Abstract

As opposed to slow waves, spontaneous and stimulus-induced oscillations in the gamma-band show no polarity reversal in cortical depth, which cannot be explained by the classical equivalent current dipole model usually proposed as a model of pyramidal cell synaptic activity. Here we propose a ring-shaped distribution of dipoles as a source model for these fast oscillations. This distribution generates a field potential that does not reverse through cortical depth. Such a geometry could correspond to horizontally oriented dendritic fields. Moreover, this distribution generates a potential field, but no, or weak, magnetic field on the scalp surface, which corresponds to the observation that visually-induced gamma-band oscillations are detectable in EEG data, but not in simultaneously recorded MEG data.

Keywords: Oscillations; Gamma rhythm; 40 Hz; Potential field; Current source density; Interneurons

1. Introduction

Epochs of oscillatory synchronization in the gamma-band (30–70 Hz) have been described in a variety of species and experimental conditions, and have been suggested to play a functional role in binding (for review see König and Engel, 1995; Singer and Gray, 1995). Nevertheless, several types of fast oscillatory synchronous activity can be differentiated (Galambos, 1992; Steriade et al., 1996): spontaneous, stimulus-induced (appearing with a jitter in latency from one trial to the next), and stimulus-locked or evoked activity (appearing at a fixed latency on successive trials). The issue of the neuronal circuitry generating these synchronized oscillations remains open. In this paper, we shall focus on the cortical generators of spontaneous and stimulus-induced fast oscillations.

Steriade and Amzica (1996) and Steriade et al. (1996) reported the existence of spontaneous or stimulus-induced fast oscillations in motor, somatosensory and association areas of anaesthetized cats. In most cases these fast oscillations do not show any polarity reversal in the depth of the cortex. They are probably not due to volume conduction of distant active structures: their amplitudes decrease significantly in the underlying white matter, and their negative fields are associated with neuronal firing in both upper and deeper layers. The cortical profile of gamma-band oscillations induced by a moving bar in cat’s area 17 does not show any polarity reversal either (Eckhorn et al., 1998; Gray, unpublished data).

On the contrary, spontaneous or stimulus-induced slow waves are often reversed across the cortex (Steriade and Amzica, 1996; Steriade et al., 1996). The same holds true for most early components of the averaged evoked potential (Mitzdorf, 1991). The phase-reversals are mainly due to the activity of vertically oriented dendritic fields, like those of pyramidal cells (Nunez, 1981). The transmembrane primary currents that generate this type of phase-reversed field can be approximated by equivalent current dipoles perpendicular to the cortical surface.

Here we propose a simple ring-shaped distribution of equivalent dipoles able to produce a local field that shows no polarity reversal across the conducting medium in a limited area. This model is a distribution of current dipoles oriented tangentially with respect to the surface of the conducting medium, and radially distributed on a circumference (Fig. 1A). This model may account for the absence of polarity reversal observed in cats. Furthermore, it may also account for the discrepancy we observed in humans between electro-encephalographic (EEG) and magneto-encephalographic (MEG) data (Tallon-Baudry et al., 1997). Indeed, while visually induced gamma-band oscilla-
tions are detectable in EEG data, they are not in simultaneously recorded MEG data, as opposed to visually evoked oscillatory responses which can be observed also in MEG recordings (Lopez and Sannita, 1997; Tallon-Baudry et al., 1997). Furthermore, in a motor task, the amplitude variations of induced 40 Hz activity around movement onset was found to be larger in EEG than in MEG recordings (Sale-nius et al., 1996 ; Pfurtscheller et al., 1997). The current dipole distribution proposed here generates an electrical field, but no, or weak, magnetic field, outside the conducting medium.

2. Field pattern of the current distribution

The potential field generated by a distribution of current equivalent dipoles is usually determined in a spherical volume conductor. Nevertheless, no simple analytical expression to compute the electrical potential exists in the case of a distribution of tangential dipoles radially distributed on a circumference. As a first approximation, we can neglect the curvature of the brain and surrounding tissues and compute the electrical field generated in a semi-infinite plane conducting medium, this approximation being valid in the vicinity of the current generators.

Let us consider a uniform distribution of radial current dipoles with a moment per unit length $\nu$ on a circumference of radius $a$ (Fig. 1A). We consider the dipoles oriented outward. The results are equally valid for a ring of dipoles oriented inward – it indeed only requires changing the sign of the potential values. Let us suppose that this distribution is located in an infinite medium of conductivity $\sigma_1$. The electric potential value at a point $P(z,R)$ is given by (Durand, 1996):

\[
V(z,R) = \frac{V(0,0)}{\pi} \frac{d}{r} \left\{ J_1(k) + \frac{a^2 - R^2 - z^2}{(a-R)^2 + z^2} J_2(k) \right\}
\]

with:

\[
V(0,0) = -\frac{\nu}{2a\sigma_1}
\]

\[
r = \sqrt{z^2 + (a + R)^2}
\]

\[
k = \frac{2aR}{r}
\]

$J_1(k)$ and $J_2(k)$ are the elliptic integrals of the first and the second kind:

\[
J_1(k) = \int_0^{\pi/2} \frac{d\psi}{\sqrt{1 - k^2 \sin^2 \psi}}
\]

\[
J_2(k) = \int_0^{\pi/2} \frac{\sin^2 \psi d\psi}{\sqrt{1 - k^2 \sin^2 \psi}}
\]

These integrals can be approximated by analytical functions with errors, respectively, inferior to $2 \times 10^{-7}$ and $4 \times 10^{-4}$ in the range $0 \leq k < 1$ (Hastings, 1955). Now let us assume that the current dipole distribution is placed in a semi-infinite medium of conductivity $\sigma_1$, limited by a plane boundary, the above conductivity being $\sigma_2 = 0$. Let $h$ be the distance from the distribution center to the plane. The potential in the conducting medium can be calculated by the method of images. This potential is given by the superposition of the potentials created by two distributions:

\[
V = V_1 - A \cdot V_2
\]

$V_1$ is the potential created by the distribution placed in the semi-infinite medium of conductivity $\sigma_1$. $V_2$ the potential created by the same distribution, but placed at a distance $h$ above the boundary plane.

\[
A = \frac{\sigma_2 - \sigma_1}{\sigma_2 + \sigma_1} = -1
\]

A cross-section of this potential field passing through the center of the distribution is represented in Fig. 1B. The potential does not reverse throughout the depth of the conducting medium, inside a cylinder of radius $a$ and whose axis is passing through the center of the current dipole distribution. A maximum of potential can be observed at the depth of the current distribution. As the

Fig. 1. (A) The ring-shaped distribution proposed: current dipoles are uniformly distributed along a circumference, parallel to the surface of the conducting medium. (B) Cross-section of the electric potential field produced by a circular distribution of current dipoles below a plane interface. $\sigma_1$ and $\sigma_2$ are the lower and upper conductivities. $z$ and $R$ coordinates are expressed in arbitrary units ($a = 1$, $h = 3$). The location of the circular dipole distribution is indicated by two vectors. Maximum negativity is coded in blue and maximum positivity in red. Thick black lines correspond to $V = 0$. (C) Potential (thin line) and second derivative with respect to $z$ of the potential (thick line), computed along the dashed line in (B).
ratio h/a decreases, the global characteristics of the field potential distribution in depth are not modified. Outside this cylinder, the potential reverses twice in depth (for instance, as R = 2 in Fig. 1B).

In order to compare the depth profiles of ‘current-source-density’ (CSD) observed by Steriade and Amzica (1996), the second derivative of the potential has been computed along a vertical axis (dashed line in Fig. 1B). The depth profile of this second derivative shows alternatively positive and negative values across cortical layers (Fig. 1C).

It should be noted that the potential at point P due to a ring-shaped distribution can also be expressed, in spherical coordinates, as the following multipole expansion:

$$V(\rho, \theta) = V(0, 0) \left( \frac{a}{\rho} \right)^3 P_2(\cos \theta) - \frac{3}{2} \left( \frac{a}{\rho} \right)^5 P_4(\cos \theta) + ...$$

where \( \rho \) is the distance between P and the center O of the ring, \( \theta \) the angle between OP and the z axis, and \( P_n() \) the Legendre Polynomial of degree \( n \). This means that, at distance from the ring, the first term of the series is dominating, and the field distribution of ring-shape sources becomes equivalent to that of a quadrupole, i.e. two very

Fig. 2. (A) Alignment of 3 ring-shaped source distributions along the horizontal axis. The reversal-free area is increased as compared with Fig. 1B. (B) Combination of 9 parallel quadrupoles. Although this configuration increases the area of negative polarity along the horizontal axis, very focal polarity reversal still exists near the sources.
close dipoles of same magnitude located at the center of the ring, perpendicular to it and of opposite direction.

To explain the measured field potential depth profiles without polarity reversal, reported by Steriade and Amzica (1996) and Steriade et al. (1996) (Fig. 3), one may consider a combination of ring-shaped sources along the horizontal axis of the cortex (Fig. 2A), as well as a combination of parallel quadrupoles (Fig. 2B). Both source configurations will enlarge the reversal-free region in a given cortical area. As opposed to ring-shaped sources, the combination of quadrupoles still create a focal double inversion pattern.

3. Magnetic field generated by a ring-shaped distribution

To determine the magnetic field generated by such a
current distribution, Ampere’s law can be used to determine the magnetic field $B$ from currents. The current distribution $j$ is invariant by rotation around the $z$-axis. Consider a circular path $C$ centered on the $z$-axis, of radius $r$, and in a plane parallel to the boundary interface. From the symmetry of the problem, $\mathbf{B}$ has the same magnitude at all points on this circle, with $\mathbf{B} = B_\phi(\rho, z) \hat{\mathbf{e}}_\phi$, $\hat{\mathbf{e}}_\phi$ being a unit vector tangent to the circle. According to the Ampere’s law, we have:

$$\iint_S \mathbf{B} \cdot d\ell = 2\pi \rho B_\phi = \mu_0 \iiint_V j \cdot d\mathbf{s}$$

$S$ is any surface spanning $C$. Above the boundary plane $j = 0$, thus yielding to $\mathbf{B} = 0$. The ring-shaped distribution of current dipoles does not generate any magnetic field outside the conducting medium. For similar symmetry reasons, this also holds true for a quadrupolar source.

4. Topography generated by such a ring-shaped distribution in a sphere

The potential and magnetic field distributions generated by these ring-shaped dipoles have been computed by summing up the contribution of each discrete dipole, using the classical formula in a 3 layer spherical model (Sarvas, 1987). EEG and MEG topographies are presented in Fig. 3A. Two different orientations of the ring have been tested. When the ring is oriented tangentially with respect to the scalp surface, it generates a monopolar topography. As in the semi-infinite medium and due to the symmetry of the spherical model, no magnetic field can be observed. When the ring is oriented radially with respect to the scalp surface, it generates both an electrical and a magnetic field, with complex topographies. For comparison, the topographies generated by a single tangential dipole are shown, and the maximum amplitude value is used to normalize the maps obtained with different ring sources. Fig. 3B shows the variations of the normalized amplitudes versus ring depth, for potential and magnetic fields. The normalized magnetic amplitude of the tangentially oriented ring is low and independent of ring depth. The normalized potential amplitude is higher, especially for tangentially oriented ring-shaped distributions, and decreases slowly with depth.

At distance from the source, similar topographical properties can be obtained with a quadrupole.

5. Discussion

We have proposed a simple model of current sources generating a potential field which shows no polarity reversal across the conducting medium in a limited area. Outside this area the potential decreases rapidly. When studying fast oscillatory activity, Steriade and Amzica (1996) have described a pattern of positive and negative values of the second derivative of the potential with respect to $z$, across the cortex. We have shown that ring-shaped sources exhibit the same pattern.

Similarly, horizontal distribution of quadrupoles tends to increase the reversal-free area. Both source types seem to be possible models for the intracortical field potentials and the scalp potentials observed during fast oscillatory activity, but each model should be related to distinct synaptic activities. Quadrupoles, i.e. opposing dipoles, would mimic synaptic currents at intermediate cortical depth on a radially oriented dendrite (of a pyramidal cell for instance). This requires that the active synapses should be precisely located midway along the apical dendrites (Nunez, 1981), thus leading to very focal polarity inversions in the vicinity of the sources. However, ring-shaped sources would rather mimic the activity of synapses which are located on horizontally oriented dendrites distributed all around the soma. This later geometry fits with the idea that interneurons (stellate cells) may be involved in a network generating a coherent oscillatory activity (Whittington et al., 1995; Wang and Buzsaki, 1996). However, a possible contribution of pyramidal neurons (basal dendrites for instance) to this network cannot be ruled out (Linâas, 1988; Jagadeesh et al., 1992; Gray and McCormick, 1996). Still, our model suggests that neurons with horizontally oriented dendritic fields may play an important role in the generation of stimulus-induced or spontaneous cortical fast oscillations.

We have also shown that in a spherical model of the head, the ring-shaped distribution of current dipoles proposed here generates an electric field, but either no, or weak, magnetic field on the scalp surface. Since in our model, rings are parallel to the cortical surface, rings oriented tangentially with respect to the scalp surface would be found in the superficial cortex, while radially oriented rings would be found deeper in the brain, along sulci. Consequently, the electrical field observed on the scalp will be predominantly due to eccentric and tangentially oriented rings, while the magnetic field will remain very weak. This model may thus account for the discrepancy between EEG and MEG data we observed in simultaneous recordings (Tallon-Baudry et al., 1997). Deep or radial dipolar sources would also explain the EEG/MEG discrepancy we observed in humans, but they would not account for the absence of polarity reversal observed in cats.

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References

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