Evoked potentials in cat auditory nerve: Suppression by prior tonal stimulation

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Action potentials (AP) recorded from the eighth nerve of a cat to a tone pip, S_1 , were suppressed when preceded by a monotic or dichotic conditioning tone, Tc. The suppression increased when (1) the interval between Tc and S_1 was decreased, (2) either the intensity or the duration of Tc was increased, or (3) the difference in frequency between the two stimuli was reduced. Thus the nerve action potential amplitude correlates strongly, but inversely, with the loudness enhancement effects seen in man (Galambos, Bauer, Picton, Squires & Squires, *Journal of the Acoustical Society of America*, 1972, 52). Since Coats and Dickey (*Journal of the Acoustical Society of America*, 1972, 52) found that the human AP can be diminished by a preceding noise without reducing the loudness of a click, the available results suggest that a central mechanism functions to compensate for the reduction in AP amplitude. The dichotic effects could be accounted for by cross-hearing, thereby providing no evidence for a role of the olivocochlear bundle in the effects observed.

When human subjects hear two brief auditory stimuli that follow one another in time, the first can enhance the loudness of the second (Buytendijk & Meesters, 1942; Elmasian & Galambos, 1973; Galambos, Bauer, Picton, Squires, & Squires, 1972a, b; Gol'dburt, 1963; Irwin & Zwislocki, 1971; Sokolich & Zwislocki, 1972). Throughout this report, the first signal (a "conditioning tone") is designated Tc, the second signal (the "enhanced" one) is S_1 , and the interval between them is ΔT .

Galambos et al. (1972a, b) investigated several parameters in a dichotic loudness enhancement task by matching the loudness of S_1 with a third stimulus, S_2 , which followed S_1 by 1,500 msec. S_1 (8 KHz, 2 msec) was enhanced by as much as 15 dB in these experiments. They found that loudness enhancement (1) disappeared as the duration of ΔT was increased, (2) increased as the intensity or duration of Tc was increased, and (3) was greatest when the frequency of Tc was the same or nearly the same as the frequency of S_1 . In the monotic loudness enhancement task, even greater enhancements of 20 dB or more have been obtained by Elmasian and Galambos (1973).

The following experiments examine the effect of Tc on the eighth nerve response to S_1 in a cat. They were done with stimulus parameters similar to the ones used in the loudness enhancement study of Galambos et al. (1972a, b), with the objective of determining the role of the auditory nerve in loudness enhancement. The N_1 - P_1 component of the eighth nerve action potential (AP) was measured to S_1 in three conditions:

S_1 alone, S_1 with a monotic Tc, and S_1 with a dichotic Tc, while the different parameters of the stimulus configuration were varied. If loudness enhancement is mediated at the eighth nerve level, the variations in the amplitude of the AP to S_1 produced by Tc should correlate positively with the enhancements of S_1 loudness produced by Tc in man. As we shall see, they do not.

METHODS AND PROCEDURES

One healthy young female cat was used in this experiment. She was studied in about 40 2- to 3-h sessions spread over a 3-month period. A bipolar electrode chronically implanted in her left-eighth nerve yielded all the data reported here. The electrode was a Teflon-coated stainless steel wire with a tip diameter of approximately 200 μ ; it had been implanted 7 months earlier using a stereotaxic instrument and standard operating procedures. The bipolar pair and a grounding electrode (skull screw) were terminated in a subminiature connector attached to the skull. At a second operation, the middle ear muscles on the implanted side were sectioned by electrocautery without damage to the ossicles. Data recording began 2 months later.

Recordings were made with the cat unanesthetized and lightly restrained in a box inside a double-walled acoustic chamber. The bipolar recordings were first differentially amplified 100 times by a Grass P-15 with a bandpass of 30 to 3,000 Hz and were further amplified 100 times by a Tektronix 122 between 8 Hz and 10 KHz, for a total amplification factor of 10,000. The output of the Tektronix was sampled by the analog-to-digital converter on a PDP-9 computer to a 12-bit accuracy at a sample rate of 20 KHz. The output of a MB Type 302 accelerometer attached to the pedestal on the cat's head was amplified 100 times by a Grass P-15 between .1 Hz and 1 KHz and then sampled for 25 msec at a 10-KHz sampling rate by the A-to-D converter prior to the presentation of stimuli on each trial. If the maximum peak-to-peak voltage from the accelerometer was greater than 100 mV, which indicated that the cat was moving or making noises, the trial was not recorded.

Trials were presented in blocks of 40 with an intertrial time of 2 sec. The trials within a block alternated between trials with S_1 alone and trials with TC preceding S_1 by the interval ΔT . On the

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monotic trials, S_1 and Tc were presented to the left ear, and on dichotic trials, S_1 was presented to the left and Tc to the right ear. Tc was generated by a Wavetek 116 voltage control generator (VCG) and S_1 by a Wavetek 150 VCG. Both Tc and S_1 were bandpass filtered by a Krohn-Hite 3550R set at 100 Hz above and below the stimulus frequency. The stimuli were delivered through audiovox 9C earphones positioned inside the pinna at the entrance to the external auditory meatus. Four different parameters were varied; ΔT interval duration, Tc intensity, Tc duration, and Tc frequency (at two different S_1 frequencies). Intensity functions were obtained for S_1 presented to both the ipsilateral (left) and contralateral (right) ear in order to obtain a measure of the cross-hearing. The order of the parametric values presented and whether the condition was monotic or dichotic on a given block of trials was determined randomly. The usual values of all parameters except the one being investigated were as follows: S_1 , 80 dB SPL, 1 msec, and 8 KHz; Tc, 100 dB SPL, 250 msec, and 8 KHz; and ΔT was 10 msec. All measures of intensity are for a continuous tone. ΔT varied in the interval duration experiment between 10 and 500 msec. Tc in the intensity study ranged from 50 to 100 dB SPL in 10-dB steps and in the duration experiment from 1 to 500 msec. In the Tc frequency study, when S_1 was 8 KHz Tc varied between 5 and 11 KHz in 500-Hz steps. In the second half of the experiment, S_1 frequency was set at 5 KHz and Tc frequency varied between 2 and 8 KHz in 500-Hz steps with no change in the other parameters. In the S_1 intensity series, the S_1 level ranged from 50 to 100 dB SPL in 10-dB steps. All stimulus presentations were controlled by the PDP-9 computer.

The eighth nerve action potentials (AP) recorded to S_1 by the computer's analog-to-digital converter were segregated depending upon whether or not Tc had been presented and then summed with like trials. On each trial, the computer measured and recorded the latency and peak-to-peak amplitude of each wave of the waveform. At the end of the block of trials, the computer calculated the means and standard deviations for the latencies and amplitudes for both the trials with and without Tc, and the difference between the trials with and without Tc for all the measurements. The difference in N_1 - P_1 amplitude between Tc and no-Tc trials is the statistic reported here to demonstrate the effect of Tc on the eighth nerve response to S_1 .

RESULTS

Figure 1 shows sample waveforms of the AP as a function of S_1 intensity when presented both ipsilaterally and contralaterally to the ear with the electrode. Note the similar morphology of the responses to ipsilateral and contralateral stimuli, and that the response to an ipsilateral stimulus is greater than that to a contralateral one. The fact that it takes an increase of 21 ± 3 dB in the intensity of the contralateral S_1 to produce an N_1 - P_1 amplitude equal to that of an ipsilateral S_1 demonstrates the amount of cross-hearing in this cat for 8-KHz 1-msec signals. Figure 2 plots the amplitude of the N_1 - P_1 wave as a function of S_1 intensity for both conditions. The contralateral S_1 starts to generate a substantial response when its level is some 20 dB above that which produces a response in the ipsilateral case. Since both functions increase linearly and essentially in parallel thereafter, the cross-hearing effect of approximately 20 dB appears to be the same at 60, 70, 80, and 90 dB as well.

The graph in Figure 3 plots the difference in N_1 - P_1 amplitudes between Tc and no-Tc trials. A positive

Figure 1. Cat eighth nerve action potentials to S_1 (1 msec, 8 KHz) presented monaurally to the ear ipsilateral and contralateral to the electrode site. Calibration: 100 μ V, 2 msec.

value means that Tc enhanced the AP to S_1 , while a minus value means that Tc suppressed it. Figure 3 shows that Tc reduces the amplitude of the N_1 - P_1 wave in both the monotic and dichotic conditions. The ipsilateral Tc is more effective than the contralateral by 17 ± 4 dB (as measured from the 70-, 80-, 90-, and 100-dB points on the dichotic amplitude difference curve to the equal amplitude levels on the monotic curve). Since a *t* test between the difference in cross-hearing seen in Figure 2 and the difference

Figure 2. Amplitude of the N_1 - P_1 component of the AP to the same signal (S_1) presented ipsilaterally and contralaterally.

Figure 3. The reduction in the amplitude of the N_1 - P_1 component to a signal (S_1) as a function of the intensity of a prior stimulus (T_c). Both the monotic and dichotic conditions are shown.

between the dichotic and monotic conditions of Figure 3 was insignificant, the effect of a contralateral T_c can be accounted for by cross-hearing alone.

The reduction in N_1 - P_1 amplitude induced by T_c becomes smaller as ΔT is increased, as shown in Figure 4. When ΔT reaches about 350 msec, the effect of T_c upon the response to S_1 disappears. Further examination of the curves shows that for short ΔT intervals, 25 msec or less, a monotic T_c suppresses N_1 - P_1 amplitude by 40 to 60 μV more than a dichotic T_c , and that for longer ΔT intervals, the monotic and dichotic T_c s produce about the same amount of reduction in N_1 - P_1 amplitude. This suggests that there may be more than just cross-hearing involved in the dichotic condition.

Figure 5 shows that increasing T_c duration gradually reduces the amplitude of the AP to S_1 similarly in both the dichotic and monotic conditions. Each asymptotes at about 100 msec, beyond which there is no reduction in the AP. The average difference between the monotic and dichotic reductions in AP amplitude is $21 \pm 17 \mu\text{V}$. The difference between the monotic and dichotic curves for the T_c intensity function is $27 \pm 14 \mu\text{V}$. Since the dichotic effect in the T_c intensity function can be accounted for by cross-hearing, and since the difference in T_c effectiveness between the monotic and dichotic conditions for both the T_c intensity and duration functions are statistically the same, there is no evidence that the dichotic effect in the T_c duration experiment is due to anything more than cross-hearing.

Varying the frequency of T_c away from the frequency of S_1 in either direction reduces its suppressive effect on S_1 s of either 8 KHz (Figure 6) or 5 KHz (Figure 7). When using a 5-KHz S_1 , the N_1 - P_1 amplitude is quite small, especially when S_1 was

preceded by T_c (Figure 8). Therefore, N_2 - P_2 was measured and the effect of varying T_c frequency on this component is plotted in Figure 7. At both 8 and 5 KHz, the maximum suppression occurs at the frequency of S_1 or just below it, and decreases as T_c frequency is varied away from S_1 frequency. All of the curves show a significantly steeper rise in the recovery from suppression for the frequencies above S_1 than for the frequencies below S_1 [$T(10) = 2.89$, $p < .01$, monotic and 8 KHz; $T(10) = 2.64$, $p < .025$, dichotic and 8 KHz; $T(10) = 4.63$, $p < .005$, monotic and 5 KHz; and $T(10) = 2.85$, $p < .01$, dichotic and 5 KHz]. That the suppressive effects of T_c on the S_1 AP is frequency-dependent for two different frequencies of S_1 tends to confirm that the middle ear muscles were successfully sectioned, or at least not producing the effects observed in these experiments.

DISCUSSION

The objective of the experiments just reported was to determine whether the auditory nerve plays a role in

Figure 4. The reduction in amplitude of the N_1 - P_1 component to S_1 by a prior T_c as a function of ΔT , the interval in milliseconds between T_c and S_1 . Both the monotic and dichotic conditions are shown.

Figure 5. The reduction in amplitude of the N_1 - P_1 component to S_1 as a function of the duration of a prior T_c . Both the monotic and dichotic conditions are shown.

Figure 6. The reduction in the amplitude of the N_1 - P_1 component to an 8-KHz S_1 as a function of the frequency of the prior stimulus, T_c . Both the monotic and dichotic conditions are shown.

Figure 7. The reduction in amplitude of the N_2 - P_2 component to a 5-KHz S_1 as a function of the frequency of the prior stimulus, T_c . Both the monotic and dichotic conditions are shown.

loudness enhancement. To do this, the AP generated by S_1 was examined in both the absence and presence of T_c . The results suggest a strong, but inverse, correlation between the AP amplitude and loudness enhancement. For every parametric variation that increases the enhancement effect in man (increasing T_c intensity or duration, shortening the ΔT interval, or matching the frequency of T_c to that of S_1) there is a greater suppression of the S_1 AP amplitude in cat.

That T_c consistently suppresses the AP to S_1 suggests that the cat perceived S_1 to be masked by T_c . In man, however, a study on the recovery of both click loudness and AP amplitude by Coats and Dickey (1972) suggests that this may not be the case. They found that, although the amplitude of the human AP to a click is reduced by a preceding burst of noise and has not completely recovered after a ΔT interval of 500 msec, its loudness recovered within 150 msec of

the offset of T_c .¹ This shows that the AP amplitude cannot be equated with the perceived loudness of a stimulus and so it is not impossible that the cat in our study actually perceived S_1 as enhanced. Coats and Dickey (1972) suggested a way to reconcile the differences between the recovery functions of the AP and the loudness of the click. They proposed that there was a more central mechanism which compensates for the reduction T_c produces in the AP to S_1 so that the "suppressed" S_1 is perceived to be as loud as a control S_1 without T_c . If such a mechanism were to overcompensate for the suppressive effects of T_c on S_1 , then loudness enhancement could occur despite the results obtained here.

The relationship between the present electrophysiological results and loudness enhancement contrasts strongly with the relationship between eighth nerve AP amplitude and auditory sensitization (Hughes, 1954; Hughes & Rosenblith, 1957). Auditory sensitization (Hughes, 1954) is a lowering of the psychophysical threshold of tone pips produced by a preceding intense tone of several minutes' duration. Hughes and Rosenblith (1957) have shown a strong, positive correlation between the variations in AP amplitude produced by a preceding "sensitizing" tone in cats and the time course of the auditory sensitization effect observed in man under a variety of similar stimulus conditions. This suggests that these two similar psychophysical phenomena—sensitization and enhancement—are quite different in that one is probably due to a peripheral mechanism while the other seems to be due to a more central process.

Since the effects of both an ipsilateral and contralateral T_c on the AP amplitude of S_1 were investigated, it is possible to assess the role, if any, of the olivocochlear bundle (OCB) on the effects observed here. Galambos (1956) and Desmedt (1962) have demonstrated that shocking the crossed OCB reduces the AP of the eighth nerve to clicks. And

Figure 8. Eighth nerve action potentials to an 8- and a 5-KHz S_1 (1 msec, 80 dB) with and without a monotic T_c (250 msec, 100 dB) of 8 and 5 KHz, respectively. Calibration: 100 μV , 2 msec.

Neider and Neider (1970) showed that APs to clicks reduced by presenting noise return to their full amplitude when the OCB is shocked. It has also been demonstrated that sounds to one ear can activate both the crossed (Fex, 1962) and uncrossed (Fex, 1965) OCB. It seems, however, unlikely that the effects observed here can be attributed to the action of the OCB. Our findings on the effects of Tc (its intensity and duration, whether delivered to the ipsilateral or contralateral ear) are all statistically consistent with the idea that they are due solely to cross-hearing. To be sure, in the ΔT experiment, the monotic and dichotic curves converge at ΔT s longer than 25 or 30 msec, which suggests that something in addition to cross-hearing might be occurring in the dichotic condition. However, an explanation simpler than one invoking the OCB is available. Rosenzweig and Rosenblith (1953) demonstrated that the recovery functions to monotic Tcs of different intensities converge as ΔT is increased. If the contralateral Tc in the present studies is considered to be just a weaker, ipsilateral Tc, then the convergence of the monotic and dichotic curves is also consistent with the cross-hearing hypothesis. Consequently, there is no evidence from these studies that the OCB plays a role in the suppressive effects of Tc observed here.

An interesting aspect of the suppressive effect of Tc on the AP to S_1 is its frequency specificity, which earlier investigators have not reported. Coats (1964) found no "qualitative" effects of varying Tc frequency on the suppression of the AP produced by a .01-msec square-wave S_1 . Rosenblith, Galambos, and Hirsh (1950) found no systematic differences between Tc frequencies of 200, 500, 1,000, and 4,000 Hz on the recovery of AP amplitude to a .1-msec pulse S_1 . In both of these prior studies, the S_1 being suppressed had a broad energy spectrum, so it would not be expected that tonal stimuli would show differential suppressive effects; by contrast, the 1-msec tone pips used in this study have approximately 90% of their energy concentrated between 1,000 Hz above and below the nominal frequency of S_1 (Wightman, 1971). As we show, recovery from the suppression produced by Tc is more rapid when Tc is higher than S_1 in frequency, which agrees with the well-known observation that low frequencies mask high frequencies better than high mask low (Egan & Hake, 1950; Wegel & Lane, 1924).

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NOTE

1. One might expect that the subjects of Coats and Dickey (1972) would have shown loudness enhancement, which they do not report. However, in their study, the differences in intensity between Tc and S_1 were small, which limits the amount of enhancement attainable. Furthermore, their interval between S_1 and the reference (S_2) was often less than 1 sec, which means that S_2 itself could have been enhanced. Finally, it is at this time not known how well a noise Tc like theirs enhances a click S_1 , nor how much is produced by the 3-sec Tc they used. Consequently, their failure to report enhancement may have been due to an unfortunate choice of stimulus parameters.

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