daltons (1), giving an estimate of 0.023disintegrations per 5S RNA molecule per 2 months. The emulsion, NTB2, detects tritium disintegrations with nearly a 10 percent efficiency (12); therefore, 15 to 30 grains would accumulate over this region if the hybridization yield was between 3 to 6 percent. Such hybridization efficiency places the transfer RNA genes with their redundancy of 13 times or more (13) within the limits of resolution of the system. Indeed, certain sites along the chromosome arms are frequently lightly labeled with fractions containing transfer RNA (Fig. 2, region 60 BC) and need only to be cataloged to cytologically mark the location of the numerous transfer RNA genes.

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### **Cochlear Summating Potentials: Composition**

Abstract. The potential difference across the cochlear partition and the overall potential level of a given cochlear cross section were measured as functions of stimulus parameters and spatial location. It was confirmed that the potential difference is negative in the vicinity of greatest excitation, and it was discovered that in the same region the overall potential level is positive.

Upon presentation of a brief tonal stimulus a d-c potential shift can be recorded from the cochlea (1). This potential, the summating potential (SP), is reported to be an elusive phenomenon and difficult to quantify (2), even though a large number of experiments have been devoted to it (3, 4). The SP, just as the other inner-ear potential, the cochlear microphonic (CM), is presumed to originate in the hair cells; it is generally stated, or tacitly assumed, to appear in opposite polarity (referred to an indifferent reference electrode) in the two perilymphatic scalae at a given cochlear location. We show here that the latter contention is not generally correct, and that the recorded SP at any point in the cochlea can be thought of as the algebraic sum

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of the potential difference between scala vestibuli and tympani (heretofore designated as differential component or DIF) and the common potential of these scalae (to be identified as average component or AVE). These components vary independently; both are functions of stimulus parameters and cochlear recording site.

Data were obtained from 39 guinea pigs. The experimental animals were anesthetized with urethane; the auditory bulla was approached ventro-laterally and was opened widely; small holes were drilled through the bony cochlear wall at appropriate locations; and fine wire electrodes (Tu or Ag-AgCl) were introduced through these holes into the perilymphatic scalae. Electrodes were placed in pairs, one in the scala vestibuli

and one in the scala tympani of a given turn. Either one or two pairs of electrodes were used. The indifferent electrode was an Ag-AgCl disk placed on the neck muscles. The signals from the two active electrodes were independently amplified (60-db gain, 3 second time-constant) and processed. The stimuli consisted of tone bursts 40 msec long, with 100 msec between bursts, and virtually instantaneous rise and fall times. The sound signal was delivered to the bony meatus of the animals in a closed acoustic system; it was continuously monitored near the eardrum with a calibrated probe-tube microphone. The amplified signals were processed with an averaging computer. The gated sinusoidal signal that provided the speaker voltage was not synchronized with the onset of the burst; consequently the cochlear microphonic phase was changing from burst to burst with the result that this a-c signal was simply averaged out. What remained was the onset and offset action potential, some onset CM in response to ringing in the acoustic system, and the SP. This method of eliminating the CM is much superior to filtering because it avoids wave-form distortion. The number of samples averaged ranged between 16 and 1024. This number depended on the magnitude of the signal; at high stimulus levels a few samples sufficed, but at low levels larger numbers were required. We would either average the scala vestibuli and scala tympani potentials (SV and ST) or utilize electronic means to subtract or add these signals before averaging. These latter two signals are defined as SV - ST = 2 DIF and SV + ST =2 AVE. It is easy to demonstrate that either arithmetic or electronic generation of DIF and AVE components from SV and ST potentials yield virtually identical results. It should be noted that when obtained by electronic addition or subtraction, the DIF and AVE components are similar to the results of classic differential electrode recording when either action potential or CM is rejected (5).

The only difference between our method and the usual differential electrode recording is that we do not utilize an electronic balancing technique; instead, simple addition or subtraction is performed. Appropriate symmetry between the two electrodes is achieved by their careful placement and by the rejection of inadequate preparations (6). The DIF component should be in-



Fig. 1. Averaged scala vestibuli (SV) and scala tympani (ST) summating potential responses to tone bursts 40 msec long with 100 msec between bursts. Stimulus frequency and sound pressure level are indicated as the parameters. Vertical bars provide voltage calibration. Panels a, b, and c show recordings from one electrode pair in the first turn, whereas panel d depicts responses from the third cochlear turn. Positive polarity is up.

terpreted as the potential difference across the cochlear partition, and thus as an indication of the combined output of the sources that are located between the two electrodes. The AVE component has been generally considered to reflect remote activity, and indeed until now it was used merely to reject local CM and to emphasize whole-nerve action potential which is, of course, a "remote" potential. We wish to extend this interpretation. It appears to us that the AVE component might reflect both remote potential and a local response which, however, has the same polarity in the two opposite perilymphatic scalae. We will show that for certain stimulus conditions this latter constituent of the AVE response predominates, and in these cases this response should be interpreted as the potential level of a cochlear location (SV and ST) in reference to indifferent tissue (7).

In Fig. 1 some sample SP waveforms are shown. These are SV and ST recordings to demonstrate possible polarity relationships between the two potentials in the two scalae. The first two traces are from the basal turn at a low frequency and a relatively high sound pressure level (SPL). The polarity is opposite in the two scalae; SV is positive, ST is negative. The second two traces are from the same location

at the same frequency but at a low signal level. Here both traces are negative and virtually identical. The third pair of traces are again from the basal turn, but here the frequency is high and so is the intensity. The polarity is opposite, but here SV is negative and ST is positive; the magnitudes of the two responses are unequal. The final two traces were recorded from the third cochlear turn at a midfrequency at high stimulus level. Both traces are positive but not equal in magnitude. These traces simply serve to demonstrate some of the varieties of relationships that can be seen for SP polarity. Note that the magnitude of the SP changes in some cases during the presence of the stimulus. The change is asymptotic, and the response generally levels off around 40 msec. All readings of SP magnitudes are obtained by taking the difference between the baseline and the average magnitude of the SP during the final 5 msec of the response.

There are many possible ways to depict the quantitative behavior of the SP as a function of stimulus parameters. It is not our purpose to provide a complete parametric picture of the dependence of the SP on stimulus intensity and frequency and upon recording location. Such will be given in a more detailed communication. Here we

merely chose to present one example which, however, is sufficient to demonstrate our main points of contention. In Fig. 2 the magnitudes of the DIF and AVE SP components are given as the function of stimulus frequency with intensity as the parameter. These plots are obtained from one guinea pig that had electrodes placed in scalae vestibuli and tympani of the second cochlear turn. The following trends are evident. At low frequencies the DIF component is positive at all intensities, and the magnitude is directly related to stimulus strength. Around 4000 hz the DIF component is negative at all levels and again the magnitude increases with increasing sound pressure. At high frequencies the DIF component vanishes. Note that the width of the negative band around 4000 hz increases with increasing signal level, but significantly the spread is toward the low frequencies. At first glance the AVE plots appear to be the mirror image of the DIF plots; this however is not the case. Around 4000 hz there is a positive band in the AVE plot; the width of this band also widens at higher stimulus levels, and the spread is again primarily toward the low frequencies. The zero-crossing points are generally not the same in the DIF and AVE plots. For frequencies below and above the positive band the AVE response is negative.

If the recording electrodes are placed at another cochlear site, then a similar but displaced pattern of DIF and AVE responses is obtained. To explain, with an electrode pair in the first turn the maximum DIF negativity and AVE positivity occurs around 10,000 hz. When the electrodes are in the third cochlear turn, these characteristic peaks are seen around 1000 hz. In all cases the potentials at lesser or higher frequencies than that of the characteristic region show similar patterns to what is demonstrated here for the electrode site in the second turn.

The general trends can be studied with optimum clarity in spatial plots such as the one given in Fig. 3. Here the results from three animals, having electrodes in different cochlear turns, are combined to provide a spatial representation of the two potential components. In other words, SP magnitude is plotted as a function of distance from the stapes. Stimulus frequency is the parameter, and the intensity is constant at 60 db SPL. Each curve is based on three data points. The general trends seem to be well represented by these plots even though accuracy of spatial detail might be lacking.

Three zones are seen in both plots; they can be best studied by following, for example, the 4000-hz graphs. In the DIF plot there is a negative peak between 11 and 12 mm; a positive peak occurs at approximately the same location in the AVE plot. Below this characteristic region the DIF response goes positive and then diminishes toward the base of the cochlea. In this same region the AVE response is negative. The latter is also negative on the apical side of the positive maximum, but in contrast the DIF response assumes zero value toward the apex. One notes similar trends and polarity zones for the other frequencies.

The two types of DIF responses (negative and positive) appear to correspond to the previously identified (3) so-called negative and positive summating potentials, SP- and SP+. If we compare the spatial patterns of Fig. 3 with available frequency maps of the guinea pig cochlea (5), then it is noted that both the prominent negative DIF peak and the positive AVE peak occur more apically than the maximum mechanical vibration of the cochlear partition. These peaks are better correlated with the distal end of the traveling wave envelope and conceivably with the hypothesized shear waves in the cochlea (8). The positive DIF response appears on the proximal slope of the traveling wave envelope, while beyond the spatial extent of the wave, the DIF response vanishes. It is highly possible that both negative and positive DIF responses originate in cochlear distortion processes as has been suggested by several authorities for SPand SP+ (9).

The properties of the DIF component strongly resemble those of the SP when recorded from the scala media of the cochlea (4); both are apparently representative of the local potential difference across the organ of Corti.

We suggest that the two likely sources that might be responsible for the generation of the negative DIF component are either the nonlinear distortion of the CM-producing process, or one-way bending of the cilia of the hair cells on the distal envelope of the traveling wave, or both. The positive DIF component is likely to arise in one-way bending of the hairs in a different direction on the proximal slope of the traveling wave. Von Békésy (8) had demonstrated that the principal motion is different on these two slopes,



Fig. 2. Magnitudes of DIF and AVE summating potential components as the functions of stimulus frequency with sound pressure level as the parameter. Electrodes were located in the second turn. By definition the DIF and AVE components are obtained from the potentials recorded from scalae vestibuli and tympani as 2 DIF = SV - ST; 2 AVE = SV + ST.

thus opposite unidirectional bending accompanying the to and fro movements is a distinct possibility.

The AVE component of the SP response had not been previously identified. This component is clearly the sum of two constituents, the negative and positive AVE response. The positive component dominates in the vicinity of maximum excitation, whereas the negative component is evident everywhere else in the cochlea. It is our contention that the negative component is a conducted remote response, reflecting distant activity (10). The identification of the narrow positive potential zone



Fig. 3. Composite spatial plot (based on data obtained from three animals having electrodes in turns one, two, and three, respectively) of DIF and AVE summating potential component magnitude. Abscissa is the distance from the stapes in millimeters; the parameter is stimulus frequency in kilohertz. All data are obtained at 60 db SPL. By definition the DIF and AVE components are obtained from the potentials recorded from scalae vestibuli and tympani as 2 DIF = SV - ST; 2 AVE = SV + ST.

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in the region of the maximum activity is probably the most important contribution of this study. This positivity is a stimulus-related cochlear response that is confined to a limited spatial extent of the inner ear, and which is an independent response from the familiar CM and DIF-SP components which appear as voltages across the organ of Corti. The positive AVE-SP component is the polarization of an entire segment of the cochlea. Since the only electrical connection between the membranous cochlea and the rest of the body is through the internal auditory meatus, via the eighth nerve and blood vessels (11), it can be conjectured that the positive AVE component can serve as a hyperpolarizing electrical agent acting on the dendrites that originate in the region of maximum positivity. The source of this positive AVE response is not yet identified with certainty. This response is possibly due to a voltage drop caused by longitudinal current flow within the cochlea between regions of strong and weak excitation.

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- Under ideal recording conditions the DIF and AVE responses can be registered inde-pendently from one another. If the electrodes are well placed and if the electrical paths from them to the various sources of potential are symmetrical, then any change that might occur in the potential difference across the coch-lear partition is manifested by the DIF re-sponse only. Conversely, under such condi-tions any overall shift in voltage level by a cochlear cross section would modify the AVE component alone. In practice the electrodes are never perfectly balanced, and consequently the recorded components are not completely independent. The errors resulting from a given independent, The errors resulting from a given electrode imbalance can be estimated, and thus one can guard against unwarranted use of the data. The electrode imbalance can be obtained, at least as a first approximation,

from the comparison of the cochlear microhonic outputs of SV and ST electrodes at high frequencies (6). It is important to point out, however, that even when perfect a-c balance (that is, that for CM) exists between two electrodes, they are not, in general, "balanced" for SP. For example, in Fig. 1c the responses are shown from scalae tympani vestibuli from the first turn at and a high frequency. In this situation the CM's from the two electrodes are virtually identical in magnitude but opposite in phase; there is balance. Note, however, that the SP magni-tudes are not the same; the SP from the ST is considerably greater than that from the SV. This indicates the presence of a "common-mode" d-c potential, the very item of inter-est in this communication that is labeled as the AVE component.

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to be contradictory to the findings of I. Tasaki and C. Fernández [J. Neurophysiol. 15, 497 (1952)] that the electrical spread in cochlea from turn to turn is negligible. Actually there is no contradiction. Tasaki and Fernández obtained their attenuation figure of 6 db/mm from differential electrode recordings; in other words, this attenuation constant would apply for our DIF component. When not using differential electrodes, one observe much less attenuation of electrical potentials, probably of the order of 1 to 2 db/mm (6). This latter figure is applicable for the AVE component. Thus, it is quite reasonable to as-sume that the negative AVE component is a response that results from current spread from active remote regions. That this is so can be highlighted by the prominence of this re-sponse in regions and at frequencies where no local traveling wave activity exists, that is, in the higher cochlear turns at high frequencies.

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# **Intelligence Quotient Pattern over Age: Comparisons** among Siblings and Parent-Child Pairs

Abstract. Comparisons between sibling and parent-child pairs with unrelated control pairs matched for year of birth and parental education were made to determine the relative heritability of the general level of intelligence quotient as opposed to that of the sequential pattern of IQ change over age (3 to 12 years). There was greater similarity among related siblings relative to matched controls for general level than for pattern of IQ over age. Relationships between the IQ's of children and that of their parents as children were not consistent across age.

A recurring question concerns the relative heritability of general IQ. One position is that IQ can be altered by certain environmental factors, such as programs of enrichment (1). The opposite position suggests that the genetic component of IQ is so significant that it is unrealistic to hope that enrichment programs will be able to change IQ very much, particularly for relatively normal children (2).

The issue is exemplified by two sets of apparently contradictory findings: (i) the IQ's of severely deprived youngsters can be raised by certain programs of stimulation and compensatory education (1, 3); but (ii) the correlation between the IQ scores of pairs of individuals increases dramatically and consistently with the degree of their genetic, as opposed to their environmental, relationship (2, 4).

Part of this controversy may be resolved by distinguishing between the general level of IQ as reflected in an IQ score assessed at a single age and the sequential pattern of IQ change that might occur over age. It is likely that many normal children display substantial changes in IQ during childhood and that these shifts over age constitute meaningful and reliable trends (5).

Since much of the current emphasis on compensatory education programs is concerned with changing IQ, it would be valuable to determine if such patterns possess as much heritability as the general level of IO.

Most of the evidence for the genetic basis of intelligence has been determined with single-age (or at least separate-age) correlations between genetically related individuals. These data demonstrate the heritability of the general level of IQ, but they do not demonstrate the heritability of IQ changes over age. Even if these methods suggest that the genetic contribution to the general level of IQ is substantial, meaningful changes in IQ over age are still possible (as produced by enrichment programs, for example).

In this paper I report an examination of the relative heritability of the general level of IQ as opposed to the pattern of IQ change over age. This issue was addressed by a comparison of the similarity of patterns of IQ change over age among siblings and among parent-child combinations with the similarity of patterns for unrelated subjects matched for/year of birth and parental educational level. These comparisons were made first when both the general