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Do Electrode Properties Create a Problem in Interpreting Local Field Potential Recordings?

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Local field potential (LFP) recordings within the brain have become an important tool used by neuroscientists to make inferences about the activity of a population of cells near an electrode. Each passing year analysis of LFPs in neuroscience seems to bring important new insights on the possible workings of networks in the brain to produce behavior (Buschman and Miller 2007; Canolty et al. 2006; Gregoriou et al. 2009; Liu and Newsome 2006; Lubenov and Siapas 2009; Pesaran et al. 2008; Womelsdorf et al. 2006). Indeed LFPs have become a near-ubiquitous tool in neurophysiology seemingly in use anywhere extracellular spikes are also recorded.

One issue that often comes up among those who interpret LFP data is the uncertainty about how electrode impedance and other electrode parameters affect LFP recordings, presenting a potential problem in their interpretation. Indeed this is a complex question, given that current flow in the brain depends on a multitude of factors and extracellular recordings cannot uncover the precise neural events giving rise to a specific LFP voltage. Amidst this uncertainty, one commonly mentioned idea that exists today is the notion that microelectrodes of different impedances or geometries might integrate signals across space differently which could lead to differing results between experiments that use electrodes of different impedances to collect LFP data. This notion has been frequently expressed verbally by many, though direct discussions of it in the literature (Pesaran 2009) have been more rare. However, literature discussing how these electrode parameters affect spike recordings (Andersen et al. 2010; Moxon 1999; Paik et al. 2003; Ward et al. 2009) is more commonly found. Despite the relative prevalence of this question in the field, research investigating it has been lacking and no definitive answer has yet been proposed. However, we believe that the answer to this question can be found from information gleaned from a range of existing literature and published data, although most in the field are not presently aware of this. The uncertainty surrounding this issue is important to address because it creates a potential barrier for the comparison of LFP data across experiments and laboratories. Furthermore, as the interpretation of LFPs continues to move beyond its infancy further into the territory of a standard neuroscience technique, such comparisons will be increasingly common and important for building consensuses in the field.

As we describe here, we believe this issue presents one of the rare cases in neuroscience in which the answer that would make the work of trying to understand the brain easier also happens to be true. That is to say, provided that the proper recording equipment is used, the impedance and geometry of microelectrode recording sites in the ranges typically used in extracellular experiments do not appreciably affect LFP recordings. Scientists in fact do not need to attend to this issue when interpreting LFP data or when comparing such results across experiments and laboratories.

To defend this claim, the first point to clarify a priori is that an electrode can be considered to report the average voltage present at its uninsulated tip or recording site (Nunez and Srinivasan 2006; Robinson 1968). Indeed by using metal microelectrodes suspended in saline, we have verified that this was the case and that this model presented years ago by David Robinson does hold true (Nelson et al. 2008). Thus the only sense in which an electrode integrates a signal across space is by determining this average voltage. The shape and size of an electrode's recording site will not, for example, affect the way in which it responds to distant as opposed to nearby voltage sources.

Second, if the proper recording equipment is used, the voltage that is ultimately amplified and recorded will not be appreciably electrically affected by the electrode's impedance. Indeed in previous work we demonstrated this to be the case (Nelson et al. 2008). Recorded voltages in saline using electrode impedances spanning the range typically used in extracellular experiments were independent of the electrode's impedance when using a headstage with a high (>1 GΩ) input impedance. This does require some attention from neurophysiologists though. For example another commercially available headstage we tested had a lower input impedance that led to electrode impedance–dependent signal distortions. Fortunately, when they occur these distortions can be corrected post hoc (Nelson et al. 2008), as reported in several recent publications (Gregoriou et al. 2009; Siegel et al. 2009).

A separate question from whether the impedance of an electrode electrically influences the recorded voltage is the question of whether the size and geometry of the recording site have an impact on the recorded LFPs. Within the framework that we have described here, one can conceive how during a recording these parameters could affect the average voltage present over the whole uninsulated site and thus affect the recorded values.

An electrode's impedance is of course highly dependent on the size of its uninsulated surface area. Indeed impedance, which is more easily measured, is essentially used only as a proxy to describe an electrode's uninsulated surface area, which is of more interest to neuroscientists. For spike recordings, for example, the general viewpoints in the field tend to be that larger recording sites spanning more of the extracellular

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space will record more neurons at a given time (Andersen et al. 2010; Moxon 1999; Paik et al. 2003; Ward et al. 2009), whereas smaller recording sites will have more specificity and record individual neurons that are better isolated (Moxon 1999; Paik et al. 2003). These views are not established facts, however, and there is at least some contrary evidence in the literature (Suner et al. 2005).

The impact on spike recording set aside, it may be tempting for one to make the claim that LFPs are affected by recording site size and geometry. However, a closer look reveals that current estimates of the spread of LFP signals suggest that these potentials in the brain vary on a spatial scale larger than the size of uninsulated electrode recording sites used in extracellular recordings. For instance, Katzner and colleagues (2009) recently showed that LFPs are more local than previously thought, but even their newly lowered estimate still suggests that LFPs primarily originate from sources within 100 μm of a given point, with noticeable contributions coming from up to within 250 μm. Meanwhile, even a 300 kΩ at 1 kHz tungsten electrode, which is a very low impedance by extracellular recording standards and thus has a very large recording site, corresponds to a surface area of only 1,850 μm^2 (Yaeli et al. 2009). For a conical electrode at even an extreme angle of 10°, this would result in an uninsulated height near 80 μm, as illustrated in Fig. 1. Similar data published for platinum/iridium electrodes (Lemon 1984; Tielen et al. 1971) ultimately yield the same conclusion, further suggesting that this will hold true for other metals as well. Changing the size and shape of a recording site within this range would not likely appreciably affect the average potential found over the site based on current estimates of the spread of LFPs.

Thus we feel that evidence available in the literature suggests that the impedance, size, and shape of the recording sites of microelectrodes will not affect the recording of LFPs. This holds for microelectrodes spanning the range of impedances typically used in extracellular recording experiments, provided that headstages of the proper input impedance are used (Nelson et al. 2008). Of course it would be possible to produce an extremely low impedance microelectrode that may indeed report different voltages than typical microelectrodes, but it is not clear that anything would be gained by the use of such an electrode. Indeed larger electrode recording sites essentially only serve as low-pass spatial filters (Nunez and Srinivasan 2006) and it would seem that the more precise spatial measurement provided by microelectrodes currently in use would be preferred in any reasonable scientific application.

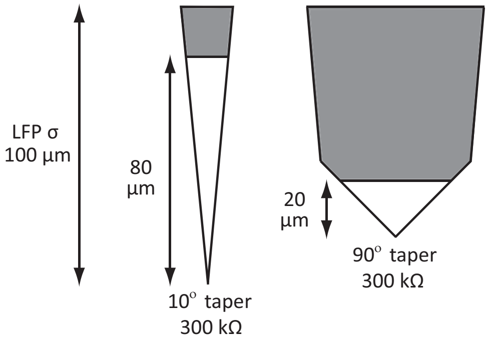

FIG. 1. Electrode recording site sizes relative to the spread of local field potentials (LFPs). Even for a low impedance (300 kΩ) electrode with an extremely fine taper angle (10°), the uninsulated recording site length is smaller than that of current estimates of the SD of the spread of LFP signals. Larger taper angles or higher impedances correspond to even smaller recording site lengths. The average potential across the electrode's tip should thus not be appreciably affected by variations of recording site size within the range of electrodes used for extracellular recordings. Data for the spread of LFPs come from Katzner et al. (2009), whereas data for electrode recording site sizes can be found in Lemon (1984), Tielen et al. (1971), and Yaeli et al. (2009).

Those who might disagree with the claim we have presented here should be clear in their reasons for doing so. The framework that we have presented describing the circuit properties of microelectrode recordings is generally accepted, although many neuroscientists may be unaware of it. Assuming that one then does not disagree with this framework, disagreeing with our claim amounts to the counterclaim that LFP voltage profiles in the brain change appreciably on a spatial scale smaller than a few tens of microns, which is the scale of microelectrode recording sites in use today. Thus for this counterclaim to be true, it is important to note that current beliefs about the spread of LFPs must then be wrong. Even if hypothetically LFPs did vary on such a small spatial scale, the very precise placement of an electrode within the brain would then likely be of more importance than the size and geometry of its recording sites. In such a case it is unclear that it would even be possible or desirable to attempt to capitalize on such a fine spatial structure of the local field potential.

Although the electrode parameters of impedance and recording site size likely have no effect on the recorded LFP, this says nothing about the effects of the mechanical disruption introduced by the electrode. Such effects would likely be dependent on electrode parameters such as size and taper angle, although an electrode's impedance or the size of its uninsulated region should not directly influence this. Additional caveats to consider are the effects of increased thermal noise and loss of signal due to shunt capacitance, both of which affect recorded voltages more as electrode impedance increases (Cogan 2008). However, we believe that again the evidence suggests these will not have sufficiently large effects on LFP recordings to be of notable concern for recordings made within typical ranges of parameters. With respect to thermal noise, its magnitude is dependent on signal bandwidth as well as electrode impedance, and LFP recordings typically take place over a limited bandwidth. Using electrode impedance spectra data from our previous work (Nelson et al. 2008) and the well-established formula for thermal noise (Johnson 1928; Nyquist 1928) we can derive estimates of the amount of thermal noise theoretically expected for different microelectrodes in the frequency band from 0 to 150 Hz given their average impedance in this frequency band, which is a generous bandwidth for LFPs. The expected root mean square value of this thermal noise was 7.7 μV for an electrode with a 3.3 MΩ impedance at 1 kHz and 4.2 μV for an electrode with a 500 kΩ impedance at 1 kHz. The different amount of noise between these electrodes, which approximately span the range of electrode impedances in use today, is all but negligible compared with the size of most LFP results of interest. With respect to signal loss through shunt pathways, the impact of shunt capacitance in recordings serves to effectively compromise the input impedance of the headstage at high frequencies (Cogan 2008; Nelson et al. 2008; Robinson 1968), which results in electrode impedance–dependent signal loss and distortions at those frequencies. However, this impact declines as frequency decreases. Indeed during test recordings with metallic resistors and electrodes suspended in saline, we found that as frequency decreased, shunt capacitance ceased to influence recordings starting in the 300 to 400 Hz range (Nelson et al. 2008), well above the LFP frequency ranges of interest. We should be clear, however, that shunt capacitance does depend on how the recording equipment is arranged and the impacts could be different in some recording configurations. However, this has yet to be tested in the literature and the available evidence we mentioned suggests this will not be a problem for LFP frequencies.

There is still a great deal of interesting future research that is needed to better understand the details of what can be inferred about neural activity from a given LFP trace. Indeed there are many curiosities and unknowns related to this. Nonetheless, we hope that neuroscientists interpreting LFP data can more freely compare results and continue the important work of using field potentials to understand the brain without worrying about the possible effect of electrode impedance and recording site geometry as one more unknown for concern.

DISCLOSURES

No conflicts of interest are declared by the authors.

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