ON and OFF components in the auditory evoked potential

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It has been suggested that the ON and OFF components of the auditory evoked potential (AEP) may be mediated by independent physiological mechanisms and that the response to a brief tone consists of overlapping ON and OFF responses. Two experiments were performed to evaluate these proposals. First, AEPs were recorded to tonebursts of various durations presented at a fixed rate. As the tonebursts were made longer, they evoked smaller ON responses and larger OFF responses, particularly when either response followed the other by less than 5 sec. This indicates that ON and OFF responses are not physiologically independent. Second, the AEP to a 25-msec tone was compared with the ON response to a 2,000-msec tone. At an interstimulus interval of 4 sec, the difference wave formed by subtracting the latter AEP from the former contained clear N_1 (ca. 100 msec) and P_2 (ca. 180 msec) components, which have been interpreted as an OFF response by some authors. These components in the difference wave were greatly reduced or even inverted at 10-sec interstimulus intervals, however, where interactions between ON and OFF responses to successive stimuli were minimized. This result indicates that any residual OFF response in the AEP to a brief tone is very small in amplitude, if present at all.

Changes in the intensity, frequency, or location of an auditory stimulus evoke a negative-positive sequence of waves from the vertex region of the scalp, with latencies in the 50-250-msec range. The most prominent components in this auditory evoked potential (AEP) are the N_1 (peaking at 50-150 msec) and P_2 (150-250 msec) waves. The N_1-P_2 complex, or "vertex potential," is elicited both by the onset and offset of a sound, with the OFF response usually having an amplitude of between one-quarter and one-half the size of the ON response for equal stimulus ON-OFF periods (Onishi & Davis, 1968; Spychala, Rose, & Grier, 1969).

There is some controversy in the literature as to whether these ON and OFF responses are mediated by the same or similar physiological mechanisms. On the one hand, it has been postulated that ON and OFF responses are manifestations of a common process which registers changes in the environment (e.g., Clynes, 1969; McCandless & Rose, 1970). Supporting this view is evidence of sequential interactions between successive ON and OFF responses. With decreasing tone durations, the OFF response is

reduced in amplitude, while the ON response becomes smaller when it is preceded more closely by an OFF response (Pfefferbaum, Buchsbaum, & Gips, 1971; Picton, Woods, & Proulx, 1978a). The N_1-P_2 response is also greatly diminished to a stimulus change that follows within 500 msec after a preceding change in that stimulus (Clynes, 1969). These results suggest that the OFF response to a very brief tone (under 100 msec) should be very small.

Other investigators, however, have argued that there is little or no interaction between successive ON and OFF responses. In one study, no significant differences were reported in the N_1-P_2 peak-to-peak amplitude of the OFF response when stimulus duration was varied between 300 and 1,300 msec (Johannsen, Keidel, & Spreng, 1972; Keidel, 1976). If, as suggested by these results, there is little interaction between ON and OFF responses at short intervals, the AEP to a brief sound would consist of overlapping, independent responses to its onset and offset (Spreng, 1969). Recent experiments by Schweitzer (1977) were interpreted as supporting this hypothesis. Subtraction of the ON response to the beginning of a 2,000-msec tone from the AEP to a brief (25 or 75 msec) tone yielded a waveform that was grossly similar in amplitude and morphology to the OFF response which occurred at the end of a 2,000-msec tone. From these results, Schweitzer con-

cluded that the AEP to a short-duration tone is "the result of overlapping responses to the onset and offset of stimulation" and suggested that "the ON and OFF responses are mediated by independent physiological mechanisms."

These data of Schweitzer are subject to a completely different interpretation, however, which takes into account the long refractory periods of the N_1-P_2 waves (Davis, Mast, Yoshie, & Zerlin, 1966; Nelson & Lassman, 1968). Since tones were presented at a rate of one every 4 sec, the ON responses to the 25, 75, and 2,000-msec tones were elicited at different intervals after the OFF response to the preceding tone (3,975, 3,925, and 2,000 msec respectively). If there was interaction between the OFF and ON responses to successive tones, then the AEP to a brief tone would be larger than the ON response to the 2,000-msec tones, not because it contained an additional OFF response, but because it consisted of a more fully recovered ON response.

This paper presents two experiments performed in an attempt to clarify this controversy. The first experiment evaluated the interaction between ON and OFF responses over periods of time between 1 and 9 sec. In order to investigate possible interrelations between the ON and OFF responses and the auditory-evoked sustained potential (Keidel, 1971, 1976; Köhler & Wegener, 1955; Picton et al., 1978a, 1978b), dc recording techniques were used. A second experiment investigated whether the AEP to a

25-msec toneburst could be "dissected" into separate ON and OFF responses (Schweitzer, 1977) when the confounding variable of interstimulus interval was controlled.

EXPERIMENT 1

Methods

One-kilohertz tonebursts at an intensity of 80 dB above normal adult threshold (HL) were presented at a rate of once every 10.24 sec to the left ear. Rise and fall times were 10 msec. The durations of these tones were set at 1, 3, 5, or 9.24 sec. The stimuli were presented in blocks of 48 or 64 at each duration. Each block was replicated once, and the resulting eight blocks were presented in random sequence to obviate any possible order effects.

EEG activity was recorded using Ag/AgCl electrodes. A vertex electrode was referred to a balanced frontal-mastoid electrode adjusted to cancel out eye-blink artifact (Cooper, Osselton, & Shaw, 1974). The EEG was amplified and filtered with a bandpass of 0-20 Hz (Picton et al., 1978a). Evoked potential averaging was carried out on-line. The final AEP waveforms were based on averages of 96 or 128 responses.

Recordings were made from 10 young normal adults, all paid volunteers. The subjects read a book during the experiment, blinking occasionally but not making any large eye movements.

AEP components were measured according to the diagram shown in the upper left of Figure 2. The N_1 component was identified as the maximum negativity between 50 and 150 msec after the beginning of the onset or offset of the tone; the P_2 component was the maximum positivity in the 150-250-msec range. Except for the N_1 component of the OFF response (denoted N_{1X} in the figure), all measurements were made relative to a baseline determined as the average voltage of the waveform in the ½ sec prior to stimulus onset. The sustained potential (SP) was
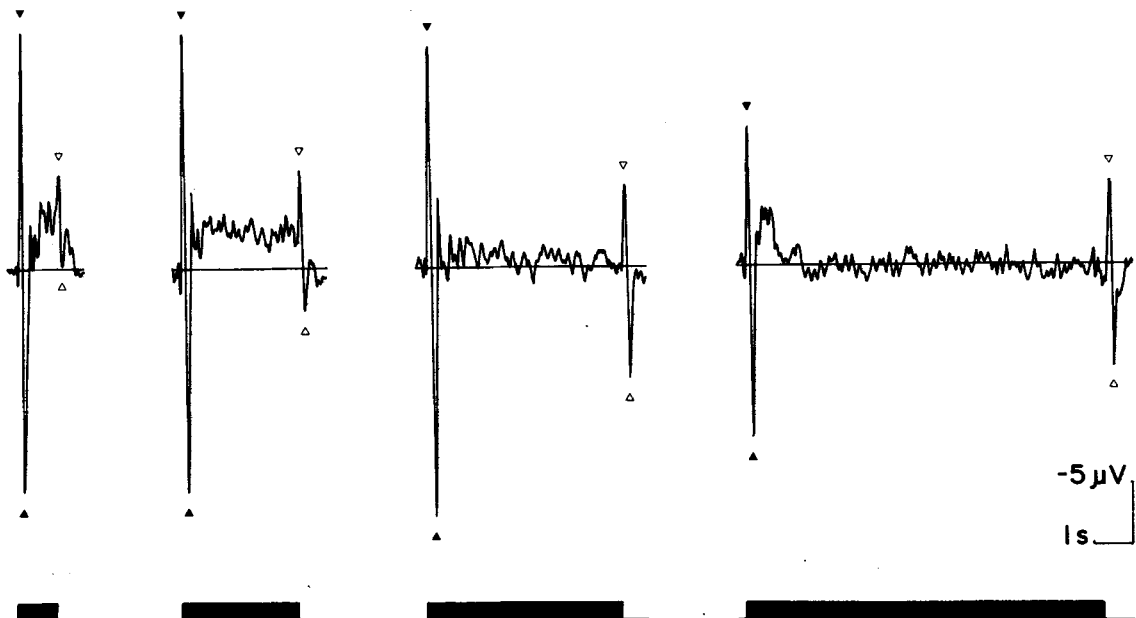

Figure 1. AEPs to 1-kHz 80-dB HL tonebursts of 1, 3, 5, and 9.24 sec duration. The N_1-P_2 components to the onset of the tone are indicated by filled triangles and to the offset by open triangles. Note that the ON response is smaller at tone durations of 9.24 sec than at the other durations, while the OFF response becomes smaller at tone durations of less than 5 sec. Negativity at the vertex is represented as an upward deflection in all figures. Each tracing represents the average of 96 individual responses. Time calibration = 1 sec (1s). Subject E.S.

measured as the mean voltage level over the last ½ sec of the tone. The N_1 component of the OFF response was measured relative to this SP value.

Results

The onset of the tone evoked a large N_1 component with a mean peak latency of 108 msec, followed by a smaller P_2 component with a mean peak latency of 212 msec. During the toneburst, there was a negative SP that fell back to the initial baseline with tone cessation. The offset of the tone also elicited an N_1-P_2 complex, with mean peak latencies of 101 and 206 msec, respectively. At the shorter stimulus durations, the P_2 component of the OFF response was often identifiable only as a small notch on the falling slope of the sustained potential. The AEP waveforms from one subject with particularly large N_1-P_2 responses are shown in Figure 1.

The paradigm was such that, as the toneburst was made longer in duration, its offset came closer to the onset of the subsequent tone. Consequently, the onset response became progressively smaller in amplitude with increasing stimulus duration, particularly when the offset occurred only 1 sec prior to the onset of the succeeding tone (Figure 2). This effect of stimulus duration on the ON response was significant for the N_1 component [$F(3,27) = 20.20$, $p < .001$] and the N_1-P_2 peak-to-peak measure [$F(3,27) = 4,70$, $p < .01$], but not for the P_2 wave [$F(3,27) = 0.27$, n.s.].

Measurement of the N_1 and P_2 components in the OFF response was complicated by their temporal overlap with the SP offset (SP_X in Figure 2). The
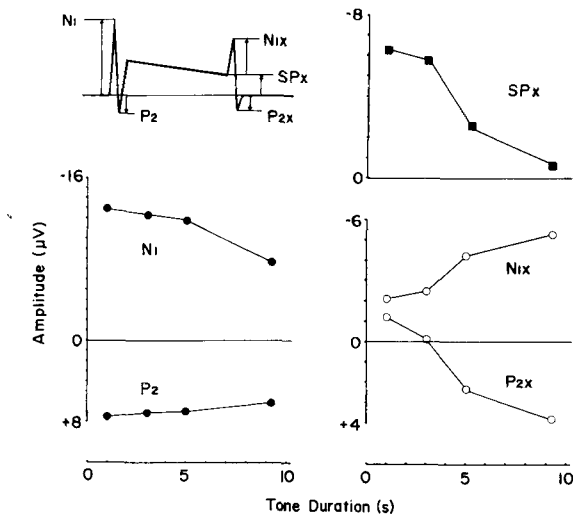

Figure 2. Average data of 10 subjects from Experiment 1. In the upper left is a diagrammatic illustration of how the AEP measurements were made. The lower left portion of the figure shows the mean amplitudes of the ON-evoked components at the different stimulus durations (in seconds). The upper right graph shows the amplitude of the falloff of the sustained potential that occurred upon tone offset. The OFF response amplitudes are plotted in the lower right.
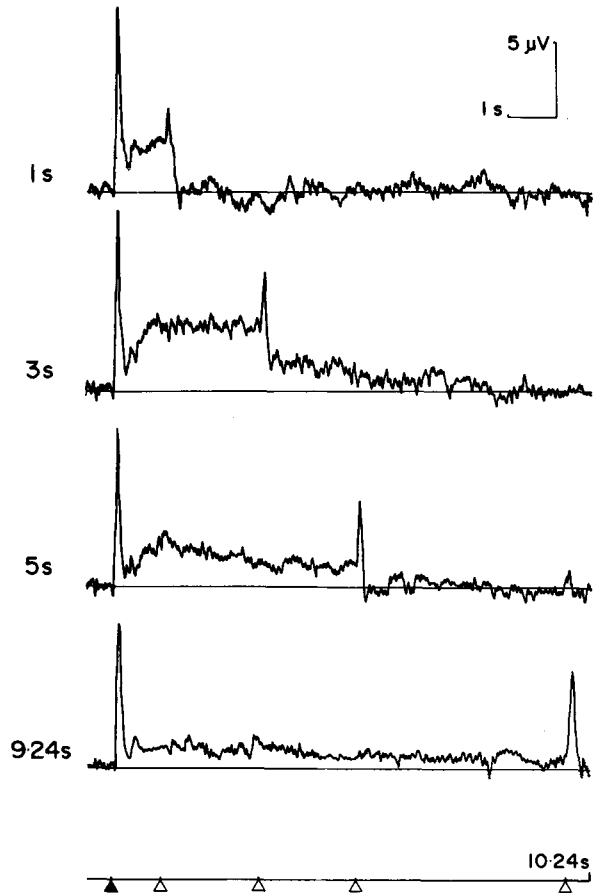

Figure 3. Changes in onset, offset, and sustained potentials as a function of tone duration from 1 to 9.24 sec (s). Each tracing represents the average of 128 individual responses. With increasing stimulus duration, the onset response and the sustained potential get smaller, whereas the N_1 component of the offset response becomes larger. Subject G.P.

N_1 component (N_{1X}), measured relative to the mean value of the SP in the last ½ sec of the tone, showed a progressive decline with decreasing stimulus duration [$F(3,27) = 5.57$, $p < .01$].

With increasing stimulus duration, the SP decreased in amplitude [$F(3,27) = 12.69$, $p < .001$]. For the tones of shorter duration, the amplitude of the SP offset was much larger than the combined amplitudes of the N_1 and P_2 components of the OFF response. Because this change in the amplitude of the SP falloff overlapped the offset-evoked N_1-P_2 response, a peak-to-peak measurement of the total offset response (i.e., the sum of N_{1X}, SP_X, and $-P_{2X}$) changed very little as a function of stimulus duration—from 7.04 μV at 1 sec to 9.64 μV at 9.24 sec duration [$F(3,27) = 1.76$, n.s.]. This is illustrated in the waveforms from a second subject shown in Figure 3.

EXPERIMENT 2

The results of the preceding experiment indicate

that the amplitude of the N_1-P_2 response to the onset of a toneburst varies as a function of the duration of the preceding silent interval. Thus, in Schweitzer's (1977) experiments, the AEP to the 25-msec tone might have differed from the ON response to the 2,000-msec tone because the former was preceded by a longer silent interval, not because it contained an additional OFF component. To evaluate this question, we first replicated one of Schweitzer's experimental conditions, using a 4-sec interstimulus interval (ISI), and compared those AEPs with AEPs elicited to the same stimuli delivered at 10-sec ISIs. If the reported difference between the AEPs to the 25-msec tone and to the onset of the 2,000-msec tone was indeed due to an OFF response to the shorter tone, this difference should be maintained at the longer ISI.

Another factor which may have confounded the results of Schweitzer's subtraction procedure is the tone-evoked SP. Since a large SP is elicited by the 2,000-msec tone and not by the 25-msec tone, the difference between their respective AEPs at both stimulus onset and offset may be determined, in part, by overlap with the SP. To evaluate this possibility, recordings at the low-frequency cutoff used by Schweitzer (0.15 Hz) were compared with dc recordings.

Methods

One-kilohertz tonebursts were delivered binaurally through earphones at an intensity of 86 dB SPL. The tonebursts were either 25 or 2,000 msec in total duration, with rise and fall times of 10 msec. They were delivered at regular ISIs of either 4 or 10 sec, measured between successive stimulus onsets. These four experimental conditions (two durations by two ISIs) were each run once and then replicated in reverse order, with each subject receiving a different ordering of the four conditions.

Recordings were made from five normal adult volunteers ranging in age between 25 and 35 years. The subject read a book while AEPs were recorded. AEPs were recorded from a bipolar, vertex-to-occipital montage (C_z-O_z), using Grass silver cup electrodes. An additional electrode was placed under the right eye (referred to O_z) to rule out eyeblink and movement artifacts. Potentials from these two channels were amplified both at a bandpass of 0.15-500 Hz (Grass Model 7P5 preamplifiers) and at a bandpass of 0-40 Hz (Grass Model 7P1 preamplifiers). At the input impedance level of the 7P1 amplifier, the scalp recordings were effectively dc (time constant greater than 10 sec).

AEPs were tape-recorded at a bandpass of 0-150 Hz (Vetter Model A) and averaged off-line using a Nicolet MED-80 computer after elimination of artifact-contaminated trials. AEPs were averaged separately for each of the eight runs, which consisted of 128 stimuli at the 4-sec ISIs and 64 stimuli at the 10-sec ISIs. The AEPs of the two replicate runs were then averaged together.

Results

The 25-msec tones as well as the onset and offset of the 2,000-msec tones all elicited prominent N_1 and P_2 components. The mean N_1 and P_2 latencies were 93 and 180 msec in the AEP to the 25-msec tones, 92 and 169 msec in the 2,000-ON response,

and 84 and 170 msec in the 2,000-OFF response (the latter measured from the beginning of the tone offset).

The effect of ISI on these components is illustrated for a typical subject in Figure 4. At the 4-sec ISI, it is seen that the 25-msec tone elicited a larger N_1-P_2 response (the 25 M.R., or "multiple response," in Schweitzer's terminology: solid line) than did the onset of the 2,000-msec tone (dotted line). The difference wave between these two AEPs (d25-OFF, or "dissected OFF response"), shown below, is similar in amplitude and morphology to the AEP elicited by the offset of the 2,000-msec tone (third row of tracings). In the lower two sets of " split" tracings, the replicate AEPs from the two halves of the experiment are superimposed to illustrate the reproducibility of the d25-OFF waveform and the 2,000-OFF response.

In contrast, at the 10-sec ISI, the AEP to the onset of the 2,000-msec tone was nearly identical to the AEP to the 25-msec tone and, in fact, slightly exceeded it in peak-to-peak amplitude. Accordingly, the d25-OFF waveform was greatly attenuated and
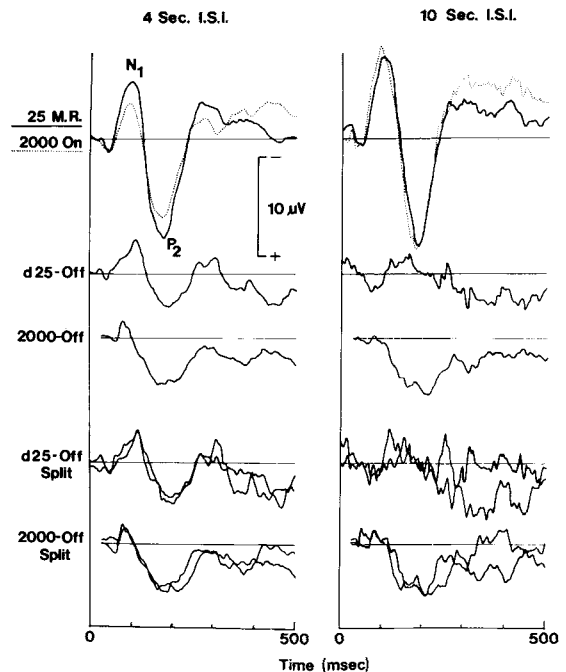

Figure 4. The top tracings show the natural AEPs to the 25-msec tones (25 M.R., solid lines) and to the onsets of the 2,000-msec tones (2,000-ON, dotted lines) from Subject 1. Below are the difference waveforms (d25-OFF) formed by computer subtraction of the 2,000-ON response from the 25 M.R. at the indicated ISI. The third set of tracings (2,000-OFF) shows the natural OFF responses to the 2,000-msec tones. The lower ("split") tracings are the superimposed replications of the d25-OFF and 2,000-OFF waveforms from the two halves of the experiment. The AEPs were averaged over 128 stimuli at the 10-sec ISI and 256 stimuli at the 4-sec ISI, with half this many averaged for each of the "split" tracings. ac recordings.

lost any clear N_1-P_2 morphology. The AEP to the offset of the 2,000-msec tone, however, remained at about the same amplitude at both ISIs.

Similar patterns of results were observed in subjects 2, 3, and 4. The N_1-P_2 amplitudes were larger to the 25-msec tone than to the 2,000-ON stimulus at the 4-sec ISI, with this difference reversing at the 10-sec ISI (see Table 1). Accordingly, the d25-OFF waveforms consisted of a negative-positive sequence of peaks at the 4-sec ISI and a positive-negative sequence at the 10-sec ISI, when measured at the latencies of the N_1 and P_2 peaks in the natural (25 M.R.) waveforms. This difference in the N_1-P_2 amplitude between the d25-OFF waves obtained at 4- and at 10-sec ISIs was significant over all subjects [$t(4) = 3.17$, $p < .02$], and is illustrated for subjects 1-4 in Figure 5; note the resemblance between the 2,000-OFF response and the d25-OFF response at the 4-sec ISI but not at the 10-sec ISI.

The N_1-P_2 amplitudes of the 25 M.R. and the 2,000-ON responses (shown in Table 1) were also submitted to a two-way (ISI by Stimulus Duration) repeated measures analysis of variance. The main effect of ISI was highly significant [$F(1,4) = 58.19$, $p < .01$], but the main effect of stimulus duration was not [$F(1,4) = 0.94$]. There was a significant interaction between ISI and duration [$F(1,4) = 10.63$, $p < .05$], since the onset response to the 2,000-msec tone showed a greater amplitude increase with ISI (57%) than did the response to the 25-msec tone (15%).
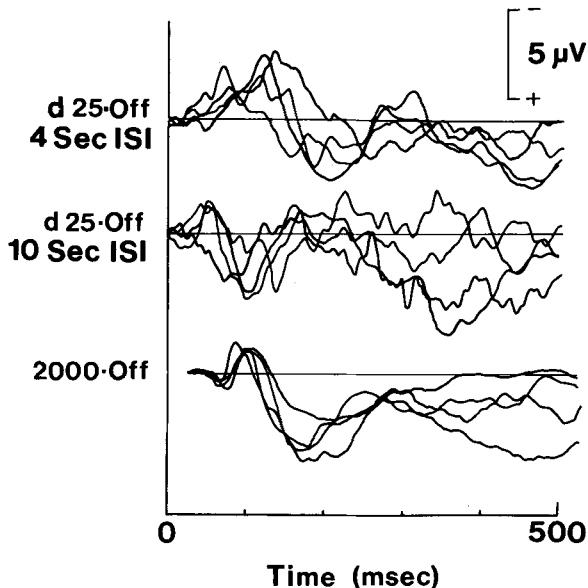

Figure 5. The d25-OFF waveforms are shown for ISIs of 4 sec (upper tracings) and 10 sec (middle tracings). The 2,000-OFF responses at the 4-sec ISI are shown in the bottom tracings. The waveforms from Subjects 1-4 are superimposed. ac recordings. The data from the Subject 5 are present in Figure 6.

Table 1
N_1-P_2 Peak-to-Peak Amplitudes (in Microvolts) for the Different Natural and "Dissected" AEPs in Each Subject

AEP	Subject	Interstimulus Interval	
		4 sec	10 sec
To 25-msec tone	1	16.7	19.7
(25 M.R.)	2	13.7	15.5
	3	15.1	14.7
	4	13.0	14.4
	5	12.7	17.3
	Mean	14.2	16.3
To 2,000-msec tone	1	11.4	21.0
(2,000-ON)	2	10.2	16.5
	3	12.0	18.3
	4	12.3	18.2
	5	11.3	15.3
	Mean	11.4	17.9
d25-OFF	1	5.3	-1.3
(at latencies of peaks	2	3.5	-1.0
in 25 M.R.)	3	3.1	-3.6
	4	.7	-3.8
	5	1.4	2.0
	Mean	2.8	-1.6
d25-OFF	1	7.1	.1
(at latencies of peaks	2	5.5	1.6
in d25-OFF at 4-sec	3	3.3	-2.8
ISI)	4	5.7	.9
	5	5.2	5.6
	Mean	5.4	1.1
To 2,000-msec tone	1	6.6	6.4
(2,000-OFF)	2	5.6	6.9
	3	5.5	6.1
	4	3.9	4.1
	5	3.5	4.0
	Mean	5.0	5.5

Note—Measurements made from ac recordings.

The components of the d25-OFF difference wave at the 4-sec ISI were also qualified as the peak negativity between 50 and 150 msec (N_1) and the peak positivity between 150 and 250 msec (P_2). As shown in Table 1, the mean N_1-P_2 amplitude measured for the d25-OFF response at these peak latencies was much smaller at the 10-sec ISI (1.1 μV) than at the 4-sec ISI (5.4 μV), a difference that was significant over all subjects [$t(4) = 3.34$, $p < .02$].[1]

One subject (No. 5) presented a different pattern of AEPs from the others. In this case, the d25-OFF responses were very similar in amplitude and waveform at the 4- and 10-sec ISIs. To get an accurate picture of the genesis of these difference waves, however, it is necessary to examine the dc recordings of the AEPs (Figure 6). At both ISIs, there was a sustained potential difference between the AEPs to the 25- and 2,000-msec tones, with the latter being more negative from about 150 msec onwards. This difference is attributable to the SP, which is present only during the long-duration tone and onsets with an earlier latency than in the other subjects. Con-
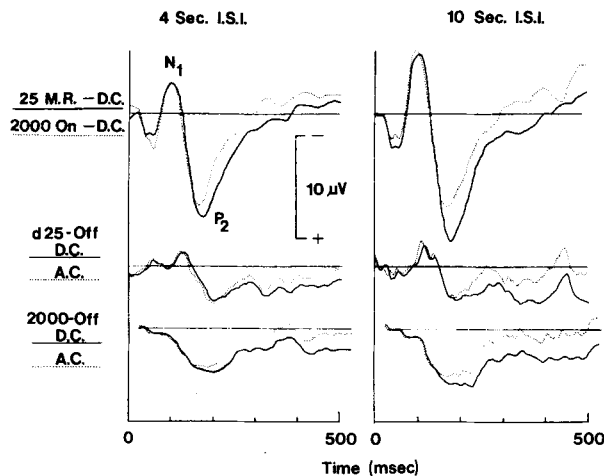
Figure 6. The top tracings show the dc recordings of natural AEPs to 25-msec tones (solid lines) and 2,000-msec tones (dotted lines) in the fifth subject. The middle pairs of tracings show the difference waveforms between these AEPs (d25-OFF), obtained with simultaneous dc (solid lines) and ac (dotted lines) recordings. The lower pairs of tracings are the AEPs to the offset to the 2,000-msec tone obtained with dc (solid lines) and ac (dotted lines) recordings. AEPs were averaged over 256 stimuli at the 4-sec ISI and 128 stimuli at the 10-sec ISI.

sequently, the d25-OFF waves contained a sustained positivity in the dc recordings (solid lines), which appeared as a more phasic positive wave in the P_2 latency range in the ac recordings (dotted lines). The earlier negative component in the d25-OFF waveforms seems to arise from a slight broadening or prolongation of the N_1 wave to the 25-msec tones in relation to the 2,000-msec tones, at both ISIs. This negative peak does not appear to correspond to any discernable component in the natural OFF responses (bottom tracings). The major part of the difference wave in this subject seems, therefore, to have arisen from the subtraction of the developing SP and is similar to the 2,000-OFF waveform which contains the "resolution" of the SP.

GENERAL DISCUSSION

The results of the first experiment demonstrate a strong interaction between AEPs to stimulus onset and offset, particularly when ON and OFF responses are separated by intervals of less than 5 sec. When either type of AEP succeeds the other within this time span, its N_1-P_2 components are markedly attenuated. These results confirm and extend the findings of Pfefferbaum and colleagues (1971) to a wider range of ISIs. It would appear, then, that the processes underlying the evoked ON and OFF responses to auditory stimuli are not independent.

The first experiment also shows that peak-to-peak measurement of the N_1—P_2 of the OFF response

will typically include, at least to some extent, the return to baseline of the auditory SP. In fact, with tonebursts of 1-3 sec duration, the SP offset can be much larger than the N_1-P_2 components of the OFF response. This effect probably explains why Johannsen et al. (1972) did not measure any diminution in the OFF response when stimulus durations were reduced from 1,300 to 300 msec. Most likely, a large portion of their N_1-P_2 measure consisted of SP falloff. The overlapping of the SP resolution with the N_1-P_2 probably also explains why we observed no significant effect of stimulus duration on the peak-to-peak amplitudes of the offset response.

With stimulus durations of 1 sec or less, the offset-evoked N_1-P_2 components became very difficult to distinguish from the falloff in the SP (Figures 1 and 3). This was also found to be the case in experiments where AEPs to 600-msec tonebursts were recorded using dc techniques (Picton et al., 1978b). It is, therefore, very unlikely that the AEP to tones shorter than 100 msec would contain an appreciable OFF response, and certainly not one so large as 4-5 μV, as reported by Schweitzer.

The second experiment provides further evidence against the presence of an appreciable OFF component in the AEP to a short one. While we replicated Schweitzer's (1977) finding that the difference wave ("d25 OFF") formed by subtracting the ON response to a 2,000-msec tone from the AEP to a 25-msec tone may resemble the natural OFF response (Figure 4), this subtraction procedure was shown to be confounded by at least two factors.

First, the form and amplitude of the components in the d25-OFF waveform were shown to be strongly dependent upon the ISI. In four of the subjects, the d25-OFF response contained clear components in the N_1 and P_2 latency ranges at the 4-sec ISI, but these waves were either reduced to noise levels or inverted in polarity at the 10-sec ISI. This effect is attributable largely to the relative reduction in amplitude of the 2,000-ON response at the 4-sec ISI, due to its being preceded by an OFF response 2 sec earlier. At the 10-sec ISI, where such refractory-period interactions are minimized, the 2,000-ON response became slightly larger than the AEP to the 25-msec tone, perhaps due to the integration of stimulus energy over the first 50 msec of the tone. Thus, the d25-OFF waveform in these subjects does not appear to represent a dissected OFF response so much as a differential between the amplitudes of the ON responses to the 25- and 2,000-msec tones, as determined by the different silent intervals that preceded them.

The second confounding factor was the presence of the tone-evoked SP, which could overlap both the ON and OFF responses to the 2,000-msec tone. This

negative SP may begin at a latency of around 150 msec after the onset of the tone (Picton et al., 1978a) and, thus, may overlay the P_2 wave evoked by the long-duration tone and reduce its measured amplitude. This overlap may account, in part, for the finding that the N_1-P_2 peak-to-peak amplitude can be slightly larger to a 30-50-msec sound than to a longer sound (Muller, 1973; Spreng, 1969). Thus, in subjects with SPs of relatively early onset (Figure 6), the d25-OFF waveform will include a positive deflection, beginning at around 150 msec, that is attributable to the negative SP to the 2,000-msec tone. In such subjects, the comparison between dissected and natural OFF responses may reveal similarities largely because the dissected OFF response contains an inverted (subtracted) SP while the natural OFF response contains the positive-going termination of an SP.

Even if the confounding effects of refractory interaction and overlapping SPs could be eliminated, there is still reason to doubt that the subtraction of the AEPs to 2,000- and 25-msec tones from one another would unambiguously reveal an independent OFF component. Since both loudness and N_1-P_2 amplitude may increase as tone duration is extended over this range (Keidel, 1976; Muller, 1973; Onishi & Davis, 1968), it is likely that these responses reflect in part the temporal integration of stimulus energy. Hence, it would be difficult to conclude that the small AEP differences between long- and short-duration tones seen in some subjects reflect the presence of OFF responses rather than the effects of temporal integration of the ON responses.

Taken together, these results support earlier findings (Pfefferbaum et al., 1971; Picton et al., 1978a, 1978b) of a strong and mutual interaction between the vertex potentials (N_1-P_2 components) elicited by closely spaced stimulus onsets and off-sets. This suggests that the ON and OFF responses arise either from the same cerebral generator or from closely related systems that strongly influence one another. Further evidence suggesting an equivalence of their cerebral generators comes from studies showing that ON and OFF responses have similar scalp distributions (Picton et al., 1978a). These findings are consistent with the concept that both ON- and OFF-elicited auditory N_1-P_2 waves are largely manifestations of a general brain system which responds to changes in the acoustic environment (cf. Clynes, 1969; McCandless & Rose, 1970).

A broader question is to ascertain to what extent the auditory ON and OFF responses are equivalent to the vertex potentials elicited by stimulus changes in other modalities. Somatosensory and visual events also elicit an N_1—P_2 complex in the 100-250-msec range (Davis et al., 1972; Gjerdingen & Tomsic, 1970), and several authors have suggested that these components reflect the activity of a common cerebral system (Goff, Matsumiya, Goff & Allison, 1969; Walter, 1964). More recently, it has been established that the N_1-P_2 waves in different modalities do not have identical scalp distributions (for review, see Goff, Allison, & Vaughan, in press), even though all are of high amplitude at the vertex. Accordingly, it has been suggested that the late evoked potentials at the vertex may be subdivided onto modality-specific and nonspecific components which are elicited in parallel (Donald, 1976). The modality-specific components seem to be generated in or near the primary sensory cortex (Arezzo, Pickhoff, & Vaughan, 1975; Goff et al., in press; Simson, Ritter, & Vaughan, 1977), but it is not yet clear what proportion of the vertex-recorded N_1-P_2 complex comprises these components.

Despite this regional differentiation of the vertex potentials in the different modalities, there is good evidence for functional similarities among them, in that they show similar, prolonged recovery periods (Gjerdingen & Tomsic, 1970), strong and sym-metrical refractory interactions (Davis et al., 1972), and are similarly affected by selective attention (Hillyard, Picton, & Regan, in press). Hence, it seems reasonable to continue to entertain the hypo-thesis that a significant portion of the vertex po-tentials (including ON and OFF responses) represents the activity of common "neural substrates of in-formation processing" in the auditory, somatic, and visual modalities (Goff et al., 1969).

Several suggestions have been made as to the nature of this common mode of processing. Walter (1964) proposed that the vertex potential represents a nonspecific arousal response which alerts the cortex that "something has happened," with later com-ponents providing the more precise details. Another suggestion is that these waves might derive from midline limbic structures, such as the cingulate gyrus, and relate primarily to the emotional connotation of a stimulus (Chatrain, Canfield, Knauss, & Lettich, 1975). Thatcher and John (1977) have considered the later components to be largely endogenous and more indicative of the interpretation of a stimulus rather than the sensory analysis per se. A similar idea is that the vertex potential reflects the activation of those cerebral processes that are necessary for the evaluation and interpretation of stimulus changes (Picton, Cambell, Baribeau-Braun, & Proulx, 1978). This activation would involve both stimulus-specific and nonspecific processing, and its duration and decay properties would parallel the long refractory period of the vertex potentials. These various interpretations of the vertex potential remain quite speculative at present, and it is altogether possible that these waves contain multiple subcomponents representing differ-ent cerebral processes.

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NOTES

1. A negative value (-2.8 μV) for the N_1-P_2 amplitude of the d25-OFF response for Subject 3 at the 10-sec ISI was possible because of the manner in which these measurements were made. The N_1 and P_2 latencies were established in the d25-OFF waveform at the 4-sec ISI, where clear components were discernible. The measurements of N_1 and P_2 amplitudes were then made at these same latencies for the d25-OFF response at the 10-sec ISI, where, it turned out, the N_1 measure was positive in relation to the P_2 measure. This polarity inversion produced the negative amplitude value for N_1-P_2.