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Dynamic synchronization of cortical rhythmic gamma-band activity: a neural code of dexterity in human somatosensory cortex

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Abstract. To investigate neural coding characteristics in the human primary somatosensory cortices, the cortical representation of two fingers with different levels of functional skill has been focused (the thumb –high dexterous– and the little finger –low dexterous–). The finger dexterity was scored by the Fingertip writing test. In the two hemispheres, dynamic neural synchronization was analysed in the three characteristic alpha ([7, 13]Hz), beta ([14, 32]Hz) and gamma ([33, 44]Hz) frequency bands of oscillatory activity of neurons connected with the investigated fingers in primary sensory cortex. The stimulation of the thumb recruited in the dominant hemisphere a neural network more phase locked selectively in gamma band than the stimulation of the little finger. The dynamic gamma band intra-regional phase locking correlated with the contra-lateral finger dexterity, suggestings to be a coding mechanism for functional prevalence, in addition to the somatotopic central map differentiation.

Keywords: gamma band synchronization; primary sensory area; magnetoencephalography (MEG); Functional Source Separation (FSS)

1. Introduction

In the present work, intra-cerebral activity was assessed by Functional Source Separation (FSS, Barbati et al., 2006) and the dynamics of rhythmic activity synchronization phenomena was estimated within the primary finger cortical representations within the first 50 ms after simple sensory stimulation. The objective was to investigate whether specific synchronization phenomena differentiated the representation of the districts with different levels of functional skill. The thumb, considered as highly dexterous, and the little finger, considered as lowly dexterous, were studied.

In electro- and magneto-encephalographic (EEG and MEG) studies, signals from recording channels are often used to estimate synchronization phenomena: if synchronization across relatively distant brain areas is studied, this method is reliable (Gerloff et al., 1998; Simoes et al., 2003; Palva et al., 2005b); but when investigating the primary hand sensorimotor cortex, all the recording channels are significantly sensitive to the activity from the same neuronal pools. Here, it is mandatory to identify the activities of the involved neuronal sources to accurately estimate synchronization levels. On this basis, the FSS procedure was used, providing cerebral source activities along different cerebral processing phases.

2. Material and Methods

Fourteen healthy volunteers (mean age 31±2 years, 7 females and 7 males) were enrolled for the study. All subjects were right-handed with an average Edinburgh Manuality Test score of 83 ± 14. The little finger and the thumb of both hands were stimulated separately (via ring electrodes, 0.2 ms electric pulses, interstimulus interval of 631 ms, stimulus intensities at about two times the subjective perceptive threshold). Brain magnetic fields were recorded via a single positioning of a 28-channel magnetoencephalographic system on rolandic area controlateral to the stimulated side. Data were bandpass filtered through a 0.16–250 Hz and gathered at 1000 Hz of sampling rate for off-line processing.

The FSS procedure (Barbati et al., 2006) was applied to extract the activity from the two cortical neural networks representing the contra-lateral thumb (FS_T) and little finger (FS_L). The phase of band-filtered analytical signal of FS_T and FS_L were obtained. The network phase locking dynamic measure was calculated both during thumb and little finger stimulation as the stimulus-locked average of the phase difference between FS_L and FS_T. For each finger representation, an intra-cortical connectivity (ICC) index in alpha ([7, 13]Hz), beta ([14, 32]Hz) and gamma ([33, 44]Hz) frequency bands was obtained by averaging the phase locking in the time interval lasting 50 ms centred in the time point corresponding to the maximal value automatically found between 20 and 100 ms after the stimulus onset. Similarly to the phase locking index, an amplitude index was calculated in the same frequency bands with the modulus of the analytical signal.

To quantitatively estimate the sensory perception skill for each finger separately, the 'Fingertip writing' test (Lezak, 1976) was used. After having a letter "written" onto a fingertip by the experimenter, the subject had to identify the letter. The score was the time required to recognize the letters; in the case of difficulty in recognizing a letter, it was repeated until recognized.

3. Results

Functional sources describing the sensory flow in primary cortex for the thumb and little finger were successfully extracted in both hemispheres in all subjects. FS_T was located significantly more lateral, anterior and lower with respect to FS_L in both hemispheres (Figure 1, left). Both FS_T and FS_L responded with a higher reactivity for the stimulation of the finger it represents (thumb stimulation for FS_T and little finger stimulation for FS_L).

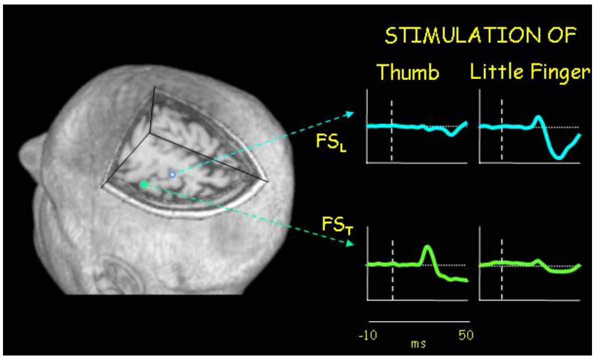

Figure 1 *In one representative subject: Left-Position of extracted thumb (green. FS_T) and little finger source (blue FS_L) in the left hemisphere. Right-Dynamics of FS_L (first row) and FS_T (second row) activities obtained as the average of the source signal timed on the stimulus onset (t=0, vertical dashed line) in the [-10, 50] ms time window following the stimulation of the contra-lateral thumb (first column) and little finger (second column).*

The right hand Fingertip writing test score was lower for the thumb than for the little finger, i.e. the thumb was more dexterous than the little finger, while the two fingers' Fingertip writing test scores were not differentiated in the left hand. No other effects were found.

Only in the gamma band, the ICC was higher for thumb stimulation than for little finger stimulation in the left hemisphere. No difference was found in the right hemisphere (figure 2, right).

Higher levels of gamma band ICC corresponded to higher finger dexterity for both thumb and little finger in the right hand, while no significant relationship was present between the left hand fingers and right hemisphere ICC (Table 1).

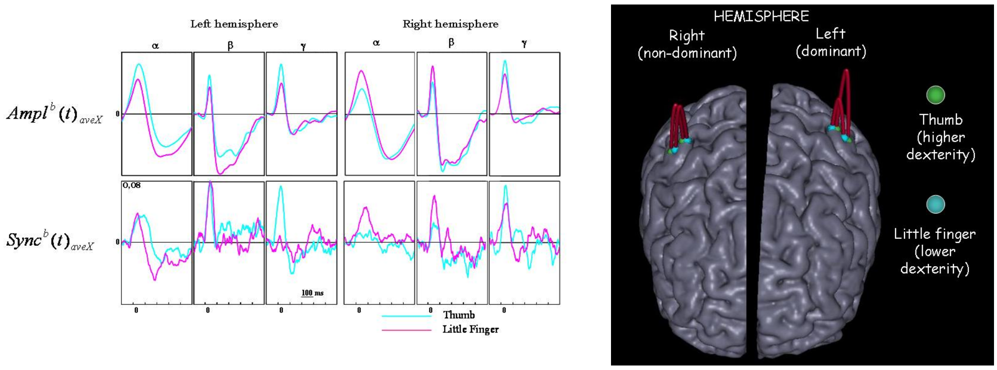

Figure 2 *Left: Phase-locking and Amplitude band dynamics. Temporal evolution (600 ms window, 0 corresponding to stimulus onset) of phaselocking (above) and amplitude (below) measures in the alpha, beta and gamma bands and in the two hemispheres, during the stimulation of the contralateral thumb (light blue line) or little finger (pink line). Scales are fixed in all conditions and the amplitude unit is omitted, as absolute values are meaningless. Right: Mean across subject of ICC in sensory areas (between finger and little finger sources) after thumb (green) and little finger (blue) stimulation. The ICC was higher for the stimulation of thumb with respect to little finger in the left hemisphere.*

	Right Hand		**Left Hand**	
	Thumb	Little finger	Thumb	Little finger
r	**-0.35**	**-0.56**	0.10	-0.05
p	**<.001**	**<.001**	>.100	>.100

Table 1 *Relationship between finger dexterity and gamma phase locking. Correlation index (r) and significance (p) corresponding to the best fitting curve* $ICC = a + b\ln(\mathrm{FtW})$ *of ICC as a function of contralateral finger dexterity. The sign of the coefficient b in the equation is attributed to r, indicating the direction of the correlation. For thumb and little finger of the right hand, higher finger dexterity (lower Fingertip Writing test score) significantly correlated with higher ICC.*

4. Discussion

In the dominant hemisphere, selectively the gamma band phase locking within the primary somatosensory neural network devoted to the more dexterous finger was found higher than that of the network controlling for the finger considered less dexterous. Moreover, the gamma band phase locking in the dominant hemisphere correlated with the contra-lateral hand finger dexterity. These properties were not present either in the other oscillatory frequency bands characteristic of the network responsiveness or for the signal amplitude. Present results indicate that synchrony with precision in the millisecond range, a key mechanism influencing goal definition, action planning and selective attention (Engel et al., 2001, 2005), becomes 'structural' of the network devoted to the most dexterous district. ICC is expression of the topology of lateral connections within cortical primary sensory areas, which are known to embody stored predictions that have been acquired both during evolution and through experience-dependent learning (Hebb, 1949; Von Stein et al., 2000; Petersen and Sakmann, 2001). The present results suggest that not only between two different executions of the same task, a network performs better when synchronizes more in the gamma band, but also between two networks executing the same task, the more intrinsically skilful synchronizes more in the gamma band.

Central information coding relies on the existence of neural links between peripheral receptors and specific cortical neuronal pools, resulting in the somatotopic, tonotopic-, retinotopic representations (Kandel and Schwartz, 1985). Present findings complement classical and unfailingly confirmed knowledge that the somatotopic representation follows the well known principle of cortical magnification, i.e. the area of the cortical surface devoted to a unit area of body surface parallels the functional importance of this latter. Thus, the thumb is represented by larger cortical areas than the little finger, as well the dominant hand cortical area is larger with respect to the non-dominant (Zappasodi et al., 2006). The presently introduced ICC index is completely independent of the number of recruited neurons, and it was higher for the finger with higher functional importance, under the same sensory stimuli impinging on the different finger central representations.

These results suggest the ICC as a coding mechanism for functional prevalence, in addition to the magnification principle of the somatotopic central maps. We suggest that a highly developed neural network uses by default the activation properties characteristic of a better performance (i.e. high gamma band synchronization), even in response to simple stimuli.

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