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Conscious auditory perception related to long-range synchrony of gamma oscillations

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ABSTRACT

While the role of synchronized oscillatory activity in the gamma-band frequency range for conscious perception is well established in the visual domain, there is limited evidence concerning neurophysiological mechanisms in conscious auditory perception. In the current study, we addressed this issue with 64-channel EEG and a dichotic listening (DL) task in twenty-five healthy participants. The typical finding of DL is a more frequent conscious perception of the speech syllable presented to the right ear (RE), which is attributed to the supremacy of the contralateral pathways running from the RE to the speech-dominant left hemisphere. In contrast, the left ear (LE) input initially accesses the right hemisphere and needs additional transfer via interhemispheric pathways before it is processed in the left hemisphere. Using lagged phase synchronization (LPS) analysis and eLORETA source estimation we examined the functional connectivity between right and left primary and secondary auditory cortices in the main frequency bands (delta, theta, alpha, beta, gamma) during RE/LE-reports. Interhemispheric LPS between right and left primary and secondary auditory cortices was specifically increased in the gamma-band range, when participants consciously perceived the syllable presented to the LE. Our results suggest that synchronous gamma oscillations are involved in interhemispheric transfer of auditory information.

Introduction

Conscious perception has been suggested to be related to synchronized oscillatory activity in the gamma-band range of widely distributed cortical regions (Hipp et al., 2011; Meador et al., 2002; Schurger et al., 2006). Thus, it is proposed that neural assemblies participating in a specific task-relevant network or processing features related to the same perception communicate via neural synchronization (Engel and Singer, 2001; Fries, 2009). Experimental evidence is based on studies in anesthetized and awake animals but also in humans using intracranial recordings, and Electroencephalography and Magnetoencephalography (EEG and MEG), demonstrating enhanced gamma-band power and synchrony in response to consciously perceived stimuli but not to unperceived stimuli (Doesburg et al., 2005; Fisch et al., 2009; Fries et al., 1997; Panagiotaropoulos et al., 2012; Singer, 1999; Tallon-Baudry and Bertrand, 1999).

Compared to the visual system less is known about the role of gamma oscillations in conscious perception in the auditory modality, e.g. in speech perception. Earlier studies of human auditory modalities have suggested that oscillatory activity near 40 Hz represents a neurophysiological correlate that may serve perceptual integration and conscious perception of auditory stimuli (Jokeit and Makeig, 1994; Joliot et al., 1994; Pantev et al., 1991; Tiitinen et al., 1993). Interestingly, EEG and MEG studies demonstrated that the presence and subjective intensity of tinnitus, as an auditory phantom percept, are related to enhanced synchronization of gamma-band activity in the contralateral auditory cortex (van der Loo et al., 2009; Weisz et al., 2007). Enhanced gamma-band activity was also found during auditory language vs. non-language processing (Eulitz et al., 1996) and word detection tasks (Pulvermüller et al., 1996).

Auditory processing is performed in a temporo-frontal network stretching across the left and right hemispheres (Friederici, 2011). Apart from regional specialization the integrity of interhemispheric interaction has been demonstrated to play an important role in syllable perception (Pollmann et al., 2002) and speech comprehension (Friederici et al., 2007; Steinmann and Mulert, 2012). The anatomical basis for this interaction is provided by the corpus callosum (CC), through the posterior third of which (isthmus and splenium) run the

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interhemispheric auditory pathways connecting right and left auditory cortices (Aboitiz et al., 1992).

An ideal paradigm for investigating conscious auditory perception as well as the interhemispheric connectivity is the dichotic listening (DL) task (Westerhausen et al., 2009). Due to the dominance of contralateral pathways and the inhibition of ipsilateral pathways (Brancucci et al., 2004; Brodal, 1981), speech syllables presented to the left ear (LE) initially access the right hemisphere and need additional transfer across the CC to be efficiently processed in the speech-dominant left hemisphere (Kimura, 1967, see Fig. 1). Thus, the conscious perception of the speech stimuli presented to the LE requires an interhemispheric interaction between both auditory cortices and similarly is an indicator for interhemispheric transfer function.

This study addresses the question of neurophysiological mechanisms underlying the dynamic coupling of bilateral auditory cortices and auditory perception during dichotic listening. Given the extensive evidence that enhanced gamma-band activity is related to perceptual processing, we hypothesized that enhanced gamma synchrony between bilateral auditory cortices is related to the conscious perception of syllables presented to the LE. Accordingly, the primary aim of the present study was to investigate the functional role of synchronous gamma oscillations between each of the right and left primary and secondary auditory cortices during the conscious perception of syllables by means of lagged phase synchronization (LPS/Pascual-Marqui, 2007b).

Materials and methods

Participants

25 German native speakers participated in the study. All subjects gave their written consent according to the Declaration of Helsinki (1964). The general procedure was approved by the local ethics Committee. Due to EEG artifacts (see EEG recording and processing section) two participants had to be excluded from the study and 23 German native speakers (13 males, 10 females; mean age = 31.3, SD = 9.16) remained. All participants were right-handed, as assessed with the empirically validated Edinburgh Handedness Inventory (mean = 87.33, SD = 15.7; Oldfield, 1971). Exclusion criteria were left-handedness or a history of hearing, psychiatric or neurological disorders as well as severe somatic conditions. To ensure normal hearing in both ears, all participants were screened with pure tone audiometry for the frequencies of 120, 250, 500, 1000, 2000, 4000, and 8000 Hz (Esser Home Audiometer 2.0). Participants with an auditory threshold higher than 20 dB, or an interaural difference larger than 15 dB in any of the frequencies were excluded from the study. All participants had normal IQ as tested with a vocabulary test (Herzfeld, 1992; mean = 112.17, SD = 9.59). Demographic data for all participants are presented in Table 1.

Stimuli: the dichotic listening task

The Bergen dichotic listening (DL) paradigm (Hugdahl, 2003) consists of six consonant–vowel (CV) syllables /ba/, /da/, /ga/, /pa/, /ta/ and /ka/ which were used as auditory stimuli. The CV-syllables were paired and presented simultaneously: two different syllables at the same time, one to the RE and another one to the LE (Hugdahl, 2003; Hugdahl and Andersson, 1986). Three of the CV-syllables were voiced (/ba/, /da/, /ga/) and had a short voice onset time (VOT) between 17 and 32 ms, and three were unvoiced (/pa/, /ta/, /ka/) with a long VOT in the range of 75 to 80 ms. VOT describes the length of time between the release of a consonant and the onset of voicing, defined by the vibration of the vocal folds. In order to control effects of syllable voicing (Rimol et al., 2006), only syllables with the same VOT were combined, resulting in 12 possible dichotic pairs (e.g., six short/short (SS): /ba/–/da/, six long/long (LL): /pa/–/ta/). Moreover, each CV-syllable combination was temporally aligned to achieve simultaneous onset of the initial consonants. All syllables were spoken by a German male speaker with constant intensity and intonation and with duration of 400–500 ms. The experiment consisted of 240 trials, which were presented in two blocks of 120 trials. Both blocks were presented to participants with the instruction to report the syllable they heard best on each trial (non-forced condition; NF). Participants were not informed that each presentation consisted of two different syllables. Responses were made by button press using the dominant (right) hand. The number of correct responses to the right and left ear was computed. A laterality index (LI) was calculated for every subject with the following formula, adapted from Hugdahl and Andersson (1986): LI = 100 ∗ (correct RE reports − correct LE reports) / (correct RE reports + correct LE reports). The scale varies between −100 and +100 and has positive

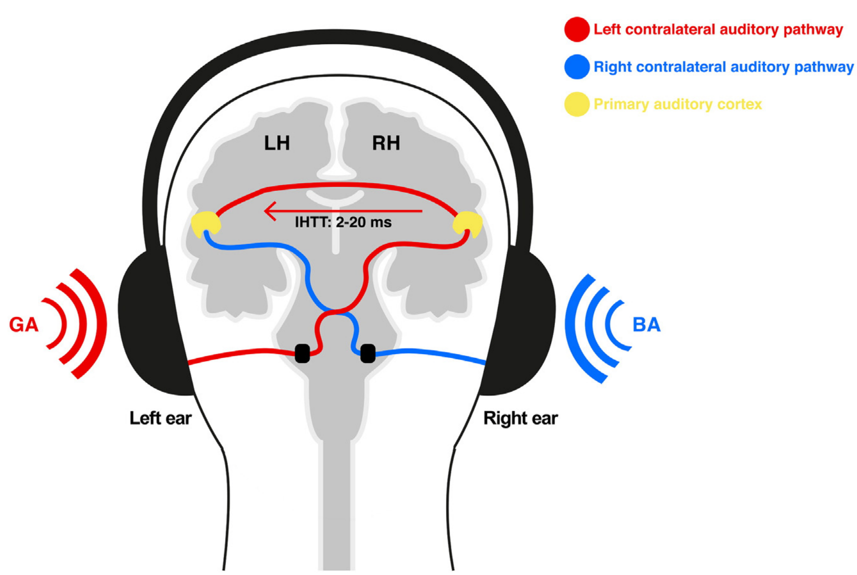

Fig. 1. Schematic illustration of the dichotic listening procedure in which two different syllables are presented simultaneously: one to the right ear (BA) and one to the left ear (GA). Although both ears are connected anatomically via ipsilateral and contralateral pathways with the auditory cortices, ipsilateral pathways are suggested to be blocked during dichotic listening (Brancucci et al., 2004). The blue line indicates the contralateral pathway connecting the RE-stimulus directly with the speech dominant left hemisphere. In contrast, the syllable arriving from the LE to the right hemisphere has to cross the CC to be efficiently processed (red line). Yellow: Right and left primary auditory cortices. LH: Left hemisphere, RH: Right hemisphere. IHTT: Interhemispheric transfer time (Henshall et al., 2012).