

EEG phase synchrony differences across visual perception conditions may depend on recording and analysis methods

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Abstract

Objective: (1) To investigate the neural synchrony hypothesis by examining if there was more synchrony for upright than inverted Mooney faces, replicating a previous study; (2) to investigate whether inverted stimuli evoke neural synchrony by comparing them to a new scrambled control condition, less likely to produce face perception.

Methods: Multichannel EEG was recorded via nose reference while participants viewed upright, inverted, and scrambled Mooney face stimuli. Gamma-range spectral power and inter-electrode phase synchrony were calculated via a wavelet-based method for upright stimuli perceived as faces and inverted/scrambled stimuli perceived as non-faces.

Results: When the frequency of interest was selected from the upright condition exhibiting maximal spectral power responses (as in the previous study) greater phase synchrony was found in the upright than inverted/scrambled conditions. However, substantial synchrony was present in all conditions, suggesting that choosing the frequency of interest from the upright condition only may have been biased. In addition, artifacts related to nose reference contamination by micro-saccades were found to be differentially present across experimental conditions in the raw EEG. When frequency of interest was selected instead from each experimental condition and the data were transformed to a laplacian ‘reference free’ derivation, the between-condition phase synchrony differences disappeared. Spectral power differences were robust to the change in reference, but not the combined changes in reference and frequency selection criteria.

Conclusions: Synchrony differences between face/non-face perceptions depend upon frequency selection and recording reference. Optimal selection of these parameters abolishes differential synchrony between conditions.

Significance: Neural synchrony is present not just for face percepts for upright stimuli, but also for non-face percepts achieved for inverted/scrambled Mooney stimuli.

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Keywords: Gamma band EEG activity; Neural synchrony; Visual cognition; Face perception; Mooney faces

1. Introduction

Empirical research in vision neuroscience has clearly demonstrated that visual stimulus features are processed at multiple spatially distributed cortical and subcortical brain regions. It has been hypothesized that neural synchronization in the gamma range (20–80 Hz) is the mechanism by which distributed features are integrated into unitary visual percepts

(Singer and Gray, 1995; Varela, 1995; von der Malsburg and Singer, 1988).¹ Neural synchronization (or neural synchrony) refers to the phenomenon in which neurons coding for a common representation synchronize or ‘phase lock’ their (oscillatory) firing activity within a restricted frequency band. The synchronous oscillations have been

¹ This definition of the gamma range follows Tallon-Baudry et al. (1998), and encompasses the range investigated by Rodriguez et al. (1999) (see Section 1.1). Other definitions place the lower range of the gamma band as being greater than 30 Hz (e.g. Fries et al., 2001).

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found to occur in various frequency bands, although the strongest covariations with perception occur within the gamma range. This mechanism may operate whenever component processes subserved by spatially separate brain regions are integrated (e.g. Varela et al., 2001).

The neural synchrony hypothesis has been supported by a large number of multi-unit recording studies in animals (for review, see Singer, 1999; Singer and Gray, 1995). Synchronous firings have been observed to occur within and across cortical areas, hemispheres and sensory/motor modalities. This synchronous behavior can reflect perceptual gestalt criteria and performance. A smaller number of EEG/MEG studies have investigated neural synchrony in humans with most supporting a role for synchrony in neural integration (Singer, 1999; Varela et al., 2001). The presence of gamma-range synchrony has been shown to correlate with the perception of sound and linguistic stimuli (Miltner et al., 1999; Pantev, 1995; Ribary et al., 1991), as well as characterizing REM dream states (Llinas and Ribary, 1993). Gamma range activity has also been linked to attention (Fries et al., 2001; Tiitinen et al., 1993) and working memory (Tallon-Baudry et al., 1998). Gamma range synchrony has been found to accompany object recognition (Gruber and Muller, 2002; Tallon et al., 1995; Tallon-Baudry et al. 1996, 1997), covarying with the binding of visual elements into unitary percepts, although the magnitude of synchrony can be reduced with stimulus repetition (Gruber and Muller, 2002).

Some human studies have failed to support a role for synchrony in human perception and cognition. For example, Menon et al. (1996) found that gamma range synchrony is restricted to less than 2 cm regions across surface cortex. This result argues against functional long-range synchrony in human perception. This study only examined a 7 cm × 7 cm region, however; EEG coherence has been found to drop at intermediate cortical distances, but then increase at long range distances (Nunez et al., 1997). Mima et al. (2001) found no between-condition differences for gamma range EEG coherence in response to black and white pictures of real and scrambled objects; although they found greater alpha range coherence for real versus scrambled stimuli. As recording and analysis methods have not been standardized, such differing results may arise from dissimilarities in methodology (e.g. Nunez et al., 1997).

We report an attempt to replicate an experiment reported by Rodriguez et al. (1999) demonstrating neural synchrony in human EEG when participants view upright versus inverted Mooney face stimuli. The pattern of neural synchrony we observed depended critically on our choice of which frequency bands to include in the grand average of the synchrony measures. When we used the criteria used by Rodriguez et al., we replicated their results. We came to believe that their criteria were not appropriate for our data set, however, and when we used a different criteria, we did not replicate their results. We found evidence for neural synchrony, although we observed a different pattern of

synchrony than Rodriguez et al. In addition, our investigation revealed that both reference scheme and wavelet size must be carefully considered in gathering and analyzing EEG data for evidence of neural synchrony.

1.1. Rodriguez et al.'s study

Rodriguez et al. (1999) reported results that they took as evidence for the direct involvement of gamma-range synchronous oscillatory activity in human visual perception. Participants were shown 200 ms exposures of fragmented black and white shapes (Mooney, 1956) while EEGs were recorded. When visual closure occurs, these Mooney stimuli are perceived as faces. Face perception is much more likely to occur for upright than for inverted versions of these stimuli (compare samples in Fig. 1a and b). Rodriguez et al. hypothesized that neural synchrony would be more likely to occur when observers perceived faces than when they did not. To investigate this hypothesis, they calculated gamma range (20–60 Hz) *global spectral power* and *phase synchrony* measures (summed across trials, electrodes, and subjects) for the EEG data separately for trials where upright stimuli were perceived as faces (Up/F trials) and trials where inverted stimuli were not perceived as faces (Inv/NF trials) (approximately 70% of the trials in each of these conditions). A note on the types of synchrony measures presented by Rodriguez et al., follows.

Global spectral power measures the consequences of synchronous activity rather than synchronous activity itself. When neuronal populations are synchronized, the resultant constructive summation of their electrical fields yields measurable potentials at the scalp surface. The power of this activity suggests the degree to which synchronization obtains because weakly synchronized activity leads to destructive interference and low measurable power at a given frequency. Thus, spectral power is an indirect index of neural synchrony at best. Nevertheless, it has been used extensively to assess neural synchrony in human electrophysiological studies (for review see Tallon-Baudry and Bertrand, 1999).

Global phase synchrony measures phase synchronization more directly. For instance, in the method developed by Lachaux et al. (1999, 2000), signal phases are extracted by use of wavelet transforms and used to compute the average complex phase difference between two signals across trials.² These differences are formed into an index of the variation in phase synchrony between two electrodes across trials, a *phase locking value* (PLV), ranging from 0 (no synchronization) to 1 (perfect synchronization). It should

² An additional method to compute synchronization has been developed by Tass et al. (1998) which has been shown to be equivalent to the method of Lachaux and colleagues (Le Van Quyen et al., 2001). It should also be noted that synchronization as indexed in these two methods differs from the more common coherence method to assess frequency-dependent interelectrode correlations, as phase synchrony is independent of relative amplitude covariations while the coherence measure is not (Lachaux et al., 1999).

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