussian distribution of power values. Mean normalized power of spectral responses was statistically evaluated for the 2×6 lateral electrodes in three time windows, 120–320 ms poststimulus onset, 320–520 ms and 520-720 ms. Data from each subject averaged over trials were submitted to ANOVAs with the factors recording site, hemisphere and wordness (word/pseudoword). In all ANOVAs, Greenhouse-Geisser epsilon values were applied to correct for lack of sphericity in the covariance matrices involving repeated measures factors with levels exceeding two.

Fig. 1 presents the results obtained from the six lateral electrodes over the left vs. right hemisphere in the frequency windows ~ 30 , 40 and 60 Hz, respectively. Because the factor electrode site did not lead to any significant main effects or interactions, data from the six lateral electrodes were averaged. Three-way ANOVAs revealed significant effects in the second time window (320–520 ms) exclusively (Fig. 2). In this interval, spectral responses ~ 40 Hz showed a significant main effect of the factor hemisphere ($F_{1,14} = 8.0$, P = 0.01) with larger signals over the right compared with the left hemisphere.

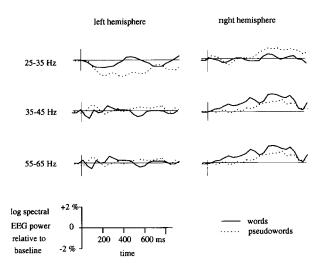


Fig. 1. Normalized spectral power (log scale) over the left and right hemisphere evoked by words and pseudowords. Data from three frequency bands (~30, 40 and 60 Hz) are presented.

Most importantly, the factors wordness and hemisphere interacted significantly in the 30-Hz frequency window $(F_{1,14} = 8.4, P = 0.01)$. Thus, between 320 and 520 ms poststimulus onset spectral power between 25 and 35 Hz reliably differentiated between words and pseudowords. Planned comparisons demonstrate that this difference was primarily due to larger power values for words compared with pseudowords over the left hemisphere (see leftmost diagram in Fig. 2). Words and pseudoword responses recorded from the left scalp were significantly different $(t_{14} = 3.07, P = 0.008)$, while there was no such difference over the right hemisphere. There was also a significant left-to-right difference for pseudowords $(t_{14} = 3.16, P < 0.007)$ but not for words. There were no reliable effects in the 60-Hz band.

In summary, evoked spectral responses revealed different activity patterns ~30 Hz evoked by meaningful words and meaningless pseudowords. Over the left hemisphere, mean 30-Hz responses to words were significantly larger compared with pseudowords in a time interval between 320 and 520 ms post-onset of visual stimuli. This pattern of spectral responses could recently be confirmed in a study investigating biomagnetic responses to auditory presentation of words and pseudowords [16].

While in the 30-Hz band a wordness by hemisphere interaction was observed, the 40-Hz band revealed a general superiority of the right hemisphere. This may reflect enhanced coherent oscillatory neuronal activity in the right hemisphere prior to onset of the finger movement (left hand) with which the lexical decision was expressed. It has earlier been reported that coherent γ -band oscillations are present in the cortex of monkeys prior to movements requiring focusing of attention [13]. In addition, enhanced γ -band activity has been observed in the ECoG, EEG and MEG of humans prior to and

during complex motor movements [12,15]. The 'right-hemisphere advantage' observed in the 40-Hz band before onset of lexical decision responses are in-line with these results.

The wordness by hemisphere interaction in the 30-Hz range cannot be due to physical differences between the stimulus classes. Words and pseudowords were equally long and they were made up of exactly the same letters. Therefore, stimuli of both classes were of equal perceptual complexity and the differences in evoked spectral responses cannot be explained as a consequence of different perceptual processes. Stronger 30-Hz responses to words compared with pseudowords are also not consistent with the assumption that enhanced oscillatory activity correlates with the state of arousal. Enhanced cortical arousal is reflected by larger negativities in the evoked potential [2]. Indeed, pseudowords usually elicit stronger negativities than words in the 300-500-ms interval [8], indicating increased arousal after pseudoword presentation. This contrasts to the 30-Hz depression after these stimuli which is, therefore, unlikely to reflect enhanced arousal.

Differential spectral EEG responses are caused by differences in neural activity in the cortex. Most effects observed in the EEG are generated by large numbers of EPSPs simultaneously present in the upper cortical layers [2]. Specific changes in the 30-Hz band of the EEG signal must be due to simultaneous activity of large neuronal populations, otherwise the signal would not spread to the recording electrodes. These populations may 'oscillate' simultaneously in the 30-Hz range. However, differential spectral responses may also result from more complex spatio—temporal patterns of neuronal activity to which large numbers of neurons contribute [1]. Coherent

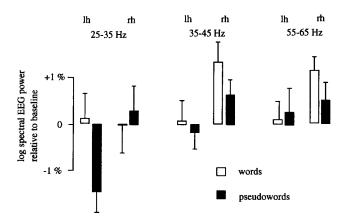


Fig. 2. Normalized spectral power (log scale) in three frequency bands (~30, 40 and 60 Hz) in the time interval between 320 and 520 ms poststimulus onset. The leftmost diagram displays the significant hemisphere by wordness interaction demonstrating depressed 30-Hz activity over the left hemisphere (lh) after pseudowords but no difference over the right hemisphere (rh). The middle diagram shows a significant main effect of hemisphere evidencing enhanced 40-Hz activity over the right hemisphere. There were no significant effects in the results from the 60-Hz band displayed in the rightmost diagram.

oscillations or repetitive spatio-temporal patterns of activity are only possible in strongly coupled cell assemblies. The present result, larger 30-Hz responses after words compared with pseudowords, is consistent with the view that neuronal assemblies are activated after word presentation but fail to 'ignite' after stimulation with pseudowords. However, words did not significantly enhance 30 Hz power above the baseline level. In contrast, pseudoword presentation led to a reduction of 30 Hz power. This can be explained if cell assembly ignition is assumed to last for several seconds, so that it can bridge the interstimulus interval between two and more trials. Word-induced 30-Hz activity would then also 'contaminate' the baseline. In this case, incoming activity which fails to lead to an ignition (pseudoword presentation) may temporarily lead to desynchronized activity in several assemblies, therefore depressing spectral responses. The fact that words and pseudowords led to different responses exclusively over the left hemisphere can be related to the left hemisphere dominance for language. Most likely, language-related neuronal activity reaches primarily the perisylvian cortex of the dominant hemisphere and differences are, therefore, visible over this site.

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