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Gamma-band activity over early sensory areas predicts detection of changes in audiovisual speech stimuli

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Oscillatory activity in the gamma-band range in human magneto- and electroencephalogram is thought to reflect the oscillatory synchronization of cortical networks. Findings of enhanced gamma-band activity (GBA) during cognitive processes like gestalt perception, attention and memory have led to the notion that GBA may reflect the activation of internal object representations. However, there is little direct evidence suggesting that GBA is related to subjective perceptual experience. In the present study, magnetoencephalogram was recorded during an audiovisual oddball paradigm with infrequent visual (auditory /ta/ + visual /pa/) or acoustic deviants (auditory /pa/ + visual /ta/) interspersed in a sequence of frequent audiovisual standard stimuli (auditory /ta/ + visual /ta/). Sixteen human subjects had to respond to perceived acoustic changes which could be produced either by real acoustic or illusory (visual) deviants. Statistical probability mapping served to identify correlations between oscillatory activity in response to visual and acoustic deviants, respectively, and the detection rates for either type of deviant. The perception of illusory acoustic changes induced by visual deviants was closely associated with gamma-band amplitude at ~80 Hz between 250 and 350 ms over midline occipital cortex. In contrast, the detection of real acoustic deviants correlated positively with induced GBA at ~42 Hz between 200 and 300 ms over left superior temporal cortex and negatively with evoked gamma responses at ~41 Hz between 220 and 240 ms over occipital areas. These findings support the relevance of high-frequency oscillatory activity over early sensory areas for perceptual experience.

Keywords: Gamma-band activity; Audiovisual integration; Magnetoencephalogram; Subjective perceptual experience

Introduction

Cortical oscillatory synchronization in the gamma band range (~30–100 Hz) has been proposed as a mechanism serving to bind together the responses of feature-specific neurons into functionally coherent assemblies representing a perceptual object (Singer, 2001). Gamma-band activity (GBA) in human electro- or magnetoencephalogram (EEG and MEG, respectively) has been observed during a variety of cognitive processes including perception of coherent visual patterns (Lutzenberger et al., 1995), selective attention (Müller and Keil, 2004) and memory (Gruber et al., 2004; Herrmann et al., 2004a), see Kaiser and Lutzenberger (2003, 2005a) for recent reviews. Findings from different paradigms have suggested that GBA may reflect the activation of internal stimulus representations and thus be related to subjective perceptual experience. For example, enhanced GBA in EEG characterized the processing of illusory Kanizsa figures compared to physically similar stimuli not forming a gestalt (Tallon-Baudry et al., 1996) and MEG (Kaiser et al., 2004). The same applied to vertical, meaningful presentations of bistable figures compared with rotated, meaningless displays (Keil et al., 1999). Keeping an internal representation active in the absence of external stimulation was also associated with increased GBA. This was shown in EEG for short-term memory maintenance of visual objects (Tallon-Baudry et al., 1998). In MEG, GBA was observed with a high topographical specificity over the putative auditory ventral, pattern processing stream during the delay phase of a short-term memory task for sound patterns (Kaiser et al., 2003) and over the putative dorsal, space processing stream during maintenance of spatial sound features both during short-term memory (Lutzenberger et al., 2002) and echoic memory (Kaiser et al., 2005a).

While in these studies enhanced GBA was shown for certain stimulus classes or types of processing, there is little empirical evidence for the notion that GBA is related to perceptual awareness. Gruber et al. (2002) demonstrated that perceptual learning influenced both subjective experience and GBA: fragmented pictures that could be identified after display of their unfragmented version elicited higher parietal GBA than pictures that could not be identified. During dichoptic stimulation in strabismic cats, Fries et al. (1997) showed that neurons responding to the stimulus that continued to be perceived increased the synchronicity of their oscillatory patterning in the gamma range, whereas neurons responding to the stimulus that were no longer perceived reduced

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the synchronicity of their discharges. In epileptic patients, detection of tactile near-threshold stimuli was accompanied by gamma coherence in intracranial recordings from contralateral primary somatosensory cortex. In contrast, nonperceived stimuli of the same intensity gave rise to similar evoked potentials but did not elicit gamma synchronization, thus supporting the role of gamma activity in conscious perception (Meador et al., 2002).

The present study aimed at identifying correlations between noninvasively recorded spectral activity in humans and perceptual awareness. As the identification of correlations between subjective experience and cortical activity requires a paradigm with a high interindividual variability in perceptual performance, we chose an audiovisual integration task with a high variance in target detection rate. Infrequent incongruent combinations of acoustic and visual speech signals were presented in a sequence of standard congruent stimuli. A previous analysis showed that both visual deviants (incongruent mouth movement producing an illusory change in the acoustic percept) and acoustic deviants (real acoustic changes) were accompanied by enhanced GBA over left inferior frontal cortex (Kaiser et al., 2005b). This area forms part of the putative auditory ventral, pattern processing stream (Rauschecker, 1998; Arnott et al., 2004). Over the same region, previous auditory pattern mismatch studies using syllables, animal vocalizations and meaningless, distorted noises have already demonstrated GBA increases during passive change processing (Kaiser et al., 2002a,b), suggesting that this area is involved in the representation of acoustic pattern changes.

While the left inferior frontal GBA increase distinguished both visual and acoustic deviants from congruent audiovisual standards, the cortical correlates of the high interindividual variability in the detection rates for both types of deviants remained to be elucidated. Here, we employed a novel statistical probability mapping procedure to identify the most significant correlations between cortical oscillatory activity and detection rate. We hypothesized that high-frequency oscillatory activity reflecting the synchronization of task-relevant networks would be correlated with detection rate. GBA should be localized over multimodal integration sites if the perception of incongruent audiovisual stimuli relies on the convergence of input from the two modalities (Calvert and Lewis, 2004). Alternatively, if integration is based on interactions between unimodal areas (Bernstein et al., 2004), correlations between detection rate and GBA should be found over those early sensory areas that process the change in the relevant modality.

Materials and methods

Subjects

Twenty healthy adults gave their informed and written consent to participate in the present study. Four subjects had to be excluded because of strong posterior electromyographic activity or electrocardiogram artifacts, leaving $N = 16$ participants for further analysis (7 females, 9 males, age range: 20–40 years). The study was approved by the ethics committee of the University of Tübingen Medical Faculty.

Stimuli

Synthesized consonant–vowel syllables /ta/ and /pa/ served as auditory stimuli (duration of both events: 165 ms, voice onset time: 60 ms). Fundamental frequency amounted to 110 Hz and decreased to 90 Hz at the end of the syllables, giving the impression of a male voice. The formant frequencies of the steady-state part of the vowel /a/ were 800, 1240, 2300, 3800 and 4500 Hz for F1–F5, respectively. The two syllables predominantly differed in the consonant bursts at the onset of the sounds which contained more high-frequency components for /ta/ than for /pa/. The auditory stimuli were presented with an intensity of 70 dB(SPL). Sound intensity was not adapted to individual hearing thresholds. Digital versions of both sounds were sampled at 22050 Hz and may be obtained on request from the authors. Visual stimuli were generated by video-recording (frame rate: 25 images per second) a male German speaker uttering the same syllables /ta/ and /pa/. Movement sequences lasted for 11 images (duration: 440 ms). The onset of mouth movements preceded the onset of the acoustic stimulus by ~150 ms. As a consequence, the decisive cue differentiating between both syllables (bilabial closure with the /p/) preceded the auditory syllable onset by about 100 ms. The stimuli subtended a visual angle of ~30° and were presented on a white background. The experiment included three audiovisual stimuli: standard stimulus (auditory /ta/ + visual /ta/), acoustic deviant (auditory /pa/ + visual /ta/) and visual deviant (auditory /ta/ + visual /pa/).

Procedure

Subjects were seated upright in a magnetically shielded room (Vakuum-Schmelze, Hanau, Germany). Auditory stimuli were presented binaurally via air-conducting plastic tubes (E-A-Rtone 3A, Cabot Safety Corporation, Indianapolis, USA). These tubes lead to distortions of higher frequencies above 2 kHz (about −6 dB at 3 kHz, −20 dB at 4 kHz and −30 dB at 5 kHz). As a consequence, the upper two formant frequencies of the present stimuli were subject to some attenuation. Visual stimuli were presented on a screen about 2 m in front of the subjects. They were instructed to respond by pressing buttons with both index fingers whenever they heard a change from the standard syllable. Responses were recorded within 1-s time windows starting from the onset of the auditory stimulus. Two blocks with 400 trials each were presented. Out of the total of 800 trials, 600 (75%) were standard trials, and there were 100 (12.5%) trials each with auditory and visual deviants. Standards and deviants were presented in randomized order with a minimum of 2 and a maximum of 6 standards preceding a deviant. The stimulus onset asynchrony amounted to 750 ms. The still face was presented in the interstimulus interval (the last frame of the visual movement sequence).

Data recordings

MEG was recorded using a whole-head system (CTF Inc. Vancouver, Canada) comprising 151 first-order magnetic gradiometers with an average distance between sensors of about 2.5 cm. The amplitude resolution of the CTF system amounts to 0.3 fT, enabling the detection of high-frequency, low-amplitude signal changes. The signals were sampled at a rate of 250 Hz. The subject's head position was determined with localization coils fixed at the nasion and the preauricular points at the beginning and the end of each recording to ensure that head movements did not exceed 0.5 cm. To reduce eye movement and blink artifacts, we