Current Source Density (CSD) Analysis

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Synonyms

CSD, CSD method, reconstruction of current sources

Definition

Current Source Density analysis (CSD) is a class of methods of analysis of extracellular electric potentials recorded at multiple sites leading to estimates of current sources generating the measured potentials. It is usually applied to low-frequency part of the potential (called the Local Field Potential, LFP) and to simultaneous recordings or to recordings taken with fixed time reference to the onset of specific stimulus (Evoked Potentials, EP).

Detailed Description

Among the different mechanisms contributing to extracellular electric potential in the tissue (Buzsaki et al., 2012, Einevoll et al., 2012) transmembrane currents in neurons are believed to dominate. These are ionic currents passing through all the different membrane channels (passive, voltage-dependent, calcium-dependent, synaptic, etc.) as well as the capacitive currents which, while charging the membrane, also contribute to the motion of ions in the extracellular space, influencing the extracellular potential and seen by the extracellular electrode. The places where net current is entering or leaving the cell are called *current sources or sinks*. While these sources are localized along the membrane of the neuron, in practice, with a finite resolution afforded by available electrode setups and limited by typical densities, we may only recover coarse-grained density. This is what we have in mind when discussing estimation of Current Source Density. Figure 1 shows the relation between the "microscopic" currents (a), coarse-grained field we usually have in mind (b) and a reconstruction of the CSD from measured potentials.

CSD analysis can be performed for signals in full spectrum or in any selected band, although it is usually applied to the Low Frequency Part (<500Hz) of the extracellular potential (LFP). We propose here such an expansion of LFP as the commonly used term Local Field Potential is actually a misnomer, since due to the long range nature of the electric field LFP can be observed millimeters away from sources (e.g. Kajikawa and Schroeder, 2011; Linden et al., 2011; Hunt et al., 2011; Łęski et al., 2013). Despite that filtering in frequencies it is known that fast processes, such as spikes, may still contribute to the LFP (Buzsaki et al, 2012, Einevoll et al., 2012; Reimann et al. 2013).

When net positive current enters the cell we speak of current sink and it corresponds to negative CSD. When net negative current enters the cell we speak of current source and it corresponds to positive CSD. Since negative CSD is observed for excitatory synaptic stimulation (positive current entering the cell / negative CSD), many researchers prefer to denote current sinks by red ("hot spot") and current sources by blue. There is a comparable number of researchers who prefer to do the opposite, according to the sign of CSD (red for positive, blue for negative). This situation has lead to two opposite conventions being in wide use. A reader is advised to always check carefully what is the convention used in a given work.

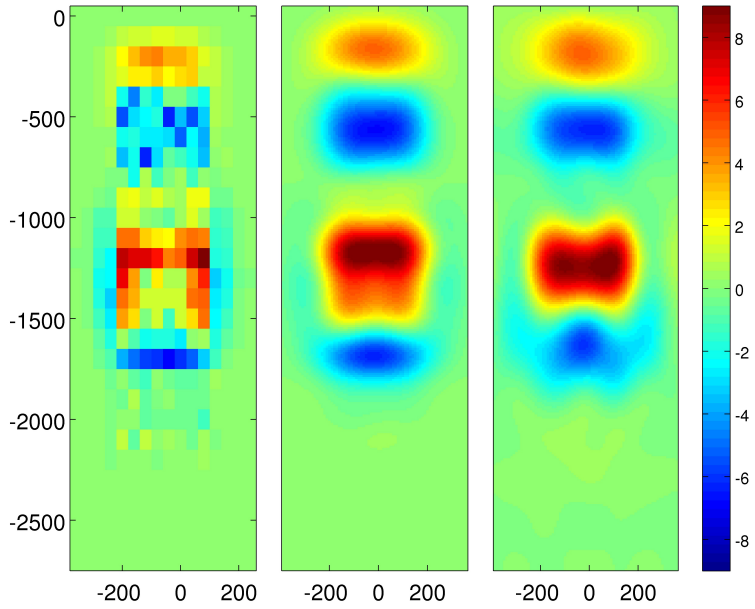

Figure 1. Comparison of the current sources obtained in a simulation (a), with coarse-grained CSD (smoothed with a Gaussian kernel of $\sigma = 75\mu m$) (b) and a reconstruction with kernel CSD method (c) from LFP computed at a grid of 8x14 electrodes from the data in (a). Data were taken from the cortical part of a simulation of 3500 cells in the model of thalamocortical loop based on Traub et al. (2005), 10 ms after simulated thalamo-cortical stimulus. Dominating contributions to CSD come from infra- and supragranular pyramidal cells. Vertical distance given in µm from cortical surface, horizontal from the center of the simulated column (H. Głąbska).

Physics behind the relation between the CSD and LFP

To get intuitive understanding of the basic relation between current sources and extracellular potential consider infinite, homogeneous and isotropic conductive medium of conductivity σ (Tranquillo, 2008). If we place a stimulating electrode and inject current *I*, it will induce current flow in the tissue with current density $\vec{J} = I\hat{r}/(4\pi r^2)$ radially at a distance *r* away from the stimulation point (Fig. 2).

In a purely conductive medium Ohm's law holds $\vec{J} = \sigma\vec{E} = -\sigma\nabla V$, which gives us the potential in space $V(r) = I/(4\pi\sigma r)$. A multitude of currents I_j located at $\vec{r}_j$ induce potential $V(\vec{r}) = \sum_j I_j/(4\pi\sigma|\vec{r} - \vec{r}_j|)$. It is natural to introduce *current source density (CSD)*,$C(\vec{r}) = \sum_j I_j\delta(\vec{r} - \vec{r}_j)$, a scalar density field which is usually coarse grained to a smooth quantity (see Fig. 1). With this definition we get the relation between the CSD and the potential as

$$V(\vec{r}) = \frac{1}{4\pi\sigma}\int d^3\vec{r'}\,\frac{C(\vec{r'})}{|\vec{r} - \vec{r'}|} \qquad \text{(Equation 1)}$$

or inverting this relation we obtain the Poisson equation

$$C(\vec{r}) = -\sigma\Delta V \qquad \text{(Equation 2)}$$

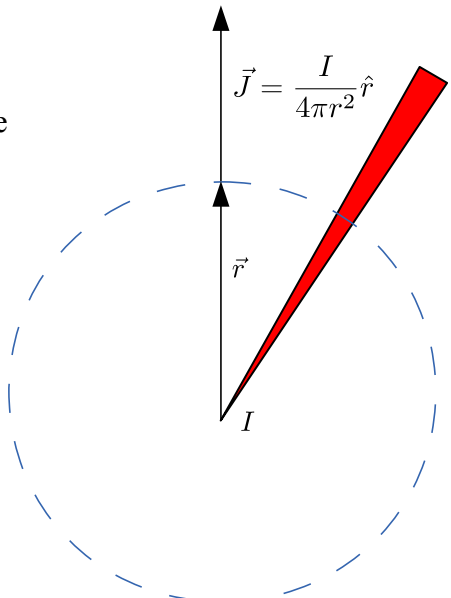

Figure 2. Current I *injected at the origin of the system spreads uniformly in all directions in infinite, homogeneous and isotropic medium.*

Equations (1) and (2) are valid only in our restricted setting. Equation (2) can be generalized for arbitrary conductivity tensor fields σ:

$$C(\vec{r}) = -\nabla\cdot[\sigma\nabla V] \qquad \text{(Equation 3)}$$

Solving (3) usually requires numerical methods. Careful derivations of (3) can be found in (Nicholson, 1973; Stevens, 1966; Nunez and Srinivasan, 2005).

Methods of CSD estimation

The simplest numerical approximation to the Laplacian is the three-point formula

$$\begin{aligned} C(x_k, y_l, z_m) \quad \approx \quad & -\sigma \left[V(x_{k+1}, y_l, z_m) - 2V(x_k, y_l, z_m) + V(x_{k-1}, y_l, z_m) \right. \\ & + V(x_k, y_{l+1}, z_m) - 2V(x_k, y_l, z_m) + V(x_k, y_{l-1}, z_m) \\ & \left. + V(x_k, y_l, z_{m+1}) - 2V(x_k, y_l, z_m) + V(x_k, y_l, z_{m-1}) \right] / \delta^2 \end{aligned}$$

which was introduced by Pitts (1952). While in the original application two-dimensional case was considered, by far the most common use of this approach has been in the study of one-dimensional cortical recordings with linear multielectrodes. One then considers lateral invariance of the potential as a consequence of laminar structure of the cortex keeping a single term in the above formula. This approach has been made popular in early 1970's by work of Haberly and Shepherd (1973) and especially Nicholson and Freeman (1975). Much of the work in this area till 1985 has been summarized by Ulla Mitzdorf in her still very useful review (1985). We refer to this approach as the *traditional CSD (**tCSD**) method*.

Methodologically, there have been few advances in the estimation of CSD from the measurements since Pitts work till 2006. The main deficiencies of the traditional approach are lack of control over the assumptions made, such as extent of the sources in the dimensions which are not probed and between the contacts, spatial and measurement noise, and the necessity of exclusion of contacts at the border. To reduce the noise, Rappelsberger et al (1981) proposed to smooth the measurements with a Hamming window obtaining a five-point formula in 1D

$$C(z) = -\sigma[0.23V(z-2\delta) + 0.08V(z-\delta) - 0.62V(x) + 0.08V(z+\delta) + 0.23(z+2\delta)]/\delta^2$$

which gained some popularity. In 1988, Vaknin et al. proposed to extend the grid of electrodes beyond the actual set of contacts copying the outmost recordings to the added contacts. While in general physically questionable, this numerical trick allowed computation of CSD values for all contact positions and was used in cortical studies.

Rapid development of new multielectrodes at the beginning of XXI century (Egert et al. 1998, Csicsvari et al 2003, Buzsaki 2004, Berdondini et al 2005, Kipke et al. 2008, Frey et al 2009) stimulated renewed interest in LFP recordings and analysis, including CSD analysis. In 2006, Pettersen et al. proposed a new, model-based approach to CSD estimation, which they termed *inverse CSD (**iCSD**) method*. The method was later generalized to three- and two-dimensional regular recording setups (Łęski et al. 2007, 2011).

The idea behind iCSD is to assume a parametric model of the sources of as many parameters as the number of measurements. For example, for measurements of potential $V_1, \ldots, V_N$ at points $\vec{x}_1, \ldots, \vec{x}_N$, we may take the values of CSD at measurement points $C_1, \ldots, C_N$ as parameters and spline interpolate in between (*spline iCSD*). Then $C(\vec{x}) = \sum_{k=1}^{N} C_k f_k(\vec{x})$, where $f_k(\vec{x})$ is a function taking 1 at $\vec{x}_k$, 0 at $\vec{x}_{l \neq k}$, and spline interpolated in between. From such a model one can compute potential at the measurement points using forward modeling formula, Eq. (1). This leads to a matrix relation between the potential and the CSD given by $V_j = \sum_k M_{jk} C_k$, where

$$M_{jk} = \frac{1}{4\pi\sigma} \int d^3\vec{x'} \; \frac{f_k(\vec{x'})}{|\vec{x}_j - \vec{x'}|}.$$

In lower dimensionality (1D, 2D), where one does not probe all directions, it is necessary to make assumptions about source behavior there. For example, in 1D one may assume invariance of CSD on disks of some radius *R* (e.g. of the size of cortical column) orthogonal to the shaft, in 2D one may assume constancy or Gaussian decay of the source on an interval orthogonal to the MEA plane. These assumptions lead to other forms of matrix elements M_{jk} which incorporate the specific form of the model (Pettetsen et al., 2006; Łęski et al., 2011).

For typical recordings the matrix relation between the LFP and CSD can be inverted leading to a formula for C_k as a function of measured potential: $\vec{C} = M^{-1}\vec{V}$, and in consequence to an estimate

of current sources in the whole probed region. A convenient feature of iCSD method is that the matrix M^{-1} is estimated once for a given setup and model of sources. Also, one can easily incorporate different boundary conditions overcoming naturally this limitation of the traditional approach (Łęski et al., 2007).

Inverse CSD is a framework which allows one to incorporate different assumptions about the structure of the sources or the properties of the tissue, e.g. its conductivity (Goto et al. 2010). An interesting variant was developed for localization of single cell current sources during action potential generation (*spike CSD,* ***sCSD***, Somogyvari et al., 2005, 2013). The flexibility of the framework is in the construction of the function space used for estimation. However, iCSD was developed for regular recording grids and under assumption of negligible recording and position noise, which could not be easily overcome within this framework.

A general solution to these problems was provided with *Kernel Current Source Density (**kCSD**) method* (Potworowski et al., 2012). While in iCSD the dimension of the function space in which one does estimation is equal to the number of measurements, in kCSD one constructs spaces of much larger dimensionality. The flexibility in tackling arbitrary electrode setups comes from separation of the construction of estimation space from the definition of the setup. The use of kernel methods allows us to use standard techniques for dealing with noise (e.g. ridge regression, etc.) as described below.

Assume potentials $V_1, \ldots, V_N$ measured at points $\mathbf{x}_1, \ldots, \mathbf{x}_N$. To construct the framework of kCSD we start with two linear spaces, the space of sources

$$\tilde{\mathcal{F}} = \left\{ C(\mathbf{x}) = \alpha_1 \tilde{b}_1(\mathbf{x}) + ... + \alpha_M \tilde{b}_M(\mathbf{x}) : \tilde{b}_i : \mathbb{R}^d \longrightarrow \mathbb{R} \right\},$$

and the space of potentials

$$\mathcal{F} = \left\{ V(\mathbf{x}) = \alpha_1 b_1(\mathbf{x}) + ... + \alpha_M b_M(\mathbf{x}) \ : \ b_i : \mathbb{R}^d \longrightarrow \mathbb{R} \right\},$$

with the dimension of the spaces, *M*, much greater than the number of measurements, *N*. The basis functions are related by a linear operator $\mathcal{A} : \tilde{\mathcal{F}} \mapsto \mathcal{F}$ so that $b_i = \mathcal{A}\tilde{b}_i$, and $V(\mathbf{x}) = \mathcal{A}C(\mathbf{x}) = \sum_{i=1}^{M} \alpha_i b_i(\mathbf{x})$. In three dimensions (isotropic, homogeneous) $\mathcal{A} = -\sigma\Delta$, in lower dimensionality we must assume properties of the sources in the directions not probed for the same reasons as in iCSD. For instance, if in 2D we assume that the sources are invariant in the direction *z* orthogonal to the electrode plane *(x,y)* within a layer of *2h,* then the physical $CSD(x, y, z)$ is $C(x, y)$ for $|z| < h$ and 0 otherwise, and

$$.b_i(x, y) = \mathcal{A}\tilde{b}_i := \frac{1}{2\pi\sigma} \int dx' \int dy' \ \mathrm{arsinh}\left(\frac{h}{\sqrt{(x-x')^2 + (y-y')^2}} \right) \tilde{b}_i(x', y')$$

We require that $\tilde{b}_i$ (b_i) are linearly independent and so they constitute bases of the linear spaces $\tilde{\mathcal{F}}$ and $\mathcal{F}$. To efficiently estimate in such a large space we construct a kernel function,

$$K(\mathbf{x}, \mathbf{x}') = \sum_{i=1}^{M} b_i(\mathbf{x}) b_i(\mathbf{x}'),$$

which introduces the structure of Reproducible Kernel Hilbert Space (RKHS) on $\mathcal{F}$ (Aronszajn, 1950). Using representer theorem from RKHS theory (Schoelhopf & Smola, 2002) one can show that minimum estimation error

$$err\left(V(\cdot)\right) = \sum_{i=1}^{N} \left(V(x_i) - V_i\right)^2 + \lambda \|\beta\|^2$$

is obtained for potential function of the form

$$V(\mathbf{x}) = \sum_{k=1}^{N} \beta_k K(\mathbf{x}_k, \mathbf{x}) \in \mathcal{F},$$

where

$$\begin{bmatrix} \beta_1 \\ \vdots \\ \beta_N \end{bmatrix} = \begin{bmatrix} K(\mathbf{x}_1, \mathbf{x}_1) + \lambda & \cdots & K(\mathbf{x}_1, \mathbf{x}_N) \\ \vdots & \ddots & \vdots \\ K(\mathbf{x}_N, \mathbf{x}_1) & \cdots & K(\mathbf{x}_N, \mathbf{x}_N) + \lambda \end{bmatrix}^{-1} \begin{bmatrix} V_1 \\ \vdots \\ V_N \end{bmatrix}$$

which can be written in more compact notation as

$\boldsymbol{\beta} = (\mathbf{K} + \lambda \mathbf{I})^{-1} \cdot \mathbf{V}$

with an obvious definition of terms. Having estimated the potential, we use the relation between the basis functions to construct a cross-kernel function,

$\tilde{K}(\mathbf{x}, \mathbf{x}) = \sum_{j=1}^{M} b_j(\mathbf{x}) \tilde{b}_j(\mathbf{x})$

with which the current sources estimated in the measurement space are given by

$C^*(\mathbf{x}) = \tilde{\mathbf{K}}^T(\mathbf{x}) \cdot (\mathbf{K} + \lambda \mathbf{I})^{-1} \cdot \mathbf{V}$ with $\tilde{\mathbf{K}}^T(\mathbf{x}) := [\tilde{K}(\mathbf{x}_1, \mathbf{x}), \ldots, \tilde{K}(\mathbf{x}_n, \mathbf{x})]$.
Parameter λ can be selected from data using, for instance, cross-validation. For further details on kCSD see Potworowski et al. (2012). Figure 3 shows an example of CSD estimation with kCSD method.

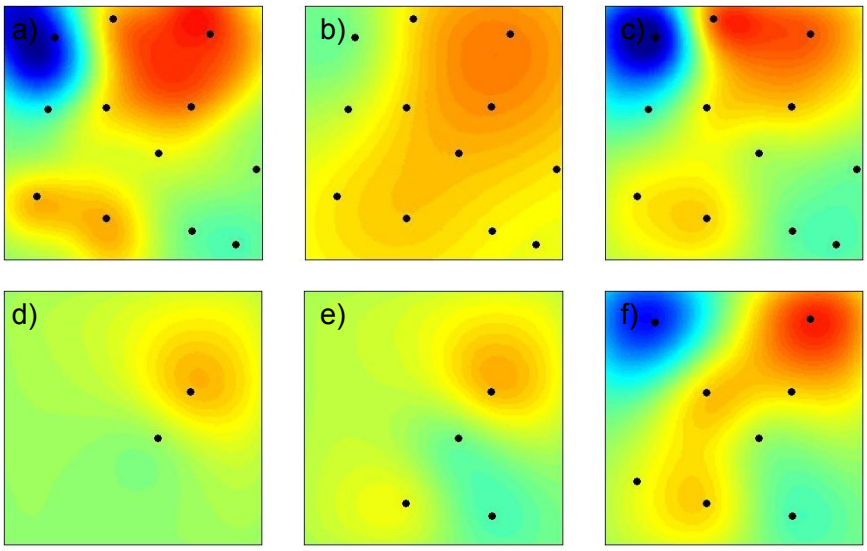

Figure 3: Example of source reconstruction with kCSD method. a) Model sources shown were used to generate potentials at randomly selected electrode locations marked with black dots. b) Potential interpolated from the potential measured at the electrode locations. c) CSD reconstructed from the random 16 measurements. d), e), f) Sources reconstructed from 2, 4, 8 measurements respectively.

Limitations of CSD analysis

The main difficulty in the interpretation of CSD profiles is that it is not possible to tell without extra knowledge what is the nature of a given observed feature, for example, if a spot of negative CSD is due to excitatory synaptic stimulation or a passive return current matching inhibitory current elsewhere. Thus one usually has to build on extra a priori knowledge of system's anatomy and physiology (Gratiy et al., 2011) or use computational models of the studied systems (Makarov et al. 2010, Potworowski et al., 2011). If possible, do both.

CSD analysis allows one to better localize neural activity by deconvolution of the inverse distance kernel. However, since usually multiple cell populations overlap, observed profile of the current sources will reflect summary activity of all of them. One way to overcome this problem is to use a method of source decomposition (see Einevoll et al., 2013 for a discussion). It seems that independent component analysis (ICA) following CSD gives functionally meaningful results (Łęski et al. 2010, Makarov et al. 2010, Potworowski et al., 2011).

To tackle both the problem of overlapping populations and unknown origin of the given source it is particularly useful to generate ground truth data as close to the system studied as possible, for instance from large scale models (Potworowski et al., 2011; Reimann et al., 2013).

Cross-references/Related terms

Local field potentials, Independent Component Analysis

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Further Reading

Scholarpedia
http://www.scholarpedia.org/article/Local_field_potential