rages as to the precise power of body weight that provides the best fit with data, but physical reasoning demonstrates that the factors limiting power output—that is, tensile strength of muscles, tendons, and bones, the rate of supply of oxygen admitted by the lungs and carried by the blood, and the rate of removal of heat from the working muscles—all are proportional to body surface area (thus, $W^{2/3}$) for geometrically similar animals. Then the power available to the heavyweight oarsmen is $K^{2/3}$ that of the lightweights, where $K$ is the weight ratio, 86/73. Therefore,

$$\frac{v_{\text{heavyweight}}}{v_{\text{lightweight}}} \propto K^{2/9} \simeq (1.2)^{2/9} = 1.05$$

The heavyweights are thus predicted to be 5 percent faster than the lightweights, as is observed. Notice that if the assumption is taken instead that the length of both light and heavy boats are equal but that the below-water cross section $A$ is proportional to displacement and thus to total weight, the result is

$$\frac{v_{\text{heavyweight}}}{v_{\text{lightweight}}} K^{1/18} \simeq 1.01$$

In this case, the heavyweights beat the lightweights by only 1 percent, which is smaller than the observed margin.

What would happen if the lightweight shell were geometrically similar to the heavyweight but shorter by the ratio $K^{-1/3}$? In this case, the wetted area of the lightweight shell would be $K^{-2/3}$ the wetted area of the heavyweight shell, but since the power available would also be $K^{-2/3}$ that of the heavyweights, the two shells would have the same speed. The remarkable conclusion becomes that, if the lightweight shell were shortened by 1.1 m in length and made 2.4 cm narrower in beam from its present dimensions, the lightweight crew could keep up with the heavyweights. The practical validity of this results is certain to be checked, sooner or later, by a sufficiently enlightened lightweight crew.

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# Human Auditory Attention: A Central or Peripheral Process?

Abstract. *The click-evoked electrical responses of the human cochlear nerve were recorded from the external ear canal concurrently with the cortical evoked potentials from the scalp. Paying attention to the clicks during a discrimination task resulted in a highly significant enhancement of the cortical response but no change in the cochlear nerve response. Hence no evidence was obtained for the operation of a peripheral gating mechanism during attention in man.*

Attention may be considered to be a process in the nervous system that enables an observer to extract more information from a selected stimulus configuration. There is controversy in both the neurophysiological and the psychological literature as to what the neural mechanisms of attention may be, and in particular whether attention involves a peripheral "filtering" or "gating" of sensory inputs (*1*).

In human observers opportunity exists to study both the behavioral and electrophysiological aspects of various well-defined types of attention. A sensitive physiological index of human attention to an acoustic signal is the amplitude of the electrical activity it evokes in the cerebral cortex. Paying attention to a sound typically enlarges the cortical averaged evoked potential (AEP) recorded from the scalp (*2*). A second electrophysiological measure of attentiveness in man is the contingent negative variation (CNV); this negative slow-potential shift precedes and accompanies perceptual judgments and reportedly varies with the degree of attention being devoted to the task (*3*).

Prompted by the recent discovery that the human cochlear nerve response can be recorded from the external auditory meatus (*4*), we decided to investigate the physiological mechanisms of human auditory attention by measuring the changes induced in the cortical AEP and the cochlear nerve response by different attentive conditions. We have determined that attending to clicks resulted in an increased AEP at the vertex without any demonstrable change in the concurrently recorded action potentials of the cochlear nerve. We thus could not substantiate the hypothesis that auditory attention involves a gating of neural transmission at the most peripheral levels of the auditory pathway.

The cochlear nerve response was recorded from a small (3-mm) tungsten needle electrode inserted beneath the skin of the superior wall of the external auditory meatus, 5 to 8 mm from the tympanic membrane, under local anesthesia. A very flexible wire leading from the electrode was glued to the skin surface of the ear canal and pinna. The auditory AEP was recorded from the vertex (*5*). The reference electrode for both these recordings was placed on the mastoid process ipsilateral to the implanted ear. Eye movements were monitored with electrodes placed on the inferior and superior orbital ridges to ensure that the AEP's were uncontaminated by electroocular artifacts. Click-evoked potentials were amplified with a polygraph and computer averaged on-line (*6*). Clicks were generated by passing 2-$\mu$sec square waves through earphones worn by the subject. The experimenters served as subjects (*7*).

In the first experiment, clicks of 55 db sensation level (*8*) were presented to the ear containing the electrode at a rate of one every 1.3 seconds. Between 10 and 20 single clicks of 51 db were randomly distributed throughout each separate series of 300 clicks. Attention was manipulated by having the subjects either listen to the clicks in order to detect the faint ones, or read a book and entirely ignore the clicks (*9*). At the conclusion of each attention series the number of faint clicks detected was reported (*10*). Attention and control conditions were alternated for successive series of clicks until the subject became fatigued. Click-evoked responses from the auditory meatus and vertex were averaged concurrently over the final 256 of the louder clicks in each series; responses evoked by the fainter clicks were not averaged.

The typical morphology of the cochlear nerve response is shown in the left columns of Fig. 1A. The most prominent features are a pair of sharp negative deflections *N1* and *N2* following

Table 1. Magnitudes of the cochlear nerve response and the cortical evoked response to clicks: comparison between the conditions of reading a book and attending to the clicks. Values are in microvolts.

| Subject (repetitions) | Component | Cochlear nerve reseponse |  | Component | Cortical evoked response |  |
|---|---|---|---|---|---|---|
|  |  | Reading | Attending |  | Reading | Attending |
| T.P. (8) | *N1* | 1.35 | 1.33 | N1-P2 | 4.95* | 6.45* |
|  | *N2* | 0.83 | 0.85 | P2-N2 | 3.86† | 5.28† |
| S.H. (8) | *N1* | .60 | .62 | N1-P2 | 3.30‡ | 4.05‡ |
|  | *N2* | .35 | .25 | P2-N2 | 4.28* | 5.36* |
| R.G. (6) | *N1* | .94 | .98 | N1-P2 | 5.23‡ | 6.30‡ |
|  | *N2* |  |  | P2-N2 | 2.68‡ | 3.75‡ |
| D.W. (5) | *N1* | .39 | .38 | N1-P2 | 7.09‡ | 8.14‡ |
|  | *N2* | .26 | .21 | P2-N2 | 7.71 | 8.33 |
| Means | *N1* | .86 | .87 | N1-P2 | 4.92* | 6.02* |
|  | *N2* | .51 | .47 | P2-N2 | 4.44* | 5.53* |

* The differences between these pairs of values in the same row are significant at the level of $P < .0005$. † $P < .005$. ‡ $P < .05$.

the click by 1.5 and 2.5 msec, respectively. The waves preceding *N1* are the cochlear microphonic potentials. The major components of the vertex AEP (Fig. 1A, right columns) consisted of negative deflections at 100 msec (N1) and 250 msec (N2) surrounding a positive peak at 150 msec (P2). The effects of attention upon these evoked responses are shown in Fig. 1, A and B, and quantitatively analyzed in Table 1 (*11*). The mean peak-to-peak measures of the vertex AEP for all subjects increased by 23 percent (N1-P2) and 25 percent (P2-N2) during attention to the clicks ($P < .0005$) (*12*), whereas there were no significant changes in the cochlear nerve response. Statistical confidence intervals were established to show that the probability was less than .05 that the *N1* amplitude would have shifted by more than ± 6.0 percent between conditions (*13*). Similar experiments using clicks of other intensities and clicks presented in various background noises gave similar results: a marked stability of the cochlear nerve response to varying attention.

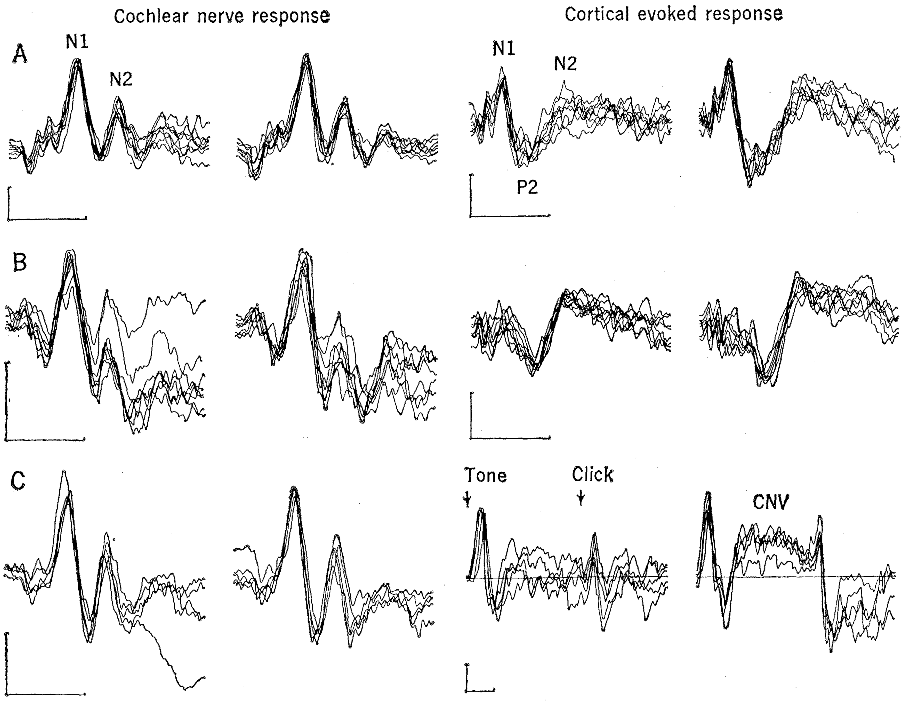

Fig. 1. (A) Comparison of changes in the cochlear nerve responses and cortical evoked responses to clicks between reading a book and attending to the clicks; subject T.P. Each of the eight superimposed responses is the average of 256 click presentations. (B) Similar responses for subject S.H. (C) The responses to clicks preceded by a warning stimulus (20-msec tone). Cochlear responses are to the clicks alone and cortical responses to the tone-click combinations. Each response (five are superimposed) is the average of 128 tone-click presentations; subject T.P. In all parts of the figure, the vertical calibrations represent 0.5 $\mu$v for the cochlear response and 2.5 $\mu$v for the cortical evoked response; the horizontal calibrations represent 2 msec and 200 msec, respectively. Negativity of the active electrode is upward in all records.

This experiment was modified to record the CNV during the same click intensity discrimination: a warning signal (a 20-msec, 1-khz tone pip at 50-db sensation level) was presented 0.80 second before each click, and the interval between successive tone-click pairs was randomized (between 4 and 8 seconds). The subject again alternated between attending to clicks (and reporting the number of fainter ones) and reading a book. Responses were averaged over 128 tone-click pairs. The results are shown in Fig. 1C. With attention there was a significant increase in both the CNV ($P < .025$) and the vertex AEP to the click ($P < .005$) but no change in the click-evoked cochlear response (*14*).

A third experiment tested whether selective attention to one ear under binaural listening conditions alters the click-evoked responses. On each channel of a stereo tape we recorded several series of 55-db clicks. Every 1.2 to 1.6 seconds a single or double (200-msec separation) click was recorded on one channel according to a random sequence with single and double clicks equally probable; a separate sequence of clicks was simultaneously recorded on the second channel. The subject was required to attend to the clicks in one ear by writing down the order of single and double clicks in that ear. Cortical and cochlear responses to the clicks presented to the electrode ear were averaged over each series of 512 clicks, and attention was alternated between the two ears in successive series. The vertex AEP was significantly larger ($P < .01$) with attention, but the cochlear nerve response remained constant in amplitude when attention was shifted from one ear to the other (*15*).

These three experiments therefore show that neural transmission in the auditory nerve is unchanged by attention, whereas the nonspecific AEP and the CNV proved to be highly sensitive to our experimental manipulations. It is well known from animal research that auditory evoked potentials are enhanced at many brain sites when the signals are made biologically significant. Considerable controversy exists, however, over the extent to which the gating of impulses in the peripheral sensory pathways contributes to this enhancement. Much of the research which purported to show lability of the response of the cochlear nerve and nucleus (*16*) has been effectively criticized for incomplete control of acoustic field variations: with such controls transmission at all auditory relay nuclei below the thalamic level was found to be stable with changing levels of arousal and attentiveness (*17*). Our findings are consistent with these reports and suggest that attention is mediated not by selective gating of inputs at the periphery but by specialized processing of relevant stimuli at higher levels of the sensory system.

Although the efferent olivocochlear pathway when electrically stimulated suppresses click-evoked transmission in the cochlear nerve (*18*), its role in sensory behavior is unknown. Recent evidence suggests that it acts as part of a feedback system involved in frequency discrimination or the detection of signals in noise (*19*). Our present experiments offer no evidence that the olivocochlear bundle is active in several types of human attention.

The negative results of this first direct inquiry into whether attention can influence peripheral auditory transmission in man must be interpreted with certain qualifications. Since only two of the varieties of auditory attention—intensity discrimination and selective binaural listening—were investigated, and these only with click stimuli, it is still possible that discriminations of more complex and significant sounds such as speech might be susceptible to peripheral gating. Most importantly, the response that we recorded at the ear represents the summed activity of many auditory nerve fibers (*20*) and so we cannot rule out the possibility that attention-induced alterations in the responses of some of them might pass undetected. Nevertheless, there seems to be no gross modulation or suppression of the cochlear nerve response with inattention.

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### References and Notes

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5. All electrodes on the scalp and face were nonpolarizable Ag-AgCl pellets (Beckman Instruments).
6. The Grass 7P5 preamplifiers were set with low-frequency half-amplitudes of 10 hz for the cochlear responses and 0.3 hz for the scalp responses. For the contingent negative variation experiment the latter setting was changed to 0.15 hz. High-frequency half-amplitudes were 3 khz. The cochlear nerve response was averaged with a Fabritek 1052 signal averager, and the vertex AEP and ocular potentials were averaged with a Mnemetron CAT 400A computer.
7. Because of the mild discomfort involved in the insertion of the electrode we did not think it proper to use volunteers as subjects. The use of sophisticated subjects opens the question of whether they can deliberately control their responses to conform with the known experimental predictions. We believe that such effects are achieved by regulating one's level of attentiveness. Whatever the mechanism, there seems to be no voluntary control of the cochlear nerve response.
8. Measurements on all four subjects showed that the intensity of 55-db sensation level yielded a cochlear nerve response that lay on a steep portion of the intensity-amplitude function [see (*4*)], so that any attention-related changes in effective click intensity would be reflected in changed cochlear potentials.
9. Subjects made no movements during the attend condition and their gaze was fixated. In the control condition, however, saccadic eye movements occurred during reading. Since certain eye movements have been shown to reduce the cortical response to clicks in cats [J. S. Ebersole and R. Galambos, *Electroencephalogr. Clin. Neurophysiol.* **26**, 273 (1969)] the possibility exists that the reduced AEP in the control condition is related to eye movement. In our third experiment, however, eye movements were similar in both the attend and control conditions.
10. The intensity discrimination task was reasonably difficult. The percentage of the fainter signals correctly detected by each subject was: T.P., 96 percent; S.H., 82 percent; R.G., 92 percent; D.W., 76 percent.
11. The amplitudes of *N1* and *N2* were measured relative to the baseline at the onset of the wave. The amplitudes of the vertex AEP were measured peak to peak. All statistical significance levels were obtained with one-tailed *t*-tests. Because of the great intersubject variability, the statistical tests for the overall means were made after converting each measurement into a percentage of the mean reading amplitude for that subject.
12. In one of the subjects, an early positive-negative wave with a latency of 25 to 40 msec was consistently recognizable in the vertex AEP; attention did not significantly change this wave. If this wave represents activity of the primary auditory cortex, its constancy implies that attention is effected after signal analysis is completed through the entire afferent pathway.
13. Confidence intervals are based on the assumption that the difference between the means of attend and control conditions followed a *t* distribution.
14. The mean responses (in microvolts) for the single subject in this experiment were: cochlear nerve response: *N1*, 1.53 (reading) and 1.58 (attending to the clicks); *N2*, 1.50 and 1.47; maximum CNV amplitude, 2.36 and 4.50; vertex AEP to clicks, 7.00 and 11.33.
15. The mean response amplitudes (in microvolts) for the single subject in experiment 3 were: cochlear nerve response: *N1*, 1.60 (attending to the electrode ear) and 1.64 (attending to the opposite ear); *N2*, 1.15 and 1.11; cortical evoked response, N1-P2, 4.53 and 2.95. These results differ from those of D. B. D. Smith, E. Donchin, L. Cohen and A. Starr [*Electroencephalogr. Clin. Neurophysiol.* **28**, 146 (1970)] who found no significant changes in the vertex AEP with selective binaural attention. We believe that our discrimination was more difficult than theirs and required more constant attention.
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## Recovery of Function after Serial Ablation of Prefrontal Cortex in the Rhesus Monkey

Abstract. *Rhesus monkeys with one-stage or serial ablation of sulcus principalis (prefrontal association cortex) were compared on three spatial tasks. On all tests, the serial monkeys made fewer errors than did the monkeys with one-stage lesions. These results indicate that partial recovery of function can occur after extensive destruction of association cortex in the mature primate brain if the damage is distributed over a number of operations.*

While recovery of function after infant brain damage has often been noted (*1, 2*), recent investigations suggest that such recovery is also possible in mature organisms following sequential surgery. Thus, rats (*3*) and cats (*4*) with multiple-stage bilateral removals of cortical or subcortical structures are less impaired than are animals with single-stage ablations of identical tissue. These ameliorating effects of serial lesions have been demonstrated also in monkeys after ablation of primary sensory cortex (*5*), but recovery of function following damage to the association cortices involved in cognition and learning has not