Far-field potentials generated by action potentials of isolated frog sciatic nerves in a spherical volume

Don L. Jewett a, David L. Deupree a and D. Bommannan b

a Department of Orthopaedic Surgery, and b Department of Bioengineering, University of California at San Francisco, San Francisco, CA (U.S.A.)

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Summary Previous results in cylindrical volumes have shown that action potentials generate far-field potentials when experimental conditions are such that quadrupolar components of the action potential are reduced to an equivalent dipole. We now show that the same conclusions are also reached within a spherical volume, again recording far-field potentials from isolated bullfrog nerves. A mathematical proof is given that shows that in a sphere, antipodal electrodes primarily detect far-field potentials from dipole generators and not quadrupole generators. A revised conception of the 'far-field' in evoked responses is discussed which equates far-field recordings with dipole detection.

Key words: Far-field potentials; Stationary potentials; Action potentials; Virtual dipoles

The purpose of the present study was to extend the results of our previous studies, involving far-field potentials generated by a nerve in a hemicylinder (Deupree and Jewett 1988; Jewett and Deupree 1989), to recordings from a nerve in a spherical volume. The spherical shape of the volume allowed us to further test the assumptions of the 'leading/trailing dipole' (LT/D) model by measuring the distribution of far-field potentials to see if the angular dependence of the potentials at a given instant was that expected from a dipole generator. Our findings show that a simple mental model, the LT/D model, permits qualitative estimation of the characteristics of generators of far-field potentials and, thus, will help in experimentation which attempts to explain the observed potentials in terms of neural generators. This is important since none of the following characteristics of far-field potential generation is readily intuited without the LT/D model: short axons, bent axons, transected axons, conduction across changes in volume conductor boundaries, or conduction across non-homogeneities in the volume.

Recent work has shown that far-field potentials are recorded when the dipole characteristics of an action potential predominate, rather than quadrupole or higher order terms. Evidence has come from both computer modeling (Cunningham et al. 1986; Stegeman et al. 1987) and also from experimentation with human subjects (Desmedt et al. 1983; Kimura et al. 1984, 1987; Scherg and Von Cramon 1985; Møller et al. 1988), cats (Nakanishi et al. 1986), and with isolated frog sciatic nerve (Nakanishi 1983; Nakanishi et al. 1986; Deupree and Jewett 1988; Jewett and Deupree 1989).

Previous work in our laboratory studying isolated nerves in hemicylinders supported the results of computer simulations (Stegeman et al. 1987) and demonstrated that these potentials could be understood as being the result of detection primarily of the dipole components of the quadrupolar action potential which become manifest un-
nder different conditions (Deupree and Jewett 1988; Jewett and Deupree 1989). The electrical equivalent of an action potential in a straight nerve is a 'linear quadropole' (Plonsey 1969), which has a source-sink/sink-source configuration. When an axon is straight and long enough to encompass the entire action potential at a single instant, the far-field effects of one of the 'dipoles' in the quadropole at that instant is canceled by the effect of the other, oppositely oriented dipole (assuming that the far-field recording points are symmetrically oriented with respect to the generator and that the generator and recording points are symmetrically oriented to boundaries). However, when the dipole components are not equal and opposite, the generator is recorded as a dipole. A 'leading/trailing' dipole model (LT/D) of the action potential was developed that so far has been successful as a qualitative explanation of these far-field potentials (Jewett and Deupree 1989). For example, when an action potential is just beginning the depolarization-propagation process, just the leading dipole of the quadropole, is present and detected. Another asymmetrical condition that leads to far-field recording of the leading dipole occurs when the action potential traverses a boundary between differently sized volume conductors (e.g., when it enters the volume that contains the recording electrodes). However, when the action potential reaches the cut-end of the nerve or a sharp bend in the nerve, only the trailing dipole is detected at the far-field electrodes, being of opposite polarity to the leading dipole's field.

Methods and materials

Sciatic nerves were obtained from 8 pithed and decapitated bullfrogs by dissection from the spinal cord to just above the ankle. Potentials were recorded using Grass P511J amplifiers with bandpass filters set at 1 Hz and 3 kHz (half amplitude, 6 dB/octave). Averages of 10,000 sweeps were stored in a computer with a 20 kHz/channel sampling rate. Just as with Chimento et al. (1987), who used the same sphere, the number of responses needed to obtain an adequate average is large because both the spherical shape and higher-than-brain conductance of the volume markedly attenuate the signal. A stimulator generated a 0.01 msec pulse at the distal (ankle) end of the isolated nerves so that all axons stimulated would conduct along the entire length of the nerve.

The stimulating tube, which was of similar design as the one reported previously (Deupree and Jewett 1988), was constructed using a 1 ml syringe with Ag/AgCl wires placed across the diameter, which served as anode and cathode (see Fig. 1A). The stimulating tube was encased in a plastic syringe cover with a hole drilled in the end allowing for nerve passage into the sphere. Encasing the stimulating tube helped to decrease the capacitively coupled stimulus artifact. The distance between the cathode and the point where the nerve exited the outer casing was 50 mm.

The glass sphere (radius = 80 mm) had Ag/AgCl recording electrodes which traversed holes in the sphere at various locations along planes formed by 3 orthogonal axes (X, Y and Z; see Fig. 1B). The sphere was filled with frog Ringer's solution which was maintained at room temperature (usually 23°C). The conductivity of the Ringer's was measured to be 82 Ω·cm at that same temperature. The stimulating tube was positioned in the sphere along the Z axis, such that the action potential traveled toward the surface Z+ electrode. The nerve segment extending out of the stimulating tube was centered along the Z axis of the sphere, such that potentials occurring as the action potential emerged from the stimulating tube and as it reached the end of the nerve segment were both located close to the center of the sphere. Far-field potentials were recorded using antipodal electrode pairs located along the 3 orthogonal axes, with the exception that the Z− electrode placement was 30° from the Z axis in the X-Z plane (see Fig. 1B); thus, it was not actually antipodal or fully orthogonal to the X and Y axes. This positioning of the Z− electrode was necessary because the stimulating tube occupied the space at the point antipodal to Z+. The conductivity volume was grounded at one of the surface electrodes on the Y plane not being used for recording. In all figures presented, a positive input to the G-I electrode (positive up, or abbreviated: p-up) gave an upward deflection in the trace.
Several other antipodal electrode pairs were also placed on the surface at varying degrees of rotation from the X, Y or Z axes. Far-field potentials recorded using these electrode pairs allowed for a comparison of observed amplitude values with those predicted from a dipole source (a cosine function), at any particular instant in time. The angular separation between electrodes was computed from the distance between the p-up electrode of any pair and the surface site Z+ (rotation occurring either in the X-Z or the Y-Z plane) as a fraction of the spherical circumference. The Z
axis was used in determining the angle between two electrode pairs because this was also the nerve axis. The amplitude values were measured at 2.08 msec following the stimulus artifact, which was the peak value of the far-field potential recorded from the Z channel (best signal-to-noise ratio). The predicted amplitudes at various angles were computed as a cosine function using as the initial value the mean value of the measured amplitudes of 3 electrode pairs which were at 30° from Z, since the Z axis electrode pair was not antipodal. Since there is agreement with the cosine function within the accuracy of our experiment, any effects of the size of the action potential on its not being centered are not sufficient to affect our conclusions.

Results

Fig. 2 shows far-field potentials recorded from a straight nerve segment at the center of the sphere and oriented along the Z axis. Note that the magnitude of the potentials is small, comparable to those obtained in human far-field recordings; the size of the sphere is about that of a human head. Also note that the size of the potentials is much smaller than those reported in our previous studies (Deupree and Jewett 1988; Jewett and Deupree 1989), which were generated using similar nerves. This indicates that the amplitudes of these far-field potentials, generated in a sphere, decrease with distance from the generator, as opposed to similar potentials generated in a cylinder, which did not appreciably decrease in amplitude with distance from the generators in an axial direction. Thus, for these experiments, a very large number of responses were averaged (10,000), and the signal-to-noise ratio is smaller than seen in our previous reports. With centrally located dipoles, antipodal electrode recordings will have potentials with larger amplitude than non-antipodal recordings, because of differential amplification, and the opposite polarity at antipodal points, due to the dipole.

The traces recorded from the two channels that were at right angles to the axis of the nerve show no discernible potentials after the stimulus artifact (Fig. 2A and B). However, along the Z axis a biphasic potential is recorded (Fig. 2C), similar to that obtained in a cylindrical volume. As with our prior data in the hemicylinder (Deupree and Jewett 1988; Jewett and Deupree 1989), the positivity is the leading dipole as the action potential enters the spherical volume from the stimulating tube, while the negativity is due to the trailing dipole, as the action potential reaches the end of the nerve.

The conduction velocity of the action potentials during these experiments was estimated to be about 25 m/sec (25 mm/msec), based upon the latency from the stimulus onset to the time the sink of the action potential enters the volume (peak of far-field potential). In our hemicylinder experiments (Deupree and Jewett 1988) greater than 50 mm of nerve length in the volume was needed in order for a return to baseline between the entry and end-of-nerve potentials. One can see from Fig. 2C that there is no discernible flat area in the trace between the positive and negative aspects of the tracing, indicating that the exposed area of nerve is not great enough to have complete separation of the two potentials. Therefore, there is some overlapping of the two potentials in Fig.
2C, which could account partially for the fact that the two potentials do not appear as equal but opposite in magnitude. Also, temporal dispersion along the nerve would be greater for the end-of-nerve potential, as compared to the entry potential. It should be noted that even if the opposing dipoles of a straight nerve (leading and trailing) are not spatially the same, they can still cancel each other if the products of current and distance, integrated along the axon, sum to equal values. Said in another way, there will be cancellation in the far-field if the integrated dipole moments (current times dipole separation) are equal. For a single axon, this equality is easily seen in the axial currents of the two opposing dipoles (first derivative of the membrane potential) which have equal areas (Plonsey 1969: Fig. 5.12, p. 237; Jewett and Rayner 1984: Fig. 7-6, p. 156).

If the potentials of Fig. 2 were plotted in 3 dimensions (3-channel Lissajous’ trajectory or 3-CLT; Jewett 1987), then the result would be a straight line along the Z axis, confirming the results of Chimento et al. (1987) with respect to straight axons, entry and end-of-nerve potentials.

Fig. 3 shows far-field potentials recorded using the 3 major electrode pairs after the last 10–15 mm of a straight nerve segment was crushed. The negative potential is now absent, which is consistent with our previous results that showed crushing the end of the nerve segment eliminated the cut-end potential (Jewett and Deupree 1989). As hypothesized in detail in our previous paper (Jewett and Deupree 1989), the trailing dipole is thought to disappear on the recording following crushing of the end segment because when the sink of the action potential ceases to propagate into the crushed region, the passive (axial) currents in the crushed area are still present. Therefore, the leading and trailing dipoles cancel as the action potential disappears at the crush.

Fig. 4 shows far-field potentials generated by the same nerve segment from Fig. 3, recording from antipodal electrode pairs, each located at a different angle relative to the axis of the nerve. Note that as the angle from the nerve axis increases to 90° (Fig. 4A and B), the amplitude of the potential decreases, becoming flat at 90° (Fig. 4C). As the angle increases passed 90°, the potential...
TABLE 1
Comparison of observed vs. predicted values of far-field potential recorded using antipodal electrode pairs at various degrees off the nerve axis. When repeated values are given at the same angle, they are from different electrodes in the glass sphere, giving an indication of experimental variability with our experimental noise.

<table>
<thead>
<tr>
<th>Degrees</th>
<th>Amplitude (in μV)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
</tr>
<tr>
<td>30</td>
<td>0.083</td>
</tr>
<tr>
<td>30</td>
<td>0.090</td>
</tr>
<tr>
<td>30</td>
<td>0.103</td>
</tr>
<tr>
<td>60</td>
<td>0.050</td>
</tr>
<tr>
<td>60</td>
<td>0.053</td>
</tr>
<tr>
<td>90</td>
<td>0.007</td>
</tr>
<tr>
<td>90</td>
<td>0.023</td>
</tr>
<tr>
<td>90</td>
<td>0.007</td>
</tr>
<tr>
<td>120</td>
<td>−0.063</td>
</tr>
<tr>
<td>150</td>
<td>−0.096</td>
</tr>
</tbody>
</table>

Fig. 5 shows far-field potentials recorded from a nerve segment that had been bent 90°, the bend located at the center of the sphere. The prebend nerve axis was still oriented along the Z axis with the action potential traveling toward Z+. While the postbend segment was oriented along the X axis, with the action potential traveling toward X+. Thus, the nerve was bent in the X-Z plane. Between 10 and 15 mm of the end of the nerve
segment had been crushed before placing the nerve in the sphere so that there would be no potential from the trailing dipole due to the cut-end (along the X axis). Along the Z axis a biphasic potential is observed (Fig. 5C), the positivity being due to the leading dipole as the action potential enters the sphere from the stimulating tube, and the negativity being due to the trailing dipole at the bend. The time of arrival of the action potential at the bend is shown by the near-field recording (Fig. 5D). Along the Y axis, no potentials are observed (Fig. 5B), the nerve being symmetrically located with respect to this antipodal electrode pair. Along the X axis (Fig. 5A) only a positive potential is recorded, due to the leading dipole as it went around the bend (there being no trailing dipole potential because of the nerve crush). The latency of start of the X axis positive wave corresponds to the time that the action potential is at the bend (start of negative-going portion of near field recording – Fig. 5D). The 3-CLT of these data can be readily intuited. Since the Y channel is zero, the 3-CLT points must lie in the X-Z plane. The plot is not a straight line since X and Z are out of phase (for the plot to be linear, they would have to be in phase and proportional). The planar curvilinear 3-CLT for the data of Fig. 5 is in agreement with the findings of Chimento et al. (1987) with regard to a bent nerve. The data of Fig. 5 differ from their prior experiments in that the recordings here were made along the axis of the bend, the end of the nerve was crushed in the present experiment, and the origin of the potentials relating to the L/T/D model is now clear.

Discussion

The polarity and occurrence of the far-field potentials of the present study are consistent with the LT/D model developed in our previous report (Jewett and Deupree 1989) to account for the generation of far-field potentials. Thus, the results from the hemicylinder are now extended to include the sphere, although the potentials diminish with distance in different ways in the two volumes. In the cylinder, far-field potentials do not appreciably diminish with axial distance, only with radial distance; in contrast, in the sphere, potentials diminish in all directions.

Further, we have confirmed that the action potential, when recorded with widely spaced electrodes, at some distance away from the generator, under conditions previously shown to accentuate LT/D detection, has amplitude and polarity characteristics of a dipole; the potentials recorded using antipodal electrodes vary as the cosine of the angle between the nerve axis and the recording axis (see Nunez 1981, p. 146). This provides another definition of 'far-field' in the context of evoked response recordings. Originally 'far-field' was operationally defined (Jewett and Williston 1971) as occurring when the responses at two electrodes were not significantly different, based upon the criteria of the analysis of the wave form appropriate to the response. Now we can suggest that far-field recordings primarily detect dipolar characteristics of the generator. If the electrodes are close to a neural generator, then the potential can best be described by means of an equivalent multipole generator, i.e., higher order terms in the expansion of the governing equation are significant (see Appendix). However, if the electrodes are not close to the neural generator, and a dipole approximation is sufficient for an accuracy appropriate to the experiment, then such recordings can be defined as far-field. With respect to a spherical volume, Nunez (1981, p. 117) has shown that the radius of the sphere must be 3 times the dipole separation in order for the error of the dipole approximation to be less than 3%. The differences between near-field and far-field are summarized in Table II, where we now include the idea of the far-field as defined by the degree of dipole approximation.

Table II emphasizes that closely spaced electrodes (as do the differences between recordings made when the electrode is moved) detect the spatial gradient of the potential field and, hence, detect near-field responses, but not far-field responses. For a fixed distance between electrodes, the absolute difference in potential at the two electrodes is greatest in the near-field. For closely spaced electrodes the spatial gradient diminishes inversely with distance from the generator, at a power higher than that for a single point, e.g., for
TABLE II
Comparison of near- vs. far-field recordings.

<table>
<thead>
<tr>
<th>Field</th>
<th>Dipole approximation</th>
<th>Change of electrode position</th>
<th>Widely spaced electrodes</th>
<th>Closely spaced electrodes</th>
<th>Detection of other, distant generators</th>
</tr>
</thead>
<tbody>
<tr>
<td>Near</td>
<td>poor (higher order terms detected)</td>
<td>large effect (high spatial gradient)</td>
<td>one ‘active’ electrode at generator, one ‘reference’ electrode, potential affected only by position of active electrode</td>
<td>detects potential only if near to generator (high spatial gradient)</td>
<td>small</td>
</tr>
<tr>
<td>Far</td>
<td>good ($r^{-2}$ term predominates)</td>
<td>little change (lower spatial gradient)</td>
<td>detects potential at distance, generator location uncertain, both electrode positions can affect recorded potential</td>
<td>no potential detected (lower spatial gradient)</td>
<td>algebraic summation</td>
</tr>
</tbody>
</table>

For a dipole the potential in a spherical conductor is inverse to $r^2$, but the spatial gradient is inverse to $r^3$. Since the electrical equivalent of an action potential in a straight long nerve is a quadrupole (Plonsey 1969, p. 237), the detection with closely spaced electrodes of an action potential at a distance within a volume conductor is even more difficult since the potential is inverse with the 4th power of distance. Thus, closely spaced electrodes can be used to detect potentials only when near the generators. Because widely spaced electrodes are not subject to such severe drop-off, detection of electrical activity is more likely with such an electrode spacing when the electrodes cannot be placed near the generators.

For the special case of a centrally placed dipole in a spherical volume, antipodal electrode positions (those on opposite sides of the sphere) have unique properties. Far-field potentials recorded from non-antipodal electrodes have effects which are not easily intuited, as is described in the Appendix. At antipodal points dipoles generate potentials equal in magnitude but opposite in sign, with the result that a differential amplifier records a potential twice that which would be recorded if one electrode were at zero (e.g., on the equator). On the other hand, a quadrupole generates a surface potential distribution with potentials at antipodal points that are equal (see Appendix). (Intuitively, opposite points on the sphere must be equal and of the same sign because of the symmetrical arrangement of the linear quadrupole: source-sink/sink-source.) In this case a differential amplifier will detect nothing.

The higher order terms in the potential field equation (see Appendix) are of no practical concern in evoked responses, because they either cancel or fall off inversely proportional to $r^4$, or at an even higher rate. In summary, because of the characteristics of potential drop-off with distance and angular dependency, antipodal electrodes on spheres primarily detect dipoles (if they are centric) in the far-field. This may explain why differences in electrode position in the cat are readily compensated for using a cosine correction (Martin et al. 1987b). If the electrodes were not antipodal, then higher order terms might also contribute to the recorded potentials, especially in the small skull of the cat. It should be noted that in the sagittal plane the brain-stem is not in the center of the human head, and that the cosine correction used in the sagittal plane in humans (Pratt et al. 1983, 1984, 1985; Martin et al. 1987a; Sininger et al. 1987) still has not been experimentally justi-
fied. Clearly, before such corrections are used the surface distribution as a function of the electrode position (expressed as an angle) must be demonstrated to be a cosine function.

It is now apparent that the paper on the 3-CLT theory (Jewett 1987) is erroneous in stating that a straight axon generates a linear 3-CLT, because if the nerve is long enough the linear quadrupole of the action potential will not be detected. What will be detected are the leading and trailing dipoles associated with the starting and stopping of the action potential in the straight nerve, and these 3-CLTs will be linear, as will the potentials from a 'short' straight nerve (one not long enough to have a full action potential occur at a single instant).

Based upon the present work an additional correction to the 3-CLT theory paper (Jewett 1987) needs to be mentioned. The cut-end potential could affect far-field potentials due to lesions (the so-called 'ghosts' previously described; see Gardi et al. 1987; Jewett 1987, p. 387). When the lesion is acute (such as a surgical lesion), lesioned axons may generate cut-end potentials. However, at some time after the lesion, once retrograde degeneration has occurred, these same axons may behave like crushed-end nerves, in which case no cut-end potentials will be detected in the far-field recordings.

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Appendix

Special properties of antipodal electrode position

The purpose of this appendix is to demonstrate the consequences of antipodal electrode orienta-

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Fig. 6. The potentials measured at a point which are due to fields generated by various current sources. A: potential measured from the field produced by a dipole. B: potential measured from the field produced by a linear quadrupole with unequal spacing of charges. C: potential measured from the field produced by a linear quadrupole with equal spacing of charges. D: potential measured from the field produced by a 2-dimensional quadrupole.
tion upon the surface-potential distribution of centrally located generators. A stepwise derivation is offered as an aid to understanding the qualitative conclusions by those without a sufficient background in mathematics (such as the first two authors).

**Dipole case**

The potential, $\Phi$, at a point due to a dipole, Fig. 6A, is given by

$$
\Phi = \frac{1}{4 \pi \sigma} \left( \frac{1}{r_1} - \frac{1}{r_2} \right)
$$

(1)

where $+I$ and $-I$ are the source and sink, $\sigma$ is the conductivity of the medium, $d$ is the distance between the source and sink (dipole separation), $r$ is the distance from the center of the dipole to the measuring point.

We express $r_1$ and $r_2$ in terms of $r$ and $\theta$, $\theta$ being the angle as shown in Fig. 6A, and express $\Phi$ as a series in $r$ and $\theta$.

$$
r_1^2 - r^2 + \left( \frac{d}{2r} \right)^2 = -rd \cos \theta.
$$

(2)

$$
r_1^2 = 1 + \left( \frac{d}{2r} \right)^2 - \frac{d \cos \theta}{r}
$$

$$
r_1 = \left[ 1 + \left( \frac{d}{2r} \right)^2 - \frac{d \cos \theta}{r} \right]^{1/2}
$$

$$
r_1 = \left[ 1 + \left( \frac{d}{2r} \right)^2 - \frac{d \cos \theta}{r} \right]^{-1/2}
$$

(3)

Similarly we express $r_2$ in terms of $r$ as

$$
r_2 = \left[ 1 + \left( \frac{d}{2r} \right)^2 + \frac{d \cos \theta}{r} \right]^{-1/2}
$$

(4)

(1) can be rearranged as

$$
\Phi = \frac{1}{4 \pi \sigma} \left( \frac{r}{r_1} - \frac{r}{r_2} \right)
$$

(5)

Comparing the left-hand side of the following binomial expansion

$$(1 + x)^n = 1 + nx + n(n-1)x^2/2! + n(n-1)(n-2)x^3/3! + \ldots$$

and the right-hand side of (3), we realize that the right-hand side of (3) could be expanded into a series where $n = -1/2$

and

$$x = \left( \frac{d}{2r} \right)^2 - \left( \frac{d \cos \theta}{r} \right)$$

We express (3) and (4) as

$$
\frac{r}{r_1} = 1 - \frac{1}{2} \left( \frac{d^2}{2^2 r^2} - \frac{d \cos \theta}{r} \right) + \frac{1}{2} \left( \frac{d^2}{2^2 r^2} - \frac{d \cos \theta}{r} \right)^2 + \ldots
$$

$$
\frac{r}{r_2} = 1 + \frac{1}{2} \left( \frac{d^2}{2^2 r^2} + \frac{d \cos \theta}{r} \right) + \frac{1}{2} \left( \frac{d^2}{2^2 r^2} + \frac{d \cos \theta}{r} \right)^2 + \ldots
$$

(6)

Similar to (6), $\frac{r}{r_2}$ expands to

$$
\frac{r}{r_2} = 1 + \frac{1}{2} \left( \frac{d^2}{2^2 r^2} - \frac{d \cos \theta}{r} \right) + \frac{1}{2} \left( \frac{d^2}{2^2 r^2} - \frac{d \cos \theta}{r} \right)^2 + \ldots
$$

(7)

Using (6) and (7)

$$
\frac{r}{r_1} = \frac{d \cos \theta}{r} + \frac{d^3 (5 \cos^2 \theta - 3 \cos \theta)}{8 r^3} + \frac{15 d^4 \cos^2 \theta}{128 r^5} + \ldots
$$

(8)

Using (8) in (5)

$$
\Phi = \frac{1}{4 \pi \sigma} \left( \frac{d \cos \theta}{r^2} + \frac{d^3 (5 \cos^2 \theta - 3 \cos \theta)}{8 r^4} + \frac{15 d^4 \cos^2 \theta}{128 r^6} + \ldots \right)
$$

(9)

If $d \ll r$, i.e., the measurement is made at much larger distances from the dipole center as compared to the dipole separation, $d^3/r^4$ and $d^5/r^6$ are negligibly small, giving rise to

$$
\Phi = \frac{1}{4 \pi \sigma} \frac{d \cos \theta}{r^2}
$$

(10)

which is the approximation used for potential in an infinite medium (Nunez 1981, p. 117). On the surface of a sphere, potentials due to a centric dipole are similarly approximated by multiplying the right-hand side of (10) by a factor of 3 to
account for the forcing of the current lines due to the spherical geometry (Nunez 1981, p. 117). Note that the second term in the expansion in (9) is sometimes called the ‘octupole term.’ We prefer to refer to it only as the \( r^{-4} \) term so as to avoid the confusion which arises from using similar words to describe generator characteristics and terms in the binomial expansion, e.g., computations regarding a generator may require an \( r^{-4} \) term if high accuracy is required, especially in the near-field.

**Antipodal measurements (dipole case)**

For antipodal electrodes, the measurements are made at points subtending an angle of \( \theta \) and \( 180 + \theta \) to the dipole axis and the potential is expressed as a difference of these two measurements.

If one were not to make the assumption of \( d \ll r \) and thereby retain the higher order terms, the result is that these terms contribute little to the surface potential. For, due to the odd powers of \( \cos \theta \), the following relations hold:

\[
\cos(180 + \theta) = -\cos \theta \\
\cos^3(180 + \theta) = -\cos^3 \theta \\
\cos^5(180 + \theta) = -\cos^5 \theta
\]

Using the above and (9), we express \( \Phi_{(180 + \theta)} \) as follows.

\[
\Phi_{(180 + \theta)} = \frac{-1}{4 \pi \sigma} \left( \frac{d \cos \theta}{r^2} + \frac{d^3(5 \cos^3 \theta - 3 \cos \theta)}{8r^4} + \frac{15d^5 \cos \theta}{128r^6} + \ldots \right)
\]

and the recorded potential between the antipodal points as

\[
\Phi_\theta - \Phi_{(180 + \theta)} = \frac{2q}{4 \pi \sigma} \left( \frac{d \cos \theta}{r^2} + \frac{d^3(5 \cos^3 \theta - 3 \cos \theta)}{8r^4} + \frac{15d^5 \cos \theta}{128r^6} + \ldots \right)
\]

As seen from (12), if we were to record a dipole by measuring the difference in the potentials at two antipodal points on the surface of a sphere, the higher order terms (all having even powers of \( r \)), do not cancel out but add together since they have the same magnitude but are of opposite sign. However, the contributions of the higher order terms in the expansion are relatively small owing to the higher powers of \( r \) in the denominator, i.e., these potentials diminish rapidly with distance from the generator. Thus, at ‘far-field’ recording points the \( \cos \theta \) dependence predominates, i.e., the complex spatial distribution of the higher order terms can be ignored because the denominator is large.

**Linear quadrupole case**

There are two possible distributions for a linear quadrupole as shown in Fig. 6B and 6C. The difference between the two quadrupoles is that the dipole separation is different, but in both cases the dipole moment (the product of current and separation) is zero, as in the case of the action potential of a straight nerve (Plonsey 1969, p. 239).

\[
\Phi = \frac{1}{4 \pi \sigma} \left( \frac{1}{r_1} - \frac{1 - 2l}{r} + \frac{1}{r_2} \right)
\]

\[
\Phi = \frac{1}{4 \pi \sigma} \left( \frac{r}{r_1} - 2 + \frac{r}{r_2} \right)
\]

Using (14) and (15) in (13)

\[
\frac{r}{r_1} + \frac{r}{r_2} = 2 - \frac{d^2}{24r^2} + \frac{3}{2^3} \left( \frac{2d^4}{2^4 r^4} + \frac{2d^6 \cos^2 \theta}{2^3 r^6} \right)
\]

\[
- \frac{5}{2^4} \left( \frac{2d^6}{2^5 r^6} + \frac{3d^8 \cos^2 \theta}{2^3 r^8} \right) + \ldots
\]

\[
\frac{1}{r} \left( \frac{r}{r_1} + \frac{r}{r_2} - 2 \right) = -\frac{d^2}{2^3 r^3} + \frac{3d^4}{2^3 r^5} + \frac{3d^6 \cos^2 \theta}{2^3 r^7} - \frac{5d^6}{2r^9}
\]

\[
- \frac{3d^8 \cos^2 \theta}{2^3 r^9} + \ldots
\]

\[
\frac{1}{r} \left( \frac{r}{r_1} + \frac{r}{r_2} - 2 \right) = \frac{d^2}{8r^3} \left( 3 \cos^2 \theta - 1 \right) + \frac{3d^4}{64r^5} \left( 1 - 10 \cos^2 \theta \right)
\]

\[
- \frac{5d^6}{128r^7} + \ldots
\]

By analogous reasoning, as we did for the dipole, if \( d \ll r \), the rest of the terms other than the first
could be neglected, which would give rise to the familiar expression for the potential on the surface of a sphere due to a linear quadrupole:

\[
\phi = -\frac{1}{32\pi r^4} (3\cos^2\theta - 1)
\]

**Antipodal measurements (linear quadrupole with equal spacing)**

If we were to make antipodal measurements, even if we do not neglect the higher order terms, owing to the even powers of \(\cos \theta\),

\[
\cos^2\theta = \cos^2(180 + \theta)
\]

which results in equation (18) for \(\Phi_{180 + \theta}\) which is the same as (17):

\[
\Phi_{180 + \theta} = \frac{1}{4\pi \sigma r^4} \left( \frac{d^4(3\cos^2\theta - 1)}{8r^3} + \frac{3d^4(1-10\cos^2\theta)}{64r^3} \right) - \frac{5d^2}{128r^6} + \ldots
\]

Therefore, an antipodal differential recording of a linear quadrupole will yield

\[
\phi\theta - \Phi_{180 + \theta} = 0
\]

which is equivalent to saying that the potentials at antipodal points are of the same magnitude and sign, i.e., no potential can be recorded by differential recording of antipodal points.

**Antipodal measurement of unequally spaced charges**

The action potential in a straight axon is a linear quadrupole (Plonsey 1969, p. 239). Although the dipole separation is unequal, the dipole moments are equal, with greater current flowing through the shorter distance. In this case, contributions from terms with odd powers of \(r\), i.e. \((1/r^3, 1/r^5, 1/r^7, \ldots)\) vanish. Because the generator is a quadrupole, the \(1/r^2\) term does not exist. Contributions from terms with even powers of \(r\) \((1/r^4, 1/r^6, \ldots)\) exist owing to the same reason (odd powers of \(\cos \theta\)) as explained in the case of the dipole. Similarly, the contributions of these terms are small because of the high powers of \(r\) in the denominator, the first term being the \(1/r^4\), and the rest higher even powers.

**Two-dimensional quadrupole (Fig. 6D)**

The potential due to a 2-dimensional quadrupole (Fig. 6D) at distances much larger than the pole separation is given by (20)

\[
\phi = \frac{3d_2 d_3 \cos \theta \sin \theta}{8\pi r^3} \quad r \gg d_2, \text{ and } d_3,
\]

Using the relation, \(2 \cos \theta \sin \theta = \sin 2\theta\), (20) could be expressed as shown in (21):

\[
\phi_{\theta} = \frac{3d_2 d_3 \sin 2\theta}{8\pi r^3}
\]

Therefore,

\[
\phi_{\theta} - \Phi_{180 + \theta} = 0
\]

which implies that an antipodal recording will be unable to detect the potential due to a 2-dimensional quadrupole, just as in the case of the linear quadrupole with equal spacing.

**Discussion and summary**

Antipodal electrodes favor detection of dipoles \((r^{-2} \text{ term})\) rather than quadrupoles \((r^{-4} \text{ term or less})\). So, it is not surprising that the 3-channel Lissajous' trajectory derived from antipodal electrode placements detects dipolar components of the auditory brain-stem response (Jewett 1987). Similarly, the cosine function surface distribution detected in this paper from the 'leading dipole' can be predicted on the basis of the derivations given here.

However, antipodal electrode placements are not common in evoked response recordings, and with any other angular positions the simplifications are lost and qualitative prediction of the effect of electrode orientations is difficult, as shown in the following mental experiment: assume an equally spaced linear quadrupole at the center of a sphere oriented along the axis. One electrode at \(0^\circ\) (north pole), and the other electrode at \(180^\circ\) (south pole). The potential difference will be zero (as described above). Now if the \(0^\circ\) electrode remains fixed, while the other electrode moves upwards on the surface, reducing the included angle, from \(180^\circ\), the difference potential observed goes from zero, to a maximum at \(90^\circ\), and then returns to zero at \(0^\circ\), following a
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(3 \cos^2 \theta - 1) function. Similar complexity will occur with a fixed (< 180°) electrode and a rotating dipole. Thus, no generalizations are possible, and the possible contributions of higher order term from quadrupole generators must be evaluated quantitatively for each situation, especially in the near-field.

References


