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SIMULATION OF 'STATIONARY' SAP AND SEP PHENOMENA BY 2-DIMENSIONAL POTENTIAL FIELD MODELLING

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Summary In order to model the distribution of potentials in the hand due to antidromic SAP propagation and in the body due to afferent conduction of the median nerve volley, 2-dimensional matrices of the appropriate shape were constructed, each containing a 'generator' consisting of up to 3 'source' and 3 'sink' points. The value of the field potential at other sites was calculated using a finite difference method.

It was shown that the potential gradient is virtually zero in matrix zones which are separated from the region containing the generator by a constriction in the boundary of the conductor. Points on the far side of the constriction remain virtually equipotential, at a level determined by the potential at the junction. This is naturally influenced by the proximity of the generator, so that as the generator approaches the constriction a potential difference will develop between points on the far side, irrespective of their distance from the junction, and other remote parts of the matrix. In the context of human SAPs and SEPs, such factors may be of paramount importance in the generation of so-called 'stationary' or 'far-field' potentials.

With additional postulates concerning the manner in which the SAP is attenuated by the termination of axons as it propagates through the hand, and the course taken by the median nerve volley between the arm and the neck, it was possible to model the majority of stationary SAP phenomena described by Kimura et al. (1984), and also the distribution and latency of the P9 SEP component following median nerve stimulation.

Keywords: *potential field modelling – stationary potentials – far-field potentials – sensory action potentials – somatosensory evoked potentials*

It is well known that a somatosensory evoked potential (SEP) with a peak latency of approximately 9 msec following median nerve stimulation at the wrist (hence labelled 'P9') can be recorded between sites on the head and remote parts of the body, due to propagation of the mixed nerve action potential through the brachial plexus (Cracco and Cracco 1976; Jones 1977; Kritchevsky and Wiederholt 1978; Desmedt and Cheron 1980; Yamada et al. 1980). This potential, which is recorded with similar amplitude and latency at all sites above the upper neck, was interpreted by Jones (1977) in terms of the volume conduction model described by Woodbury (1960), based on the theory of Lorente de Nó (1947). According to this theory the onset of the depolarised region may be considered equivalent to a dipole sheet equal in area to the cross-section of the nerve trunk, propagating along the nerve with the positive poles in advance. The potential recorded at a distance would thus be positive in polarity at all sites proximal to the depolarised region and proportional in amplitude to the solid angle subtended at the recording electrode by a cross-section through the nerve trunk. This would appear to account for the fact that P9 has a similar latency at all scalp and upper neck locations, since these sites 'see' the action potential from approximately the same viewpoint, but an observation not predicted by the model is that the recorded amplitude of P9 is also similar from the mid-cervical region to the vertex of the scalp. Furthermore, it is not clear why the onset of P9 should correspond approximately to the point at which the volley emerges from the arm into the trunk, nor why the potential should reach a peak and decline before the volley arrives at the spinal cord.

Kimura et al. (1984) described a similar phenomenon in association with antidromic propagation of the radial nerve sensory action potential (SAP) through the hand. Two successive positive/negative 'stationary' deflections were recorded from sites on the middle and distal phalanges of the index finger (referred to a site on the fifth finger) with little or no change in amplitude or latency. The second and larger of these was thought to be due to the volley approaching increased resistance at the junction of the finger with the hand. By experiments conducted in vitro, Nakanishi (1982) demonstrated that stationary potentials are produced by a moving generator wherever there is a sudden change in the resistance of the conducting medium. In a volume conductor resistance in a given direction is inversely proportional to the cross-sectional area of the medium at that point, and so will be increased wherever the volume is constricted by encroachment of its boundaries.

The object of the present study was to establish by potential field modelling in two dimensions, whether or not the stationary potentials recorded in the hand are phenomena which are simply explicable in terms of the physiological characteristics of the action potential and the geometry of the volume conductor in which it is propagated. It was then proposed to apply the same principles to modelling the afferent propagation of the median nerve volley from the arm to the spinal cord, to establish whether conductor geometry might be a major factor determining the distribution and wave form of P9.

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Methods

Field potentials were calculated by solving the 2-dimensional Poisson equation using a finite difference method. The conductor was represented by an orthogonal matrix of points containing a number of fixed-voltage sources and sinks. An iterative solution (Gauss-Siedel method) was achieved by obtaining an improved estimate of the value of the field at each point $P_{x,y}^{n+1}$ from its previous value $P_{x,y}^{n}$ and the value of the surrounding points thus:

$$P_{x,y}^{n+1} = P_{x,y}^{n} + \frac{\alpha}{4}\left(P_{x+1,y}^{n} + P_{x-1,y}^{n} + P_{x,y+1}^{n} + P_{x,y-1}^{n} - 4P_{x,y}^{n}\right)$$

while maintaining the source and sink points at constant voltage. Repetition of this process for approximately 10,000 iterations reduced the mean error at each point to less than 0.5%. To speed convergence, α was set at 1.7 ('over-relaxation'). Conductivity was assumed uniform between adjacent points in the matrix and zero across boundaries. Capacitative and inductive effects were considered negligible (Plonsey 1969).

To simulate antidromic propagation of the radial nerve sensory action potential from the forearm through the hand into the finger, 3 models of increasing complexity were constructed (Fig. 1). Model 1 consisted of a matrix measuring 101 × 50 points, connected at the middle of the longer side to a 'finger' measuring 7 × 50 with a line of symmetry at $x = 51$. The 'generator' consisted of one 'source' point and one 'sink' of the same magnitude, separated by 5 divisions of y. These were initially located in the large area on the symmetry line with the source closer to the junction with the finger. The generator was then advanced step-wise along the symmetry line towards and into the finger, maintaining the source-sink separation at 5 units, and potential fields were calculated for 8 generator positions.

Models 2 and 3 employed a matrix depicting a 3-'fingered' 'hand' with 'wrist' and 'forearm,' overall dimensions 31 × 100 points (Fig. 1). The generator (located on the line of symmetry) was triphasic, consisting of 3 source and 3 sink points in the sequence '+ – – – + +,' the relative magnitudes being +8, –1, –10, –2, +3 and +2 units. Adjacent source and sink points were separated by 4 divisions of y, and the total length of the generator (20 divisions) was chosen in relation to the overall dimensions of the model in order to correspond with the typical measured duration of the SAP (1.5 msec) assuming a conduction velocity (CV) of 50 m/sec. The generator was advanced step-wise from the 'forearm' through the 'wrist' constriction into the 'hand' and the middle 'finger.' Potential fields were calculated for 16 positions of the generator, and wave forms of potential against generator position (i.e., 'time,' assuming uniform CV) were derived at points along x-line 19, with reference to a point near the base of one lateral finger ($x = 1$, $y = 76$). 'Bipolar' wave forms were

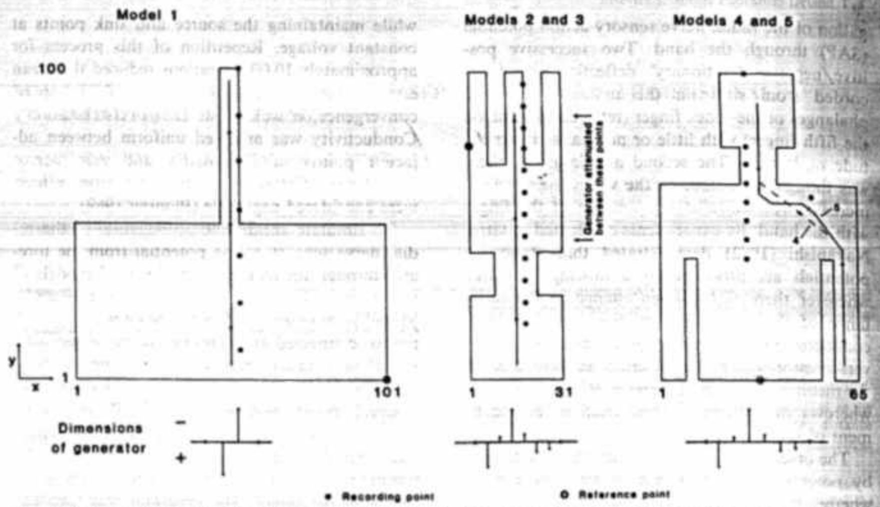

Fig. 1. Dimensions of matrices employed for models 1–5. The generator consisted of one source and one sink point in model 1, 3 of each in models 2–5. These were placed along the line of symmetry with the initial source towards the finger in models 1–3, and along the line indicated in models 4 and 5. Model 3 differed from model 2 by the manner in which the generator was attenuated between the 2 points shown (see text for details). Model 5 differed from model 4 by the course of the generator from the arm to the neck.

derived from the potential difference between adjacent 'recording' points.

Since the amplitude of the radial nerve SAP diminishes progressively on propagation through the hand (see Kimura et al. 1984), a similar property was incorporated into models 2 and 3. For model 2 the amplitudes of all generator sources and sinks were reduced progressively and simultaneously. This commenced when the major sink had reached a point in the hand distal to the wrist constriction by approximately one-sixth the length of the hand (y = 45) and was complete just beyond half the length of the finger (y = 85). Model 3 embodied a different assumption, that the sources and sinks would be attenuated independently of one another according to their position in the hand. Consequently the initial source and 3 sink points were progressively and individually attenuated between y = 45 and y = 85, and for each generator position the magnitude of the 2 trailing sources was adjusted as necessary (by adding or subtracting an equal amount to or from each) in order to preserve equality between the sums of positive and negative charges.

In order to simulate afferent propagation of the mixed median nerve volley from the arm to the head, a matrix with overall dimensions 65 × 100 points was constructed in the shape of a 'trunk' with 'neck,' 'head' and 'arms' (Fig. 1). The generator was again triphasic with 3 sources and 3 sinks in the sequence '+ − − − + +,' the relative magnitudes being the same as in models 2 and 3. The separation between adjacent source and sink points was 5 linear units, and the overall generator length of 25 units was chosen in accordance with the measured duration and CV of the mixed median nerve volley at the clavicle (2 msec and 60 m/sec respectively). The generator was initially arranged in a linear fashion within one 'arm' along x-line 60 and was then advanced proximally in steps of 5 units. On emergence from the arm into the upper trunk the direction of propagation was diverted towards the neck, initially along a diagonal in which the x-coordinate was altered by 3 units for every 4 units change in y. This kept the separation between adjacent source and sink points fixed at a distance of 5 units, although the generator itself was no longer linear. In model 4, after progression by one step along this diagonal the slope was changed to the reciprocal (3 unit change of y to every 4 of x) as far as the midline of the neck (x = 33), whereupon direct caudal-rostral propagation was resumed. In model 5 the initial diagonal was taken for 3 steps and the reciprocal for one. At this point propagation became horizontal for 2 steps as far as x = 37, resumed the shallower diagonal for one step as far as the midline and then turned vertically into the head. The magnitude of all sources and sinks was kept constant throughout. Field potentials were calculated for 14 positions of the generator and wave forms of potential against generator position plotted for selected points along x-line 29 plus the 'clavicle' (x = 48, y = 57), all with reference to the 'sacrum' (x = 33, y = 1).

Results

Model 1

The first model (Fig. 2) illustrates in general terms how the distribution of field potentials in a 2-dimensional conducting medium is influenced by the boundaries of that medium, and changes according to the position of the generator.

(1) When the generator is located in the large area (fields 1–4), the potential gradient along the finger (recording points 1–4) is virtually zero. This is because the preferred paths of current flow all lie within the large area. With very little current

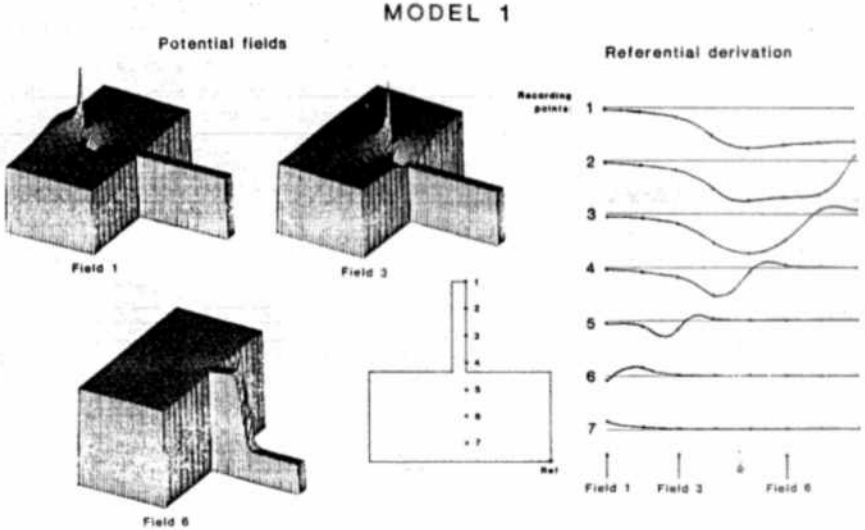

Fig. 2. Model 1: field potentials associated with propagation of a dipolar generator (positive down in this and subsequent figures) from a large area through a boundary constriction into a 'finger.' The referential derivations show the potential difference between 7 recording sites and a reference in a remote corner of the large area, plotted against generator position. Field 3 illustrates the onset of a 'stationary' potential along the finger as the initial generator source approaches the boundary constriction. Note also that in field 6 the whole of the large area is raised to a potential close to that of the generator sink.

flowing along the finger all points necessarily remain virtually equipotential.

(2) As the generator approaches the constriction at the base of the finger the whole of the latter acquires a uniform potential of the source polarity (fields 3 and 4). The potential at the base of the finger is naturally influenced by the increasing proximity of the source, and since it is still impossible for significant current to flow from the source to the sink via the finger, distal points in the finger are raised to a potential similar to that at the junction. An analogy may be drawn with a conducting lead connected to the positive pole of a battery: while the circuit remains incomplete the lead will be at one potential throughout its length.

(3) The potential difference between sites in the finger and a distant referential point in the large area reaches a maximal value as the generator enters the constriction (between fields 4 and 5) and declines only slightly thereafter, due to decreasing influence of the sink on the reference site, until the source passes by the recording point. In other words, throughout the length of the finger a 'stationary' potential is present with similar amplitude and latency of onset.

(4) Potential differences in the large area quickly diminish on entry of the generator into the finger. This is to say that, when the generator is located in the more confined space, current flow is restricted to a region within a very short distance of the generator. Note, however, that the whole of the large area is now at a potential much closer to that of the generator sink than the source. The large area is now connected to the sink as if by a conducting lead to the negative pole of a battery.

Model 2

It will be apparent from examination of the modelled potential fields in the 3-'fingered' 'hand' (Fig. 3) that with the generator situated in the 'forearm,' proximal to the constriction representing the 'wrist,' the potential throughout the hand and along the middle finger is virtually constant and identical to that at the reference site on the lateral digit. On entry of the initial source into the wrist constriction there is still little or no tendency for current to circulate via the hand, hence no potential gradient along the hand or finger (field 3). However, the wrist, hand and fingers are influenced by the proximity of the source and acquire a positive potential relative to sites in the forearm.

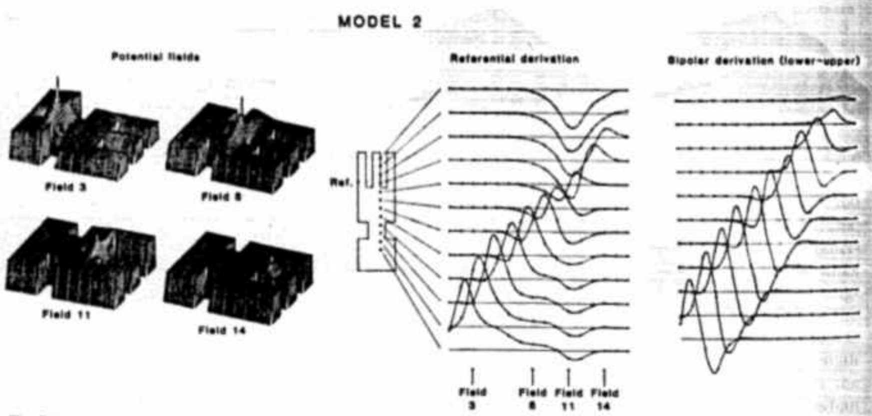

Fig. 3. Model 2: field potentials associated with propagation of a 6-element triphasic generator into and through a 3-'fingered' 'hand' with progressive, simultaneous attenuation of all sources and sinks between the points indicated in Fig. 1. Referential wave forms show the potential at 12 recording points referred to a site on the lateral finger, and bipolar wave forms the potential difference between adjacent recording points, both plotted against generator position. In field 3 the whole hand is virtually equipotential but displaced from zero (defined as the mean of the generator source and sink potentials) in a positive sense. In field 8 a 'stationary' positive potential begins to appear throughout the length of the digit, reaching a peak with field 11. In field 14 the final potential present at the distal extremity of the middle digit is of positive polarity with respect to the reference.

On emergence of the generator from the wrist constriction into the hand the magnitude of all generator sources and sinks was progressively reduced, reaching zero with the central sink distal to the base of the finger by a little more than half the length of the latter. As the initial source approaches the junction with the middle finger (field 8), all points in the latter acquire a positive potential relative to the reference on the lateral finger. The potential initially increases with the increasing proximity of the source to the junction, but as the magnitude of the generator is reduced the potential reaches a peak (field 11) and declines. Thus a 'stationary' potential is present with similar amplitude, latency and wave form at all distal locations of the finger. The potential commences while the generator is still fairly distantly located in the hand, peaks when the increasing proximity of the source is balanced by the reduction in its magnitude, and terminates with the ultimate disappearance of the generator at approximately half the length of the finger.

The triphasic wave form recorded at locations in the hand and the stationary positivity present throughout the finger are broadly similar to actual radial nerve SAP recordings obtained by Kimura et al. (1984). They also recorded a final stationary negativity, however, which was not predicted by the model. At sites proximal to and within the wrist constriction the modelled fields predict a small positive-going afterpotential of fixed latency (fields 11 and 12), due to emergence of the trailing sources from the constriction into the hand. This is not detectable in the actual recordings, perhaps because in reality the hyperpolarisation event is less abrupt and of longer duration than was assumed for the model.

Model 3

Model 3 differed from model 2 in that, after emergence from the wrist constriction, the initial source and 3 sinks were attenuated independently of one another according to their individual positions in the hand. Since it is necessary to preserve

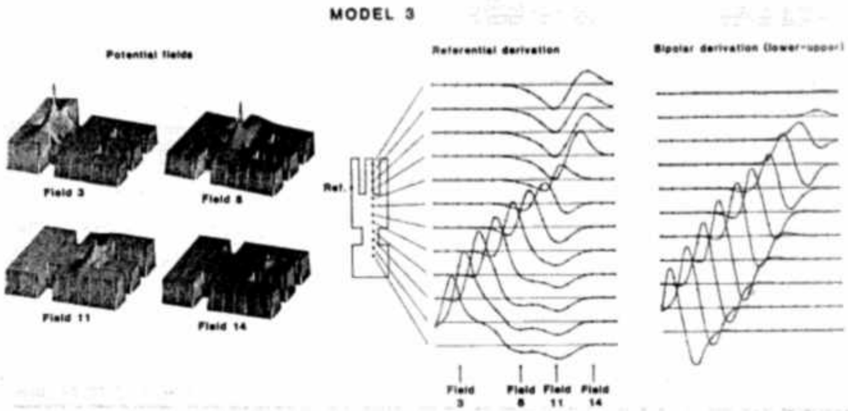

Fig. 4. Model 3: as model 2 but with independent attenuation of all sources and sinks on propagation through the hand, such that the initial source reaches zero first (chronologically). In field 14 the final potential present at the distal extremity of the middle digit is of negative polarity, as in the actual radial nerve SAP recordings of Kimura et al. (1984).

a balance of charges, the 2 trailing sources were incremented or diminished as appropriate for each position of the generator.

The major difference between models 2 and 3 visible in the field potentials and referential wave forms (Figs. 3 and 4) is that the final, positive-going stationary potential in model 2 is replaced, in model 3, by a positive/negative biphasic potential. This is of similar latency and amplitude at all sites distal to the point at which the initial generator source is reduced to zero and resembles quite closely the actual SAP recordings of Kimura et al. (1984). The one feature present in reality but not predicted by the model is a smaller, earlier deflection, also recorded from the index finger with reference to the fifth. This was proposed by Kimura et al. (1984) to be due to the volley approaching increased resistance at the wrist, and might be explained by the additional postulate of conductivity variations in the hand (see Discussion).

Model 4

Models 4 and 5 were designed to simulate afferent propagation of the mixed median nerve volley from the arm into the shoulder, neck and head. The separation between adjacent source and sink points was fixed at 5 divisions of the matrix, and on emergence of the generator from the arm into the trunk the direction of propagation towards the neck was defined by the hypotenuse of matrix triangles which preserved this 5-point separation (i.e., 3–4–5 triangles). In model 4 (Figs. 1 and 5) a diagonal course was maintained as far as the midline of the model (i.e., the 'spinal cord').

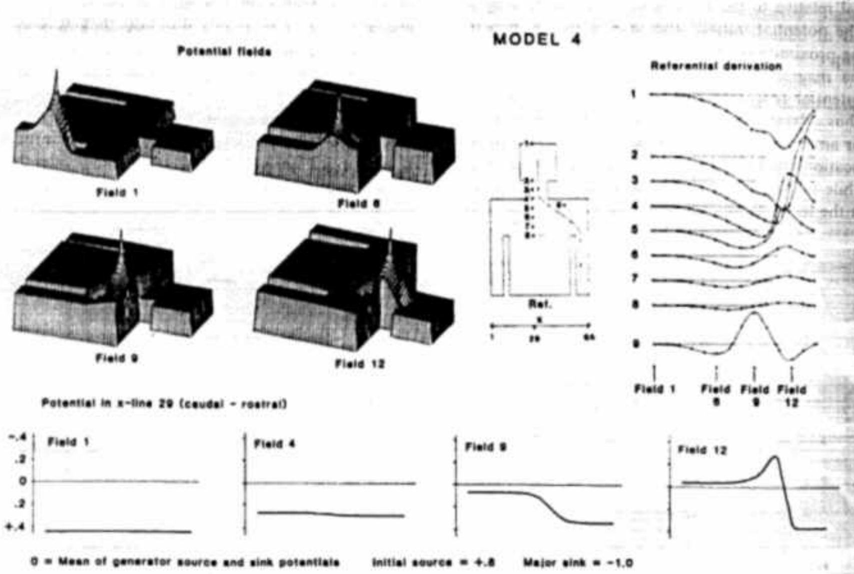

Fig. 5. Model 4: field potentials associated with propagation of a 6-element triphasic generator from the 'arm' to the 'neck' and 'head' on a relatively direct diagonal course. In field 1, with the generator confined within the arm the whole body is displaced from zero potential in a positive sense. Following emergence of the generator into the trunk (fields 4–6), a potential difference starts to develop between the head and neck and the reference on the 'sacrum,' peaking with arrival of the major generator sink at the neck (field 12). This 'stationary' potential is coincident with a 'travelling' negative wave at lower neck sites. At the 'clavicle' a triphasic wave is recorded as the generator propagates through the shoulder. The graphs of potential in the line of recording points 1–8 show the development of potential gradients along the trunk, commencing with field 4.

Fig. 5 illustrates potential fields calculated for 4 positions of the generator, graphs depicting the potential in the line of recording points 1–8 (x-line 29) in relation to the mean of the generator source and sink potentials, and wave forms of the potential recorded at 9 sites on the head, neck and trunk referred to the 'sacrum' (x = 33, y = 1) plotted against generator position (i.e., 'time'). In the latter it can be seen that there is no marked deviation from the baseline while the generator is contained within the arm (fields 1 and 2). During this time the potential gradients are confined to a region within a very short distance of the generator while the trunk, head, neck and other arm remain virtually equipotential. Note, however, that this potential is displaced from zero (defined as the mean of the generator source and sink potentials) in the polarity of the initial source, to which the trunk is connected as if by a lead to the positive pole of a battery. Once the source emerges into the trunk (fields 3–6) potential gradients begin to develop in the latter, the neck and head acquiring a positive potential relative to the sacrum. As the generator continues to approach the neck (fields 7–9), the amplitude of this stationary potential gradually increases although it is noteworthy that, on account of current flow being confined to the larger area, there is no significant potential gradient from the upper neck to the top of the head.

As the generator moves further proximally the potential difference between the head and the sacrum stabilises briefly on emergence of the trailing sources into the trunk (fields 9 and 10), but then continues to increase and reaches a peak only after the major sink arrives at the midline or 'spinal cord' and the initial source the head (field 12). The model fails to predict, therefore, that the potential difference between the head and a remote site such as the sacrum will reach a peak while the volley is still at the level of the shoulder. At the 'clavicle' (recording point 9) and sites along the neck the initial positivity is followed by a negative peak as the central sink passes its point of closest approach to the recording site. Thus a 'travelling wave' is described which increases in latency from lateral to medial and caudal to rostral sites.

Model 5

In model 5 a more devious route was proposed for the generator, to see if this might result in a more accurate prediction of the wave form and distribution of P9. Propagation was initially along a diagonal identical to that taken in model 4, but became horizontal for 2 steps and then once again diagonal before turning vertically on arrival at the midline (Figs. 1 and 6). The effect is for the initial positive potential recorded from the head referred to the sacrum to reach a peak and return briefly towards the baseline while the initial source and major sink are oriented horizontally in the shoulder (field 9). As with model 4 the onset of the positivity corresponds approximately to the point at which the initial source enters the trunk from the constricted space of the arm. The modelled wave forms now resemble more closely those seen in reality (see Cracco and Cracco 1976; Jones 1977; Kritchevsky and Wiederholt 1978; Yamada et al. 1980), with a 'stationary positive potential over the upper neck and head (of smaller amplitude caudally, and with a slightly earlier peak) followed by a second positivity which, at sites along the neck, represents the onset of a travelling negative wave.

The 'sacrum' was chosen as reference for models 4 and 5 because it is situated close to the furthermost extremity of the area of the matrix in which generator currents can circulate most freely, and is therefore one of the sites whose potential is least influenced by the generator while it propagates through the trunk. Considering other reference sites often used for SEP recordings, the potential difference between the contralateral 'shoulder' and the sacrum is fairly small for most positions of the generator. However, the shoulder acquires a significant positive potential as the orientation of the initial source and major sink changes from diagonal to horizontal, and a negative potential as the initial source enters the constricted space of the neck. Very similar potential differences are also recorded between the contralateral 'hand' and the sacrum. This is because

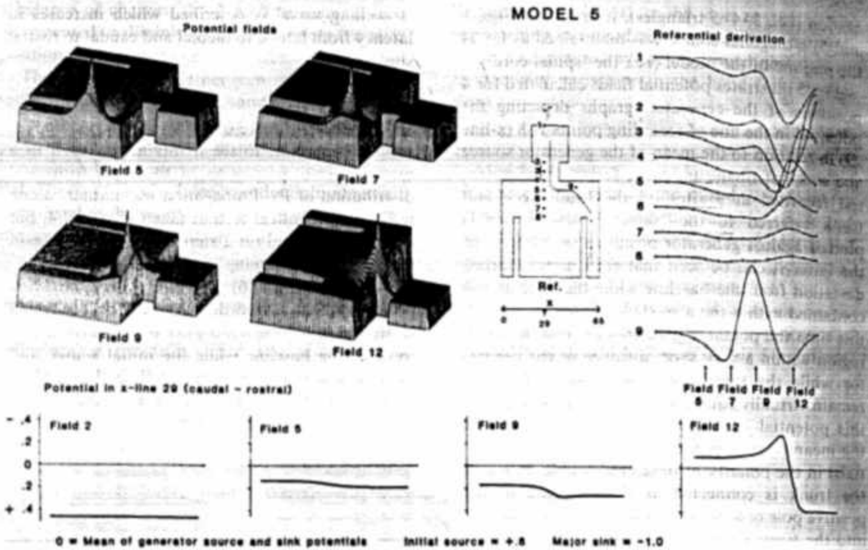

Fig. 6. Model 5: as model 4 but with the generator taking a more devious course between the arm and the neck. The effect is for the potential difference between sites on the head and neck and the sacrum to reach a peak and decline briefly while the initial generator source and major sink are horizontally oriented in the shoulder. A second 'stationary' positive peak with similar distribution is of comparable latency to the 'travelling' negative wave at lower neck sites.

there is no preferred path for current to flow between source and sink via the contralateral arm, and so distal sites acquire a potential which is virtually identical to that present at the junction with the trunk. Nakanishi et al. (1986) have shown experimentally in the cat that an electrode located on the contralateral forepaw is not indifferent to activity in the ipsilateral brachial plexus.

Discussion

In the context of a 2-dimensional, uniform conductivity model of action potential propagation, it has been demonstrated that 'stationary' potentials are likely to occur wherever there are regions in which current density is low because the preferred paths of current flow are distorted by the boundaries of the conductor from the geometry they would assume in an infinite space. Model 1 illustrates such a condition, where a chamber of large area containing the generator is connected to a second, narrow chamber through which only a tiny proportion of the current flowing from the source to the sink will pass. Penetration of current will also be low between two equally spacious chambers joined by a 'bottle-neck,' so it is unnecessary for adjoining chambers to be of unequal size for stationary potentials to develop between them. The peaking and subsequent decline of such potentials depends on other factors, such as the generator moving past its point of closest approach to the recording site, diminishing in magnitude prior to the recording site being reached (models 2 and 3), or changing its direction of propagation (models 4 and 5).

It must be emphasised that the postulates made in the context of models 2–5 have only been confirmed as *possible* explanations of stationary potential phenomena, and that other solutions may exist. It is the virtue of the modelling exercise that any number of variables may be manipulated in order to identify those which succeed best in accounting for the observed effects.

The principles governing the distribution of field potentials in a 2-dimensional conductor also apply in 3-dimensional space, although when comparing the predictions of a 2-D model with physiological data it will naturally be necessary to consider possible boundary and conductivity effects in the third dimension. The models as constructed may be considered to have a z-dimension equal to one matrix point throughout, and 3-D fields would be essentially similar provided the z-dimension were uniform and of small magnitude compared with x and y. This is approximately so for the wrist, hand and fingers, although the gradual tapering would cause the influence of the generator at remote, distal locations to be more strongly felt. Likewise, in the context of the trunk, arms and head, although constrictions in the third dimension might cause stationary potential effects to be more marked, there is no reason to suppose that this would result in qualitative differences from the predictions of a 2-D model.

Stationary potential effects will also be produced where current flow is restricted, not by encroachment of boundaries but by a reduction in conductivity (Stegeman et al. 1985). In the radial nerve SAP recordings of Kimura et al. (1984) a small, early stationary potential was recorded from the index finger referred to the fifth, which was presumed to be due to the volley approaching increased resistance at the wrist. Such a feature was not predicted on the basis of a 2-dimensional, uniform conductivity model and could neither be explained by constriction in the third dimension. It may be suggested, however, that longitudinal division of the 'hand' into compartments connected with each 'finger' and separated from one another by partial barriers of lower conductivity would cause a stationary potential to develop between the middle compartment (directly approached by the generator) and lateral compartments while the generator is at the level of the wrist.

The choice of a 'generator' consisting of 6 elements (3 'sources' and 3 'sinks') of different magnitudes and arranged in the sequence '+ − − − + +' was made with the object of producing a reasonable approximation of the compound action potential as recorded at a distance of a few millimetres. As the generator was moved through the matrix, this resulted in a smooth, triphasic wave form being recorded at sites 2 or more matrix divisions distant. Assumptions made concerning the physiological characteristics of the SAP were, in models 2 and 3, that it would be steadily diminished on propagation through the hand and, in model 3, that the sources and sinks would be attenuated independently of one another (i.e., the magnitude of each would depend on the participating axons present *at that location*, which might be lesser or greater in number and/or size than axons contributing to adjacent generator elements). It follows from the latter assumption that the initial source will disappear first (chronologically speaking), and with the sink at its final location (the most distal axon terminals) all current must be drawn from more proximal segments.

The assumption that the SAP will be progressively attenuated on propagation through the hand seems justifiable in the case of the radial nerve, innervating the dorsal surface of the hand throughout which the density of sensory endings is fairly uniform. The situation is different for the median nerve, however, which contains a high proportion of cutaneous fibres deriving from the fingertips. It may be noted that the bipolar SAPs recorded by Kimura et al. (1983) following *median* nerve stimulation show much less diminution of amplitude along the finger. The assumption that sources and sinks will be attenuated independently of one another cannot be supported with experimental evidence, but seems intuitively reasonable and accounts well for the final stationary negativity of the radial nerve SAP which would otherwise be difficult to explain. Median nerve SAPs, on the other hand, appear to exhibit no such final negativity (Kimura et al. 1983). This is anticipated by model 3, since the negativity was present only at sites distal to the final location of the sink which, for the median nerve, would be the very tips of the fingers.

The only postulate necessary for model 5 accurately to predict the distribution of the P9 SEP component produced by an afferent median nerve volley concerned the precise course taken by the nerve fibres between the axilla and the spinal cord. When the proposed course was uniformly diagonal with virtually no deviation from the most direct route, the stationary potential recorded from head and neck sites referred to the sacrum increased monotonically, reaching a peak only with arrival of the major sink at the midline. When, however, the generator was turned more horizontally such that the head and the sacrum were both, for a short time, closer to the initial source than the major sink, their potential difference declined momentarily before once again increasing. Detailed features of the P9 distribution also successfully predicted by model 5 were that its amplitude would be similar at all sites from the upper neck to the vertex, and its onset would correspond to the point at which the action potential emerges from the arm into the trunk.

Nakanishi et al. (1986) have shown experimentally in the cat that the orientation of brachial plexus fibres is an important factor influencing the polarity and distribution of potentials recorded from the skin surface. However, changes in the wave form and latency of P9 associated with the attitude of the shoulder (Desmedt et al. 1983) appear, at first glance, to be incompatible with the predictions of the model. It was reported that P9 had a later onset and also tended to merge with the following positivity (P11) when the shoulder was held in a high position, thereby presumably causing axons to be oriented more horizontally. In models 4 and 5 it was the more *diagonal* orientation which caused P9 to merge with the following positive peak. An alternative explanation for the findings of Desmedt et al. (1983) is that the more horizontal orientation may have caused the early part of P9 to be cancelled by activity at the reference location. This was the contralateral shoulder, which has been shown to be not indifferent to potentials arising in the shoulder on the ipsilateral side.

Following P9, potentials recorded from the neck and scalp are believed to originate within the vertebral column and skull, and thus are unlikely to be accurately simulated in a simple uniform conductivity model. It was demonstrated, however, that a travelling negativity recorded from the lower 'neck' and possibly equivalent to the N11 component of the SEP (Jones 1977; El-Negamy and Sedgwick 1978; Desmedt and Cheron 1980) was accompanied by a stationary positive peak of similar latency, present (as is the P11 SEP component) from upper neck level to the vertex of the scalp. In order to model potentials succeeding P11 and N11 one would need to take into account the possible contribution of excitatory and inhibitory postsynaptic potentials, plus the orientation of postsynaptic neurones in the dorsal horn and cuneate nucleus.

An attempt was made previously (Jones 1977) to account for P9 in terms of the volume conduction model proposed by Woodbury (1960). Two limitations of the latter in the present context are: (1) it defines the distribution of field potentials only in an unbounded medium; (2) the rule of proportionality between the amplitude of the recorded potential and the solid angle subtended at the recording electrode by a cross-section through the nerve trunk is only useful at relatively short distance, where the separation of the electrode from the generator is not large compared with the cross-sectional diameter of the latter. At greater distances the relationship approximates to an inverse square law, which singularly fails to account for the similar amplitude of P9 at sites located a wide range of distances proximal to the generator.

Yamada et al. (1985) recorded two negative-going stationary potentials of shorter latency than P9 from distal and proximal sites in the arm with reference to the knee. The first of these (N3) was absent above the level of the elbow and the second (N6) greatly reduced above the junction with the trunk. Similar findings have been reported by Frith et al. (1985). These deflections are perhaps best viewed as *positive* potentials present at the reference site. As the volley approaches a region of increased resistance, perhaps due to volumetric constriction at the elbow for N3 and the axilla for N6, proximal sites will acquire a stationary positive potential. This will be conducted to the rest of

the body by a 'lead' effect, will decline as the volley emerges from the proximal side of the constriction, and will be partially or completely cancelled when both electrodes are located on the proximal side.

'Far-field' potentials of latency less than 10 msec following median nerve stimulation were also recorded by Yamada et al. (1985) between electrodes on the 2 lower extremities. The implication of this, that the left and right legs were differentially influenced by the median nerve volley while it was still within the arm, seems to be incompatible with volume conduction theory, and the possibility should be considered that the potentials may have been artifactual phenomena due, for example, to leakage currents in the amplifier between one recording electrode and the earth, which was presumably located on the stimulated forearm.

Yamada et al. (1985) also recorded potentials from a second, unstimulated subject, connected to the stimulated subject by a conducting strap attached to the arm or leg of both. It was noted that the potentials were uniformly distributed over the second subject and that no activity was recorded when both electrodes were located on the latter. This finding is explained by the postulate that the second subject was raised to a uniform potential equal to that present on the first at the point of contact. The declared object of Yamada et al. (1985) was to obtain a relatively 'neutral' reference site, far removed from the generator of SEP activity in the stimulated subject. This is without any theoretical justification, since without completion of the circuit there would be no cause for current to flow through the second subject, hence no potential gradient and no tendency for any site to be more 'neutral' than the point of contact with the first.

Two points of general significance concern the nature of so-called 'far-field' potentials and whether or not there can be said to exist 'active' and 'indifferent' sites on the body. It was pointed out by Nuñez (1981) that 'far-field potential' is strictly speaking a misnomer, but the term possibly has some value in describing potentials which fail to decline in amplitude with the square of the distance from the generator. This said, the potentials occurring in conjunction with a propagating nerve volley are all governed by the same principles, whether they be recorded in the 'near-field' or the 'far-field.'

A possible definition of an 'active' site is one where there is a high density of current flow — for example the clavicular region when the action potential is at the level of the brachial plexus. This, however, does not necessarily imply that a potential difference will be present at any given time between a site in the active zone and one where current density is low. Conversely, a potential difference may be present between 2 'inactive' regions which are separated by a boundary constriction or a region of lower conductivity. Here it may be useful to make a distinction between truly indifferent locations, remote from the generator in a region where generator currents can circulate freely and therefore maintained at a potential which is roughly the average of the generator sources and sinks, and inactive but 'influenced' locations where, through an interposed boundary constriction or zone of lower conductivity, a whole area tends to acquire the potential of the nearest generator source or sink. It is intriguing to note that, according to this criterion, the whole of the body is 'influenced' by the median nerve action potential while it is contained within the arm, while caudal sites become more truly indifferent after the volley emerges into the trunk.

Résumé

Simulation de potentiels d'action somesthésiques (PAS) et de potentiels évoqués somesthésiques (PES) stationnaires par modèles de champs de potentiels à 2 dimensions

Afin d'obtenir des modèles de distribution des potentiels dans la main dus à la propagation des PAS antidromiques, et dans le corps dus à la conduction afférente de volées du nerf médian (PES), des matrices à 2 dimensions de formes appropriées ont été construites, chacune contenant un 'générateur' comprenant jusqu'à 3 points 'source' et 3 points 'puits'. La valeur des potentiels de champs au niveau d'autres sites a été calculée en utilisant une méthode de différences finies.

Il a été montré que le gradient de potentiel est virtuellement nul dans les zones des matrices qui sont séparées de la région contenant le générateur par une constriction dans les limites du conducteur. Les points du côté éloigné de la constriction restaient virtuellement à des valeurs équipotentielles, à un niveau déterminé par le potentiel à la jonction. Ce fait est naturellement influencé par la proximité du générateur, si bien que lorsque le générateur s'approche de la constriction, une différence de potentiel se développe entre les points du côté éloigné, quelque soit la distance de la jonction et d'autres parties éloignées de la matrice. Dans le contexte des PAS et PES humains, de tels facteurs peuvent être d'une importance capitale dans la genèse de potentiels ainsi appelés 'stationnaires' ou 'de champs éloignés'.

Avec des hypothèses supplémentaires concernant la manière avec laquelle le PAS est atténué par la terminaison des axones lors de la propagation dans la main, et le trajet pris par la volée du nerf médian entre le bras et le cou, il est possible de modeler la plupart des phénomènes PAS stationnaires décrits par Kimura et al. (1984), ainsi que la distribution et la latence de la composante P9 du PES à la stimulation du nerf médian.

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SCALP TOPOGRAPHY AND DISTRIBUTION OF CORTICAL SOMATOSENSORY EVOKED POTENTIALS TO MEDIAN NERVE STIMULATION

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Summary Topographies and distributions of cortical SEPs to median nerve stimulation were studied in 8 normal adults and 5 neurological patients. SEPs recorded from C4, P4, Pz, T6-A1A2 derivations to left median nerve stimulation were composed of 2 early negative (N16, N20) and 2 positive components (P12, P23), whereas those recorded from frontal electrodes (Fz, Fp1, Fp2) disclosed 2 early negativities (N16, N24) and 2 early positivities (P12, P20). N20 and P20, and P23 and N24, reversed across the rolandic fissure with no significant difference in their peak latencies. P23 was of slightly shorter latency at C4 than at more posterior electrodes (P4, T6, Pz).

In 3 patients with complete hemiplegia but normal sensation, all the early SEP components were normal in scalp distribution and peak latencies except for a decrease of N24 amplitude. In 2 patients with complete hemiplegia and sensory loss no early cortical SEPs were seen. These findings suggest that N20 and P20 are generated as a single horizontal dipole in the central fissure, whereas P23 and N24 are a reflection of multiple generators in pre- and postrolandic regions.

Keywords: *topography – scalp distribution – median nerve stimulation – cortical SEPs*

The origins of the initial negative component of the cortical somatosensory evoked potentials (SEPs) to median nerve stimulation have been discussed by various investigators. There are two theories. One is a single dipole theory with the generator located in the post-central fissure (Broughton 1969; Goff et al. 1977; Allison et al. 1980; Pratt and Starr 1981; Allison 1982; Lueders et al. 1983; Jones and Power 1984). The other is a multiple generator theory with generators located at pre- and post-central fissure (Kimura and Yamada 1982; Maccabee et al. 1983; Mauguière et al. 1983; Yamada et al. 1984; Desmedt and Bourguet 1985; De Weerd et al. 1985).

In this study we report on the scalp distribution and topography of early cortical SEPs in normal subjects and neurological patients. The purpose was to identify the generators of early cortical SEPs to median nerve stimulation.

Subjects and Methods

(1) Subjects

Eight normal healthy subjects (7 males and 1 female ranging in age from 22 to 60 years with a mean of 38 years), 4 patients with cerebral infarctions (48–60 years), and 1 patient with a brain tumor (56 years) were studied. Three patients with cerebral infarction had a complete flaccid hemiplegia without sensory abnormality (touch, pain, position, vibration and cortical sensation were normal). A low density lesion was seen in the subcortical motor area in the CT scan. In the other 2 patients, both motor and sensory functions were severely abnormal.

(2) Methods

The median nerve at the wrist was stimulated unilaterally through tin disk or needle electrodes. The stimulus was a constant current square wave of 0.1 msec in duration and 3.3/sec in repetition rate which was delivered by an electronic stimulator (Sanei 3F 37) by way of a stimulus isolation unit (Sanei 5361). The stimulus intensity was the

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