Reply to Gratiy et al.

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ELECTRIC MONOPOLES ARE INDEED COMPATIBLE WITH MAXWELL EQUATIONS

TO THE EDITOR: In their commentary, Gratiy et al. (2013) suggest that according to Maxwell theory of electromagnetism, monopoles are impossible in neurons. However, to reach this conclusion, the authors make an approximation, which we argue below may not be valid in biological media.

Maxwell theory of electromagnetism postulates that the following relation is always valid for any medium:

$$\nabla \times \vec{H} = \vec{j}^f + \frac{\partial \vec{D}}{\partial t},\tag{1}$$

where \vec{H} is the magnetic field, \vec{j}^f is the current density of free

charges, and $\vec{j}^d = \frac{\partial D}{\partial t}$ is the displacement current density. We can call the sum of these two currents, the generalized current density, $\vec{j}^g = \vec{j}^f + \vec{j}^d$. The generalized current is always conserved in a given volume, as rightly pointed out by Gratiy et al. (2013).

In a perfectly homogeneous and locally neutral medium, we have $\nabla \cdot \vec{j}^f = -\frac{\partial \rho^f}{\partial t} = 0$ because there cannot be charge

accumulation anywhere. Because the relation $\nabla \cdot \vec{j}^g = 0$ applies

to any type of medium, we also have $\nabla \cdot \left(\frac{\partial D}{\partial t}\right) = 0$. Thus, in a homogeneous locally neutral medium, we have two independent current conservation laws: one law applies to the free-charge current i^d and another one applies to the displacement current i^d . Note that in a homogeneous medium i^d is not necessarily negligible, but the application of the current conservation law on i^f can be done independently of the existence

In the Gratiy et al. (2013) commentary, the authors assume that the displacement current is negligible, which is equivalent to consider the system as a homogeneous conductor with no capacitive effect. In this case, the free-charge conservation law applies, and there cannot be electric monopolar effects. Thus the reasoning of Gratiy et al. is only true in a very particular case of Maxwell equations, when i^d is neglected.

of i^d because the two laws are independent.

However, if the medium is not electrically homogeneous, which is necessarily the case in neurons at subcellular scales (organelles, fluids, membranes, cytoskeleton, etc.), then the con-

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clusion is opposite. In this case, we have $\nabla \cdot \vec{j}^f = -\frac{\partial \rho^f}{\partial t} \neq 0$,

which implies
$$\nabla \cdot \left(\frac{\partial \overrightarrow{D}}{\partial t} \right) \neq 0$$
 because $\nabla \cdot \overrightarrow{j}^g = 0$. In other words,

there can be charge accumulation in a given region, and the displacement current cannot be neglected. A similar reasoning applies if there are frictions or inertia time to charge movement (Bedard and Destexhe 2008). In all these cases, one must use Maxwell equations without approximations (only the generalized current conservation law applies).

Thus, in media more complex than homogeneous conductors, charge accumulation and electric monopoles are possible in full accordance with Maxwell equations.

It is interesting to see that the controversy boils down to whether neurons are homogeneous and resistive. If this is the case, then there cannot be charge accumulation nor monopolar effects, and the electric fields are generated by higher order multipolar configurations such as dipoles. This "standard theory" is self-consistent, as pointed out by the Gratiy et al. commentary. However, these authors misinterpret Maxwell equations, which in their nonapproximated form are perfectly compatible with monopoles. This will be the case if the cytoplasm and extracellular media are electrically nonhomogeneous or if there are phenomena like inertia of charge movement, which may be significant if the charge mobility is low, as in neurons (Destexhe and Bedard 2012). Experiments are needed to distinguish between these two alternatives, either a homogeneous and resistive world dominated by dipoles or inhomogeneous, nonresistive media where monopolar current sources are possible. The recent Riera et al. (2012) experiments indicate that this might be possible, indeed.

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