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Modulation of early auditory processing during selective listening to rapidly presented tones *

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Summary   Two dichotic listening experiments were performed in which stimulus and task conditions were optimized for the early selection of inputs. Subjects listened selectively to sequences of rapidly presented tone pips in one ear while ignoring tone pips of a different pitch in the opposite ear. In both experiments, an enhanced positivity between 20 and 50 msec (the 'P20-50') was observed over central and frontal sites in the ERPs to the attended-channel tone pips. At longer latencies, the effects of attention appeared to include an amplitude modulation of several exogenous ERPs, including subcomponents of the central N1 (60–150 msec) and P2 (170–230 msec) waves and the temporal T complex (80–150 msec). In contrast, the attention effect prefrontally consisted of a broad negativity that appeared to be largely endogenous.

A signal processing technique (Adjar) was employed to correct for distortion of mutually overlapping ERPs elicited by successive stimuli presented at short interstimulus intervals (ISIs). It was confirmed that the P20-50 attention effect was not the result of differential overlap from previous ERPs. In addition, this technique allowed an analysis to be made of the effects of the preceding stimulus type and ISI on the attention-sensitive ERPs, which provided further support for the view that highly focused selective attention can directly modulate exogenous components of the auditory ERP. Moreover, these sequence-dependent ERP modulations were paralleled by variations in target discrimination performance. Taken together, these results provide strong support for the early selection hypothesis that attention can serve to selectively bias or gate stimulus processing before full perceptual analysis has occurred.

Key words: Modulation; Selective listening; Selective attention; ERP; Auditory; Early processing

The physiological and psychological mechanisms of selective attention can be investigated in humans through recordings of event-related potentials (ERPs) from the scalp. The earliest attention effect that has been consistently observed in the auditory ERP is a negative deflection that has been variously called the 'N1 effect' (Hillyard et al. 1973), the 'negative difference wave' or 'Nd' (Hansen and Hillyard 1980), or the 'processing negativity' (Näätänen et al. 1978). Gener-

ally, this effect can be described as a greater negativity in the ERPs elicited by attended stimuli relative to the ERPs elicited by ignored stimuli; the enhanced negativity may onset as early as 50 msec, typically augmenting the measured amplitude of the evoked N1 component at 80–120 msec.

Initially the Nd effect was viewed as an enhancement of the sensory evoked or exogenous N1 wave (Hillyard et al. 1973), but in a number of subsequent studies the attention-related negativity was found to exhibit properties of an endogenous component arising from a different source than the N1. For example, it was shown that this negativity could be dissociated in time from the N1 wave (by coming later) and could extend as much as several hundred milliseconds beyond it (Näätänen et al. 1978; Okita 1981). There is considerable evidence, however, that the Nd is not a unitary phenomenon that simply changes in amplitude and latency but rather consists of at least two overlapping phases (Hansen and Hillyard 1980; Woods and Clayworth 1987; Giard et al. 1988). The first of these

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phases (early Nd) has a scalp distribution more similar to that of the N1 itself and becomes more prominent as the two channels are made more discriminable. The second phase (late Nd) has a more frontal distribution and may last for hundreds of milliseconds. A plausible hypothesis to account for this set of results would be that the Nd attention effect is a multicomponent phenomenon, the early phase of which includes an enhancement of the evoked N1 component or one of its subcomponents during highly focused selective attention (Hillyard 1981; Donald 1983). Such a finding would be important theoretically because it would indicate that selective auditory attention can include an early gating or filtering of sensory inputs, in addition to whatever endogenous processing systems may be invoked.

ERP components at latencies earlier than the N1/Nd have generally been reported to be insensitive to shifts of attention (e.g., Picton and Hillyard 1974; Woods and Hillyard 1978; Picton et al. 1981). Woldorff et al. (1987), however, reported an earlier effect of attention in 2 dichotic listening experiments that were designed to optimize the early selection of inputs. The design features included: (1) high inter-channel discriminability, with 2 channels of tones being distinguished by both ear of entry and pitch, (2) a rapid rate of stimulation, which increased processing load and facilitated the 'tuning' of attention by rapidly repeating the channel-defining cues, (3) a difficult target detection task within the designated channel that required the subject to attend closely to all the sounds within that channel, and (4) large numbers of stimulus trials to yield ERP averages with high signal/noise ratios. Congruent with most previous reports, the brain-stem evoked responses (latency 1–10 msec) did not vary as a function of selective attention. In the midlatency range, however, a small but significant effect of attention was found in both experiments. This effect, termed the 'P20-50,' appeared as an enhanced positivity in the interval from 20 to 50 msec in the ERPs to attended stimuli and was measured as a significant increase in the Na-to-Pa peak-to-peak amplitude. The P20-50 peaked just after the Pa wave itself, a component that appears to reflect early activity in or near primary auditory cortex (Celesia 1976; Kraus et al. 1982; Scherg and Von Cramon 1986; Kileny et al. 1987; Scherg et al. 1989). Thus, the P20-50 attention effect might possibly reflect gating of auditory transmission at the level of the thalamic relay (Skinner and Yingling 1977) or primary cortex.

Although a more rapid rate of stimulus presentation appears to enhance the early selection of competing inputs, it can create problems in the analysis of ERP data due to the fact that the ERP to a given stimulus may still be in progress when the next stimulus arrives. The distortion of ERP averages due to overlapping wave forms elicited by successive stimuli has been analyzed in detail by Woldorff (1989, submitted), who described a signal processing technique (Adjar) for estimating and removing such overlap. This analysis showed that the widely used procedure of stimulus randomization in selective attention experiments does not necessarily eliminate the possibility of the ERP averages for attended and for unattended stimuli being differentially distorted by adjacent ERP overlap. If such an artifact occurred, it could mistakenly be interpreted as an experimental effect of attention on the small-amplitude, short-latency ERP components.

Another implication of rapid stimulus presentation is that the processing of each current stimulus may vary considerably as a function of what the previous stimulus was and how long ago it occurred (e.g., see Kornblum 1973; Elmasian et al. 1980). Observing the effects of such sequential interactions on different ERP components could lead to insight into the dynamic mechanisms of stimulus processing during selective attention. However, in attempting to investigate the effects of stimulus sequence on ERPs at short ISIs, the problem of overlap of successive wave forms becomes critical, since the ERPs must be sorted into subaverages based on different subsets of the possible previous stimulus types (or previous ISIs). When the ERPs overlap, any physiological effects of the prior stimulus type upon the ERP being analyzed are confounded with the differential overlapping wave forms of the ERPs to those differing previous stimuli. Because of this problem, only a few researchers have attempted sequential analyses of ERPs at short-to-medium ISIs (e.g., Woods and Knight 1986; Hansen and Hillyard 1988).

The present paper gives a more complete account of the two selective listening experiments reported in abbreviated form in Woldorff et al. (1987). The data analyses presented here were focused on 3 major aims. The first was to apply the Adjar technique to the ERPs in those two experiments in order to ensure that the P20-50 attention effect was not an artifactual consequence of differential distortion of the attended and unattended ERP wave forms due to overlap from preceding ERPs. The second aim was to analyze the attention effects on the longer-latency ERP components, since only the short-latency components (BERs and MLRs) were analyzed previously. Of particular interest was the question of whether the exogenous N1 wave or any of its subcomponents (Näätänen and Picton 1987) might be modulated by highly focused selective attention. The third aim was to study the effects of stimulus sequence on the attention-sensitive ERPs using the Adjar technique and to relate the observed ERP variations to target discrimination performance. This approach allowed an examination of the sequential dynamics of stimulus processing during selective listening to rapidly presented dichotic tone sequences.

Methods

Subjects

Subjects were paid student volunteers with normal hearing. In order to minimize myogenic contamination of the BERs and MLRs, only females were studied since they generally have less neck and head musculature than males. Only those subjects who, in a preliminary screening session, could learn to perform the task adequately while maintaining EEG relatively free from muscle activity were accepted into the study.

Experiment 1. Ten subjects (ages 19–28, 8 right-handed) who met the above criteria served as the final sample for experiment 1.

Experiment 2. The criteria for an acceptable level of muscle activity were made even stricter in experiment 2. Sixteen subjects (ages 18–26, 13 right-handed) returned to serve as the final sample, none of whom had participated in experiment 1.

Stimuli and task

Experiment 1. Subjects were seated comfortably in a reclined position and were instructed to keep their eyes fixated on a spot in front of them during the experimental runs. Acoustic wave forms were generated by a microcomputer and transduced through stereo headphones. Tone sequences consisted of 5000 Hz tone pips (duration 1.0 msec) delivered to the left ear and 3400 Hz tone pips (duration 1.5 msec) to the right ear, shaped with a 2-cycle rise time, 1-cycle plateau, and 2-cycle decay time. Auditory thresholds for these stimuli were determined for each subject, and intensity levels were adjusted to 60 dB SL. Thresholds for white noise were also determined, and about 25 dB SL of noise was added via an acoustic mixer to mask extraneous sounds.

The left- and right-ear tones were presented in random order at ISIs ranging randomly from 120 to 320 msec (rectangular distribution). The task was to listen selectively to the tones in one ear and press a button upon detecting occasional (9% per ear), difficult-to-detect deviant tones (targets) of lesser intensity than the more frequent 'standard' (60 dB SL) tones. All tones (both standards and deviants) in the other ear were to be ignored. The deviant tones were identical in wave shape to the standards in that ear, differing only in intensity. Based on the preliminary screening session, the standard/deviant intensity difference was individually adjusted for each ear of each subject to achieve a level of target detectability of around 70–80%. This was done to ensure that attention would need to be well focused on the to-be-attended ear in order to perform the task, as well as to attempt to equate difficulty between attention conditions and across subjects. These intensity differences varied from 8 to 20 dB across subjects and ear of stimulation.

Subjects were instructed to concentrate more on accuracy of target discrimination than on speed of response in order to mitigate any tendency for increased muscle tension. Verbal feedback on task performance was given to the subject after each run.

Twelve runs each of attend-left and attend-right conditions were presented in counterbalanced order. Runs in which the EEG contained myogenic artifact or the task performance was poor were deleted and redone. Each run lasted about 95 sec and consisted of 200 standards and 20 deviant tones in each ear, for a total for each subject of 2400 attended standards, 2400 unattended standards, 240 attended deviants (targets), and 240 unattended deviants for each ear.

Experiment 2. In this experiment, the parameters of the tone pip stimuli were modified, but the target probabilities, ISI range, and white noise level were identical to experiment 1. The tone pips were made longer in duration (13 msec), slower in rise/fall time (5 msec), slightly fainter (55 dB. SL), and lower in frequency (1500 Hz in the left ear, 2600 Hz in the right). Besides testing whether the effects found in experiment 1 would replicate with lower frequency tones, these changes were intended to increase the tonal quality and thereby the inter-channel discriminability of the stimuli. Target tones were again identical to the standard tones except in intensity, and the standard/deviant difference ranged from 10 to 20 dB.

The task, experimental protocol and run durations were also identical to experiment 1, but the number of runs in each condition was increased to 16.

Recording

Experiment 1. Brain electrical activity was recorded using Ag/AgCl electrodes placed at 11 scalp sites (Fpz, Fz, Cz, Pz, C3, C4, T3, T4, T5, T6, and right mastoid) of the international 10–20 system, all referenced to left mastoid. The EEG was amplified with a bandpass of 0.01–100 Hz and digitized at 500 Hz/channel onto magnetic tape. ERPs were averaged off-line (epoch length 1024 msec, beginning 200 pre stimulus) and then re-referenced by appropriate subtractions to the algebraic average of the two mastoids. Electro-ocular activity (EOG) was also recorded (from the left cheekbone referenced to Fpz) to enable artifact rejection of trials with blinks or other eye movements.

Experiment 2. In addition to the 11 scalp sites and the EOG channel recorded in experiment 1, a balanced sterno-vertebral, non-cephalic placement (also referenced to left mastoid) was included in order to be able to evaluate evoked activity at the mastoids relative to this site. Recording bandpass was set at 0.1–100 Hz. Digitization, artifact rejection and averaging procedures were identical to experiment 1. The ERP aver-

ages from all sites, including the non-cephalic placement, were again re-referenced to averaged mastoids.

In parallel to the above recording system were two high bandpass channels that performed on-line averaging of BERs and MLRs at a digitization rate of 25,000 Hz/channel. The results from these recordings were reported in Woldorff et al. (1987) and will not be presented here.

Signal processing

The recorded ERPs from the two experiments were subjected to the Adjar signal processing technique (Woldorff 1989, submitted) for removing adjacent response overlap. Relevant aspects of this procedure are outlined below.

In using the Adjar procedure, a basic distinction is made between 'full averages' and 'subaverages.' A full average ERP is defined as the average of all the ERP responses to stimuli of a particular class (e.g., attended left-tone ERP responses) without regard to the nature of the previous event. The trials from such an average can be sorted into subaverages based on the previous stimulus/response types and previous ISI subranges. In the present experiments, the 4 full averages for the standard tones (i.e., attended and unattended ERPs to left-ear tones and to right-ear tones) were each divided into 4 subaverages based on whether the stimulus was preceded by a standard tone in the same ear ('preceded-by-same') or in the opposite ear ('preceded-by-opposite') and whether the ISI since the previous stimulus was 'short' (120–220 msec) or 'long' (220–320 msec).

As described in Woldorff (1989, submitted), given a set of ERP averages obtained using short, randomly varied ISIs, the distortion due to overlap from temporally adjacent ERPs in the stimulus sequence can be estimated by performing mathematical convolutions of appropriate full average wave forms with the distributions in time of the occurrences of the corresponding adjacent stimuli. For greater accuracy, these convolutions were applied to the present data in an iterative manner (called 'level 2' in Woldorff 1989), whereby progressively better estimates are obtained for the summated ERP overlap from both preceding and subsequent stimuli. Briefly, this iterative approach involves first using the original full averages as estimates of the adjacent ERPs that overlap and distort those initial full averages. Weighted summation of these adjacent ERP estimates (each offset by the appropriate latency) provides an initial estimate of the total overlap distorting each original full average ERP. These first estimates of the distortion are then subtracted from the original full averages, thereby yielding less distorted full averages, which can then be used as still better estimates of the adjacent ERPs. In this way a convergence toward the correct (i.e., undistorted) full average wave forms is

established, the final outcome of which is used to estimate the distortion that is present in the subaverages [1].

ERP measurement and statistical analysis

All ERP measures were obtained from the averaged, Adjar-corrected wave forms of individual subjects using computer algorithms. For each ERP component, the same latency window was used for all subjects, as indicated in Tables I–III. In the midlatency range, components Na and Pa were measured in a peak-to-peak manner by comparing the largest negative peak in a latency window centered around Na to the largest positive peak in a window centered around Pa. In experiment 2 these two components were also measured baseline-to-peak, where baseline was defined as the mean amplitude across the 200 msec pre-stimulus period. For the longer-latency waves in both experiments, mean amplitudes of the wave forms within the appropriate latency window were also measured relative to the 200 msec pre-stimulus baseline.

The amplitude values obtained were entered into repeated measures analyses of variance (ANOVAs). For the full average ERPs, the ANOVA performed at midline sites was usually 2×2, with the factors being ear of stimulation (left vs. right) and attention (attended vs. unattended). Lateral sites were generally analyzed in pairs, so that a third factor was hemisphere of recording site (left vs. right). For the subaverage ERPs based on stimulus sequence, additional factors included previous stimulus type (preceded-by-same-ear vs. preceded-by-opposite-ear) and previous ISI (short = 120–220 msec vs. long = 221–320 msec).

Because experiment 2 presented more stimuli to each subject, included more subjects and used stricter criteria for acceptance of subjects, the resultant ERP wave forms had a substantially better signal-to-noise ratio than did those from experiment 1. Accordingly, the ERP results from experiment 2 will be presented in much greater detail, with only main effects from experiment 1 being given.

Target discrimination

Task performance was scored as percentage of target tones correctly discriminated. Detections were deemed correct if a button press was made within 250–1000 msec after the target onset. Only responses to targets preceded by standards were included in the analysis, and performance was scored according to

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[1] In the present analysis, the accuracy of this overlap estimation process was increased further by using only standard-tone full averages and excluding from these averages those trials that were either preceded or followed by deviant tones; this eliminated contamination from the large, highly variable P300 waves elicited by those deviants when they were attended targets.

stimulus sequence (preceding stimulus type and ISI subrange) as described above for ERPs [2].

Results

ERP full averages

To illustrate the Adjar technique, a comparison of ERPs before and after the removal of the estimates of the prior-response overlap is shown in Fig. 1. Note that even in the case of these full averages, for which previous responses were of all types and were temporally dispersed across the entire ISI range, there was still some residual overlap. In this case, however, it was not very large, and, more importantly, it did not differ between the attended and unattended ERPs.

Midlatency components

After correcting for previous-response overlap, the P20-50 attention effect was still evident (Fig. 1). This was reflected in the Na-to-Pa peak-to-peak amplitudes at central and frontal sites being significantly larger in the attended ERP than in the unattended by 10-20% in both experiments 1 and 2 (Table I) [3].

Further statistical analysis of ERPs at sites C3/C4 in experiment 2 (where the attention effect was most reliable) localized the latency of the effect to be near that of the Pa wave. In particular, the baseline-to-peak measure for Na did not differ significantly between the attended and unattended ERPs, but this measure for

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[2] Target discrimination accuracy was scored as percent correct rather than d' in these sequential analyses because of the difficulty at these high stimulus rates of analyzing false alarms as a function of sequence. The percent correct calculation is relatively straightforward, because both correctly discriminated targets and missed targets can be classified as a function of the type and ISI of the previous stimulus. False alarms, on the other hand, defined as button presses with no attended-channel target in the preceding 250-1000 msec time window were most likely to have occurred in response to an attended-channel standard tone in that time window. At the high stimulus rates in these experiments, however, several attended standards may have occurred in this time window, and thus each false alarm could not be uniquely associated with any one particular standard tone in the sequence.

In order to evaluate the possibility of sequential effects on response bias, an additional analysis was performed. Specifically, the set of all attended standard tones occurring in the time windows 250-1000 msec prior to false alarm button presses was analyzed, and the relative proportions were determined of the 4 possible types of events that could precede those tones (i.e., preceded in the same vs. opposite ear, at short vs. long ISIs). An ANOVA of these relative proportions provided an indication of whether preceding event type affected the likelihood for an attended standard to elicit a false alarm, thereby indicating whether stimulus sequence affected response bias.

[3] Because of small changes resulting from the removal of the previous-response overlap, the measured values and the corresponding statistics differed slightly from those reported in Woldorff et al. (1987). The corrected values are reported in Table I.

Pa was significantly larger for the attended responses ($P < 0.03$).

The interaction of site × ear for the Na-Pa peak-to-peak measure at the C3/C4 sites in experiment 2 was highly significant ($P < 0.002$), due to the amplitudes being larger at the site contralateral to the ear of stimulation. However, the attention effect on Na-Pa was not significantly larger contralaterally, as reflected by the lack of a significant interaction of attention × site × ear. The base-to-peak measures showed a dissociation between Na and Pa in that the Pa peak amplitude was larger contralaterally ($P < 0.001$), whereas the Na peak amplitude measure was not.

Longer-latency components: central and midline sites

The main effects of attention on the longer-latency waves were very similar in the two experiments, and hence only ERPs from experiment 2 will be shown in subsequent figures. The Adjar-corrected ERPs are shown in Figs. 2 and 3 for left- and right-ear standard tones, respectively, and the corresponding attentional difference waves are shown in Fig. 4. At central and parietal sites, there was a clear-cut separation of the attention-related negativity into two phases, the first closely overlapping the N1 component (consisting of N80 and N125 subdeflections) and the second overlapping the N2 (N290) component. In between, there was an enhanced positivity that corresponded with the P2 (P190) component. In contrast, at Fpz the attention effect consisted predominantly of a prolonged negativity. The effects of attention at Fz seemed to be a mixture of those at the central and pre-frontal sites.

From Figs. 2-4, it is clear that the attention effect did not simply consist of a unitary negative wave. To describe the complex pattern of attention effects in the difference waves, the individual subcomponents will be labeled Nd or Pd (negative or positive difference) followed by a latency value. Thus, for example, the positive attention effect overlapping the P190 will be called the Pd190, and the negative attention effect overlapping the N290 will the called the Nd290.

The attention effect in the N1 latency range at central and midline sites appeared to consist of two subdeflections, peaking at around 80 and 125 msec, respectively, as did the original ERPs themselves. This latency range was therefore divided into two time intervals, 60-100 msec and 104-154 msec, for which mean amplitude measures were analyzed separately. The attention effects on these measures will be referred to individually as Nd80 and Nd125, and collectively as the early Nd.

At central and frontal sites in both experiments 1 and 2, the mean amplitudes of both the N80 and the N125 were significantly larger (i.e., more negative) in the attended ERP than the unattended (all Ps < 0.005). Table II shows the μV values for the attended and

ORIG. UNCORRECTED FULL AVERAGE   PREV.—OVERLAP ESTIMATE   ADJAR—CORRECTED FULL AVERAGE

Expt. 1

Expt. 2

P20–50

Left Standard Tones   —— Attended   —— Unattended

1.0 μV
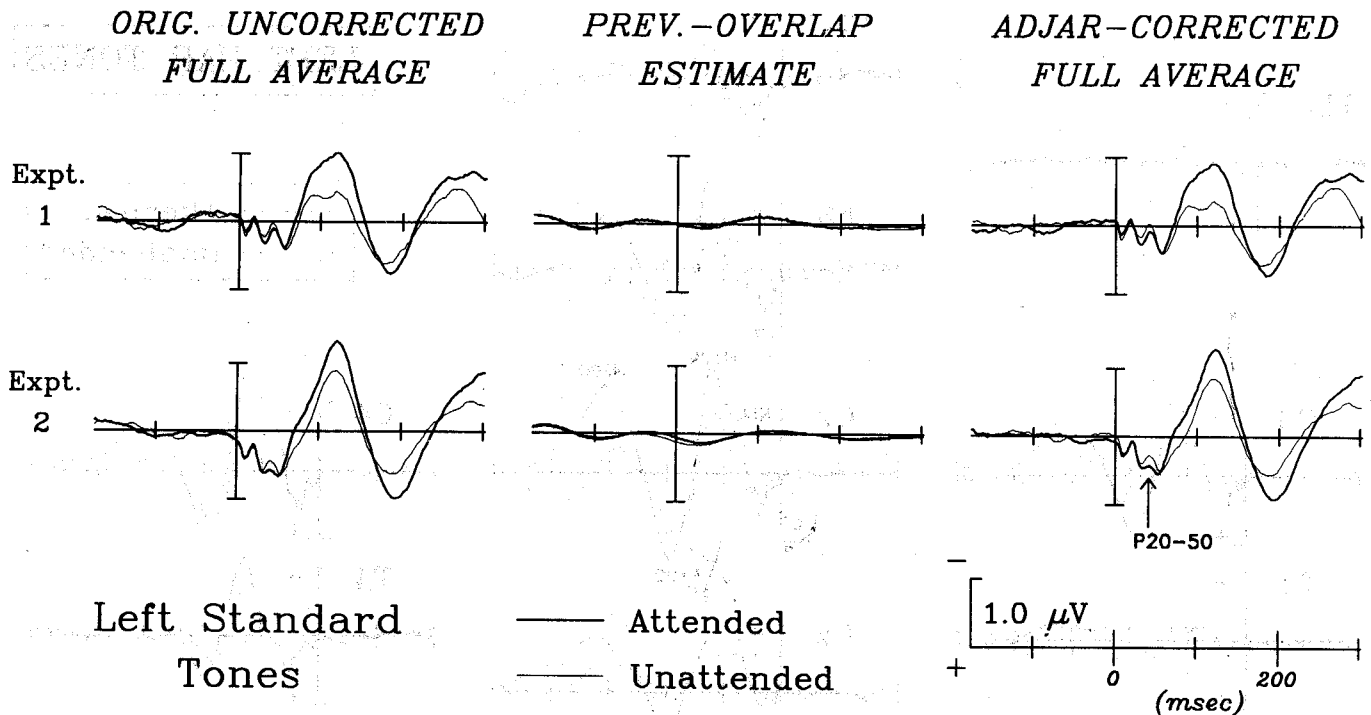
+   0   200

(msec)

Fig. 1. Uncorrected and corrected full average ERPs elicited by the left-ear standard tones at the C3 site, along with the corresponding summated overlap from previous responses that was estimated and removed. All wave forms are grand averages across subjects (N = 10 in experiment 1, N = 16 in experiment 2). Note that the distortion from overlapping previous ERPs was fairly small in these full averages and did not differ for attended versus unattended ERPs.

unattended component measures from experiment 2, along with the associated statistics.

Further analyses of laterality interactions in experiment 2 from sites C3 and C4 revealed highly significant

interactions between hemisphere of recording site and ear of stimulation for both the N80 and N125 measures (both $Ps < 0.001$), due to their amplitudes being larger contralateral to the ear of stimulation. In addition,

TABLE I

Na-Pa peak-to-peak amplitudes as a function of attention, collapsed over left- and right-ear stimuli (reference = averaged mastoids).

Experiment 1 (Na window = 14–22 msec, Pa window = 24–36 msec)

Site	Amplitudes (μV $\pm$ S.E.)		$F (1, 9)$ *	P value
	Attended	Unattended		
Fpz	0.69 $\pm$ 0.07	0.62 $\pm$ 0.06	4.0	n.s.
Fz	0.70 $\pm$ 0.07	0.58 $\pm$ 0.06	6.4	< 0.03
C3	0.57 $\pm$ 0.07	0.45 $\pm$ 0.06	8.4	< 0.02
Cz	0.60 $\pm$ 0.08	0.49 $\pm$ 0.08	15.1	< 0.004
C4	0.54 $\pm$ 0.08	0.45 $\pm$ 0.06	6.1	< 0.04
C3/C4 **	0.55 $\pm$ 0.05	0.45 $\pm$ 0.04	8.6	< 0.02

Experiment 2 (Na window = 18–24 msec, Pa window = 26–40 msec)

Site	Amplitudes (μV $\pm$ S.E.)		$F (1, 15)$ *	P value
	Attended	Unattended		
Fpz	0.61 $\pm$ 0.05	0.59 $\pm$ 0.04	0.9	n.s.
Fz	0.71 $\pm$ 0.06	0.65 $\pm$ 0.05	5.4	< 0.03
C3	0.64 $\pm$ 0.05	0.52 $\pm$ 0.04	14.9	< 0.002
Cz	0.66 $\pm$ 0.06	0.56 $\pm$ 0.04	7.1	< 0.02
C4	0.58 $\pm$ 0.05	0.48 $\pm$ 0.04	14.2	< 0.002
C3/C4 **	0.61 $\pm$ 0.04	0.50 $\pm$ 0.03	19.8	< 0.001

* Main effect of attention.
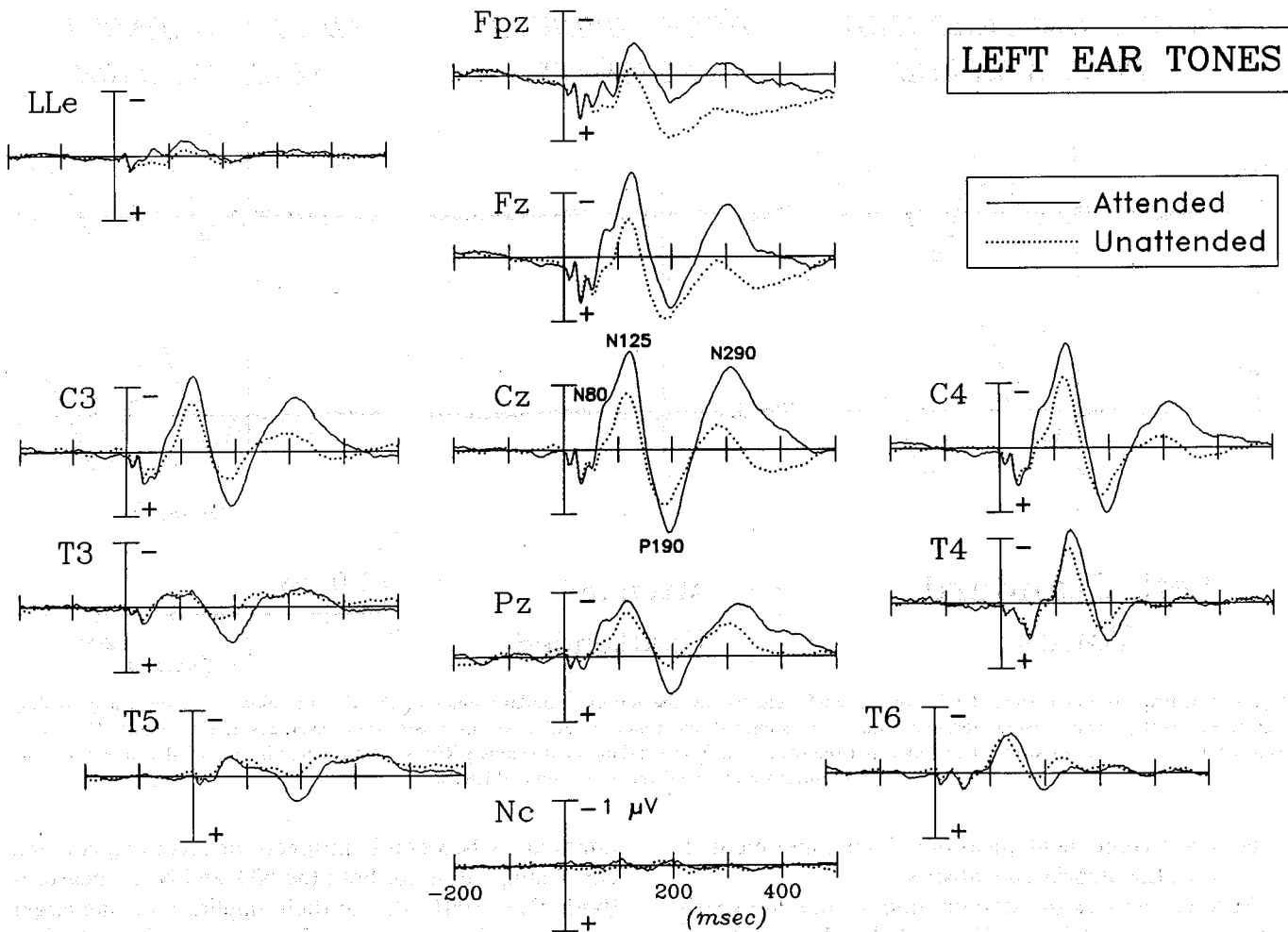** C3 and C4 sites analyzed as a pair.

Fig. 2. Adjar-corrected ERP full averages for attended and unattended left-ear tones from experiment 2, grand averaged across subjects. Reference for all sites is the algebraic average of the mastoids. Nc = non-cephalic (balanced sterno-vertebral); LLe = lower left eye (below and to the left of the left eye).

both the N80 and N125 of the unattended responses tested separately were contralaterally larger ($Ps <$ 0.001). There were also significant 3-way interactions of attention × ear × hemisphere for both of these measures, which resulted from the corresponding attention effects — Nd80 ($P < 0.003$) and Nd125 ($P < 0.03$) — being larger contralateral to the ear of stimulation. Fig. 5 depicts the contralateral preponderance of the unattended N80 and N125 components and of the attention effects on each of them.

In both experiments the P190 wave was significantly enlarged in the attended wave forms at central and parietal sites (Table II). Additional analysis at sites C3/C4 in experiment 2 found that this attention-related positivity (Pd190) was not larger contralaterally, although the P190 itself was ($P < 0.002$). At the frontal sites, on the other hand, the attentional difference wave was dominated by the prolonged negativity that extended throughout the interval 100–500 msec.

The main effect of attention in the N290 latency range in both experiments was an enhanced negativity

in the attended ERPs at central and midline sites (Table II). The N290 itself was larger ipsilaterally at the C3/C4 sites ($P < 0.001$). One possible explanation for this may be partial overlap from the P190 component, which was larger contralaterally. The Nd290, however, was not significantly different at contralateral versus ipsilateral sites.

Longer-latency components: temporal sites

At the temporal sites the component structure of the attention effect was different from that at central and midline sites (Fig. 4). In particular, the attention effect in the N1 latency range included a small positive peak near 100 msec (P100t) followed by a negative peak near 135 msec (N135t), a biphasic sequence resembling the T-complex of Wolpaw and Penry (1975). A subsequent positivity was termed the P190t. The corresponding attention effects on these waves were designated Pd100t, Nd135t, and Pd190t.
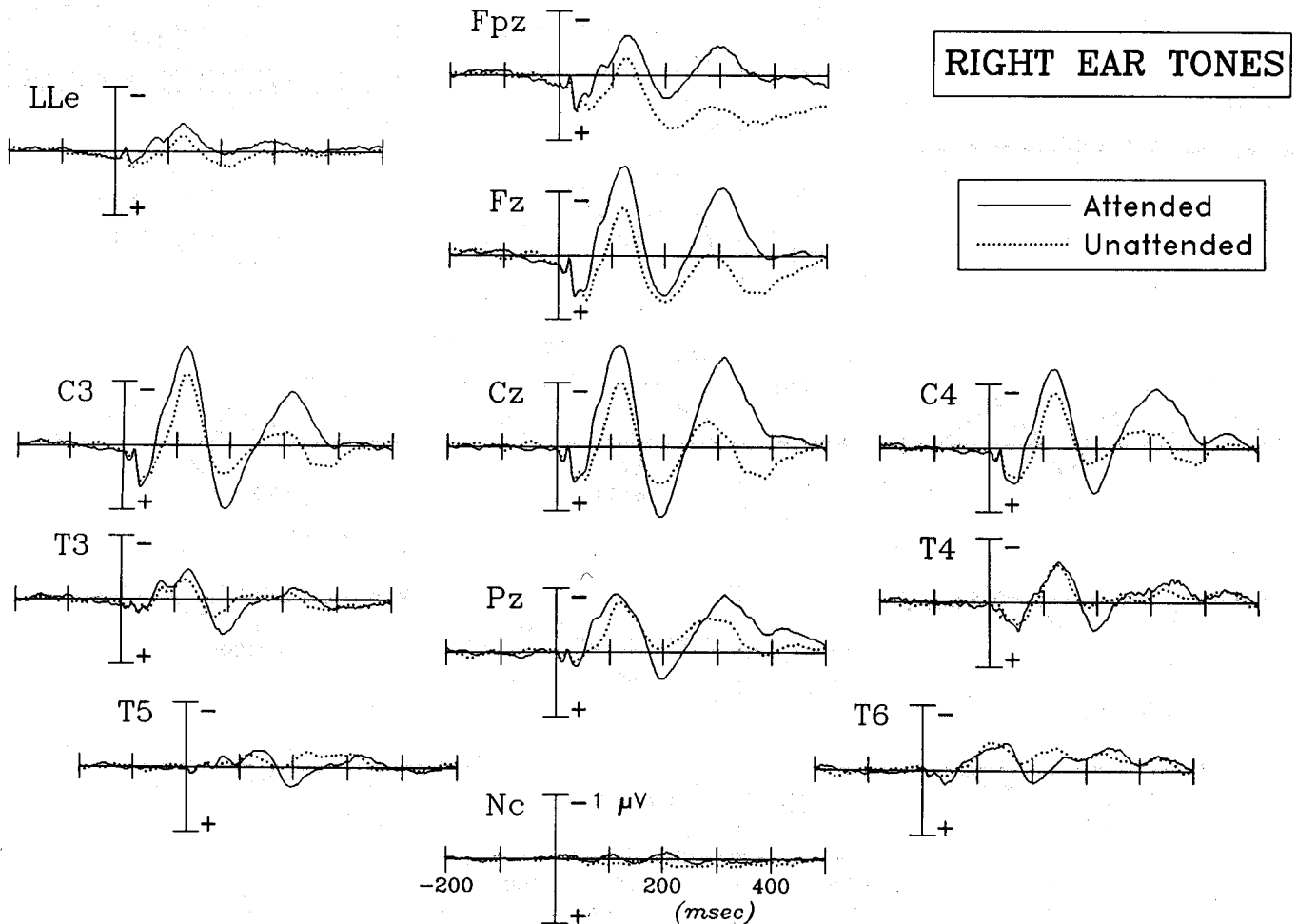
No consistent main effects of attention were ob-

Fig. 3. Same as Fig. 2 for right-ear tones.

served upon the P100t (Table III) [4]. The N135t, on the other hand, was enhanced (i.e., more negative) for attended responses at both temporal site pairs in experiment 1 (both $P < 0.01$), and at T3/T4 in experiment 2 (Table III).

Further analysis of ERP laterality in experiment 2 revealed a main effect of hemisphere for the N135t component, which was larger over the right temporal sites (T3/T4: $P < 0.001$, T5/T6: $P < 0.001$). The interaction of hemisphere × ear was significant for both pairs of temporal sites (T3/T4: $P < 0.001$, T5/T6: $P < 0.02$), as was the 3-way interaction of hemisphere × ear × attention (T3/T4: $P < 0.001$, T5/T6: ($P <$

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[4] In experiment 1 for the T3/T4 site-pair only, a significant main effect of attention on the P100t measure was observed that was due to an increased negativity for attended tones ($P < 0.001$). This effect appeared not to be the result of activity from a localized temporal generator, however, but rather to be due to the attention effect in experiment 1 including more of a slow, broadly distributed, negative shift that was largest frontally but extended to the more anterior temporal sites. Such a shift may have been partially attenuated in experiment 2 because of the use of a shorter time constant (1 sec vs. 10 sec).

0.02). These interactions resulted primarily because of a right hemispheric predominance of both the N135t and the Nd135t for left-ear tones that was absent for right-ear tones.

The attention effect on the P190t (Table III) was similar to that seen centrally and parietally, being larger (i.e., more positive) in the attended responses for both pairs of temporal sites. Testing of laterality showed that at T3/T4 the P190 was larger contralaterally ($P < 0.02$) but the Pd190t was not, a result similar to that observed for central sites.

Relationship of P20-50 to early Nd

In order to investigate whether the size of the early attention-related P20-50 was predictive of longer-latency attention effects, the subjects from experiment 2 were divided into 2 groups as a function of the size of their P20-50 (as gauged by the Na-to-Pa measure at the C3/C4 sites); group S had the smaller P20-50s, while group L had the larger. The most notable difference between these two groups (Fig. 6) was that the group L subjects had larger early Nd's than did those in group S. The Nd125 component was significantly larger for
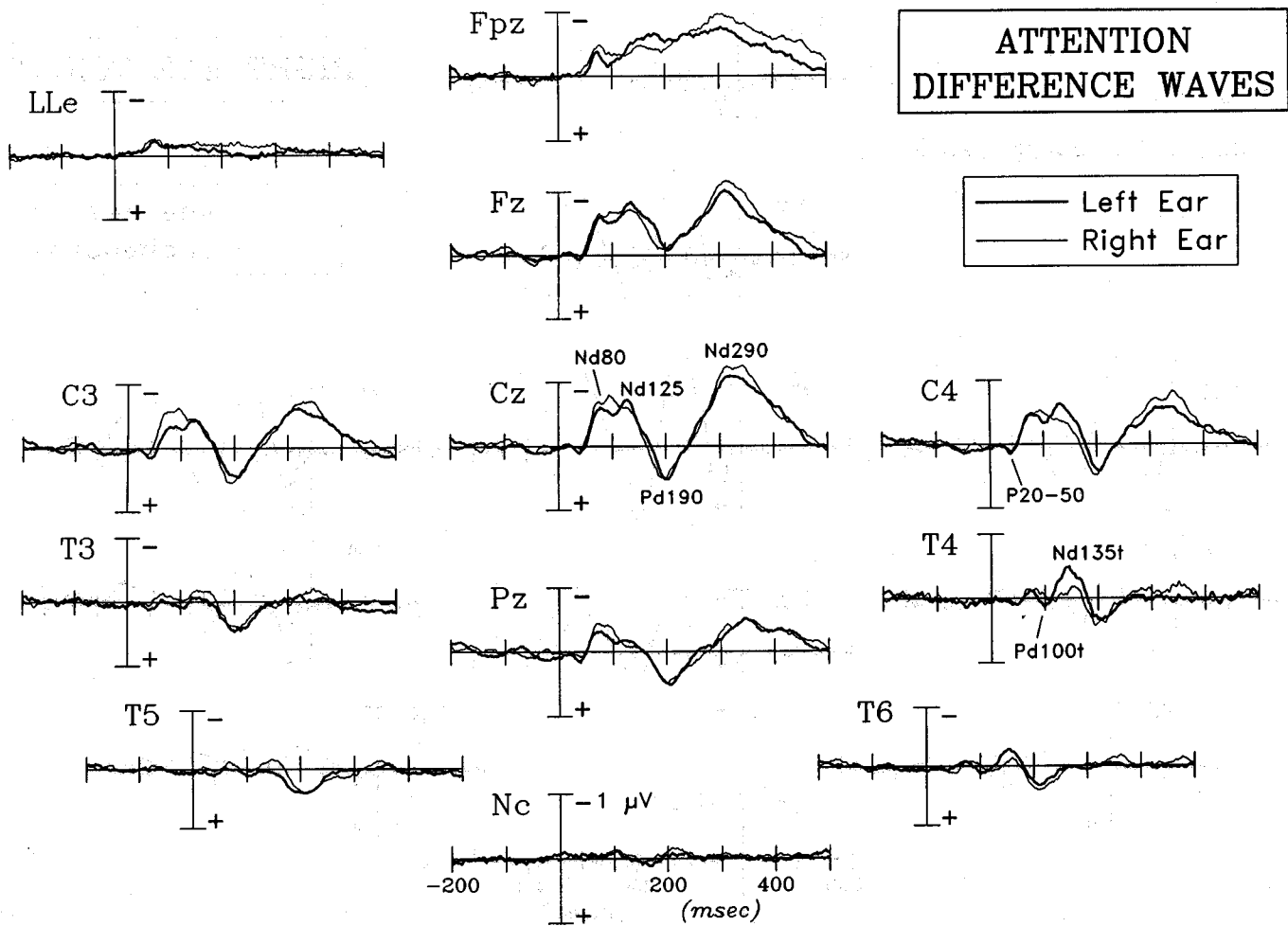
Fig. 4. Attentional difference waves (attended ERPs minus unattended ERPs) derived from the data shown in Figs. 2 and 3.
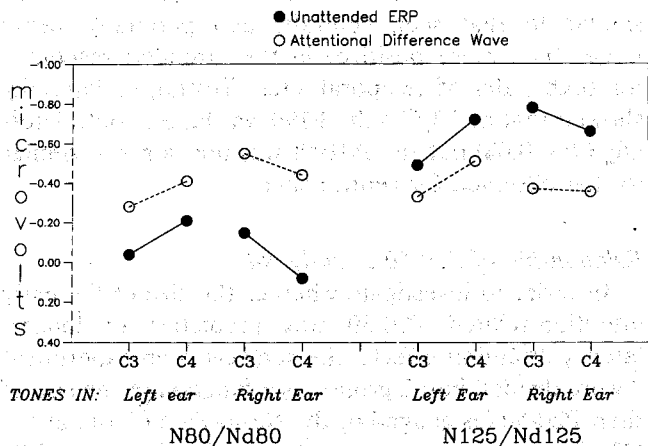

Fig. 5. Lateral asymmetry of the subcomponents of the unattended N1 wave and the corresponding subcomponents of the early Nd. Measures were mean amplitudes across 60–100 msec for the N80 and Nd80, and across 104–154 msec for the N125 and Nd125. Data from experiment 2.

group L subjects ($P < 0.01$), as was the total early Nd measured across the entire N1 latency range of 60–154 msec ($P < 0.01$). The Nd80 attention effect also appeared larger (by 0.22 μV) in group L, but this difference did not reach significance. None of the later ERP components or attention effects were different between the two groups.

ERPs to targets

The ERPs elicited by the less intense, deviant tones in these experiments are described in a separate paper (Woldorff et al. 1991) that focuses on the mismatch negativity wave (MMN) elicited by such tones. The basic findings can be summarized as follows: (1) attended target ERPs included large P300 waves (ca. 8 μV), whereas unattended targets (i.e., deviants on the unattended side) elicited essentially no P300 activity;

TABLE II

Effects of attention on longer-latency waves at midline and central sites (experiment 2) *.

Component	Site	Latency window (msec)	Attended (μV $\pm$ S.E.)	Unattended (μV $\pm$ S.E.)	Diff. (μV)	F ratio (df = 1, 15)	P value
N80	Fpz	60–100	0.07 ± 0.06	0.41 ± 0.05	−0.34	14.3	< 0.002
	Fz	60–100	−0.43 ± 0.07	0.13 ± 0.05	−0.56	29.2	< 0.001
	Cz	60–100	−0.75 ± 0.07	−0.15 ± 0.05	−0.60	43.4	< 0.001
	Pz	60–100	−0.58 ± 0.05	−0.25 ± 0.04	−0.33	19.8	< 0.001
	C3/C4	60–100	−0.50 ± 0.04	−0.08 ± 0.03	−0.42	26.8	< 0.001
N125	Fpz	104–154	−0.44 ± 0.07	−0.03 ± 0.06	−0.41	15.3	< 0.001
	Fz	104–154	−1.07 ± 0.07	−0.38 ± 0.06	−0.69	36.9	< 0.001
	Cz	104–154	−1.14 ± 0.07	−0.60 ± 0.05	−0.54	22.7	< 0.001
	Pz	104–154	−0.73 ± 0.06	−0.60 ± 0.05	−0.13	1.5	n.s.
	C3/C4	104–154	−1.05 ± 0.04	−0.66 ± 0.03	−0.39	19.2	< 0.001
P190	Fpz	170–224	0.27 ± 0.06	0.80 ± 0.07	−0.53	26.0	< 0.001
	Fz	170–224	0.55 ± 0.06	0.77 ± 0.06	−0.22	2.5	n.s.
	Cz	170–224	0.94 ± 0.07	0.60 ± 0.07	0.34	5.4	< 0.03
	Pz	170–224	0.34 ± 0.06	−0.04 ± 0.06	0.38	8.9	< 0.009
	C3/C4	170–224	0.68 ± 0.04	0.35 ± 0.04	0.33	11.8	< 0.004
N290	Fpz	270–390	−0.13 ± 0.07	0.60 ± 0.06	−0.73	24.1	< 0.001
	Fz	270–390	−0.52 ± 0.05	0.32 ± 0.05	−0.84	42.6	< 0.001
	Cz	270–390	−0.93 ± 0.05	0.04 ± 0.05	−0.97	68.6	< 0.001
	Pz	270–390	−0.64 ± 0.05	−0.31 ± 0.04	−0.33	11.7	< 0.004
	C3/C4	270–390	−0.55 ± 0.03	−0.03 ± 0.03	−0.52	32.2	< 0.001

* μV values are mean amplitudes over indicated latency windows. C3 and C4 sites are analyzed as a pair.

and (2) the unattended targets did elicit a small MMN (less than 1 μV), although it was markedly attenuated (by a factor of 4) relative to a similar negative wave elicited by attended targets. These results provided additional evidence that attention was highly focused upon the attend channel of tones in this study.

ERP subaverages based on previous events (experiment 2)

Removal of adjacent-ERP overlap. Fig. 7 (left column) displays uncorrected ERP subaverages for left-ear tones. Since these subaverages are based on differing preceding events, they are overlapped and differentially distorted by the ERPs to those events, as is evident in the pre-stimulus baselines. For example, the negative wave peaking at −70 msec in the attended

left-tone ERP in Fig. 7a (asterisk) is the residual, 'smeared-out' N1 elicited by preceding *attended* left-ear tones that occurred 120–220 msec before, whereas the smaller negative wave peaking near the same time point in the corresponding unattended wave form is the residual N1 elicited by preceding *unattended* left-ear tones occurring at those ISIs. In contrast, Fig. 7b shows a positive wave in both wave forms peaking at about −70 msec (asterisk), which is the residual P2 elicited by preceding left-ear tones that occurred at the longer previous ISIs. The distortion in Fig. 7c and d similarly results from overlap by ERPs to previous right-ear tones. In all these cases, the prior-response overlap continues well past the pre-stimulus period, differentially distorting the current wave forms. Any variation in the ERP to the current stimulus as a

TABLE III

Effects of attention on longer-latency components at temporal sites (experiment 2) *.

Component	Site	Latency window (msec)	Attended (μV $\pm$ S.E.)	Unattended (μV $\pm$ S.E.)	Diff. (μV)	F ratio (df = 1, 15)	P value
P100t	T3/T4	80–108	−0.20 ± 0.03	−0.19 ± 0.02	−0.01	0.1	n.s.
	T5/T6	80–108	−0.15 ± 0.03	−0.17 ± 0.02	0.02	0.3	n.s.
N135t	T3/T4	120–146	−0.54 ± 0.04	−0.38 ± 0.03	−0.16	9.4	< 0.008
	T5/T6	120–146	−0.33 ± 0.03	−0.30 ± 0.03	−0.03	0.2	n.s.
P190t	T3/T4	170–224	0.39 ± 0.03	0.11 ± 0.02	0.28	48.6	< 0.001
	T5/T6	170–224	0.17 ± 0.03	−0.10 ± 0.02	0.27	38.5	< 0.001

* μV values are mean amplitudes over indicated latency windows.
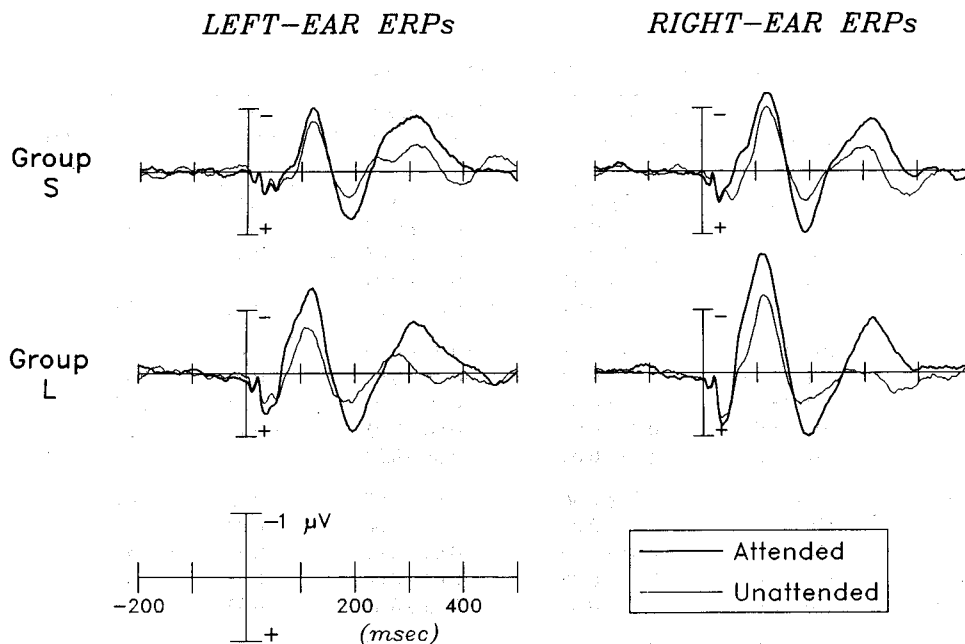
LEFT–EAR ERPs   RIGHT–EAR ERPs

Fig. 6. ERPs to attended and unattended tones from subjects in experiment 2 separated into two groups (each with N = 8) as a function of the size of their P20-50 attention effect. Group S subjects had small P20-50s, group L subjects had large P20-50s. Note that the group L subjects also had substantially larger attention effects in the N1 latency range.

function of the previous event would thus be severely confounded with this differential overlap.

By applying the Adjar technique, estimates of the previous-response overlap were obtained (Fig. 7e–h). Subtracting these from the corresponding subaverages yielded the corrected subaverages shown in Fig. 7i–l. Note that the pre-stimulus baselines have become much less distorted, indicating the accuracy of the estimation and removal of the overlapping previous ERPs.

As discussed in Woldorff (1989), the attended versus unattended comparison for each of these corrected subaverages is controlled for purely stimulus-specific ERP refractoriness, since the current and previous stimuli are physically identical for both attended and unattended ERPs. Thus, once prior response overlap is removed, comparisons of this type allow the study of attention effects as a function of stimulus sequence.

General features of the sequential interactions. Several general points were evident about the effects of stimulus sequence. First, the attended responses showed substantially more variation overall than did the unattended as a function of previous event. This is illustrated in Fig. 8, which shows the 4 types of attended left-tone ERPs at the C4 and T4 sites superimposed on each other, along with the 4 corresponding unattended ERPs. (Note that the unattended ERPs did show some variation, however, especially in the P190 component.) Second, the wave forms sorted by prior stimulus type and ISI revealed subcomponentry and complexity that tended to average out in the full

averages and therefore be more difficult to discern. Third, the effects of attention and of previous stimulus type (i.e., same ear vs. opposite ear) were generally stronger than the effects of previous ISI subrange.

Midlatency sequential effects. There were no significant interactions between attention and previous stimulus type or ISI in the midlatency range. Although the P20-50 attention effect (i.e., the Na-to-Pa enhancement with attention) tended to be larger when the preceding stimulus was in the opposite ear than when it was in the same ear, this interaction did not reach significance. However, overall Na-to-Pa amplitudes were larger when the preceding stimulus was in the opposite ear (C3/C4: $P < 0.001$; Cz: $P < 0.03$; Fz: $P < 0.007$), presumably reflecting the effect of stimulus-specific refractoriness. Na-to-Pa amplitudes also tended to be larger after the longer ISI, but this did not reach significance.

Longer-latency sequential effects: central and midline sites. Clear differences were observed between the attention effects for preceded-by-same-ear versus preceded-by-opposite-ear stimuli (Fig. 9 and Table IV). These subaverages show that the two major subcomponents of the early Nd attention effect at central and midline sites were differentially affected by previous stimulus type. In particular, the Nd80 was larger for preceded-by-opposite-ear stimuli, whereas the Nd125 was larger for preceded-by-same-ear. In addition, the interactions of these attention effects with ISI were different as a function of previous stimulus type (Fig.

ORIG UNCORRECTED
SUBAVERAGE
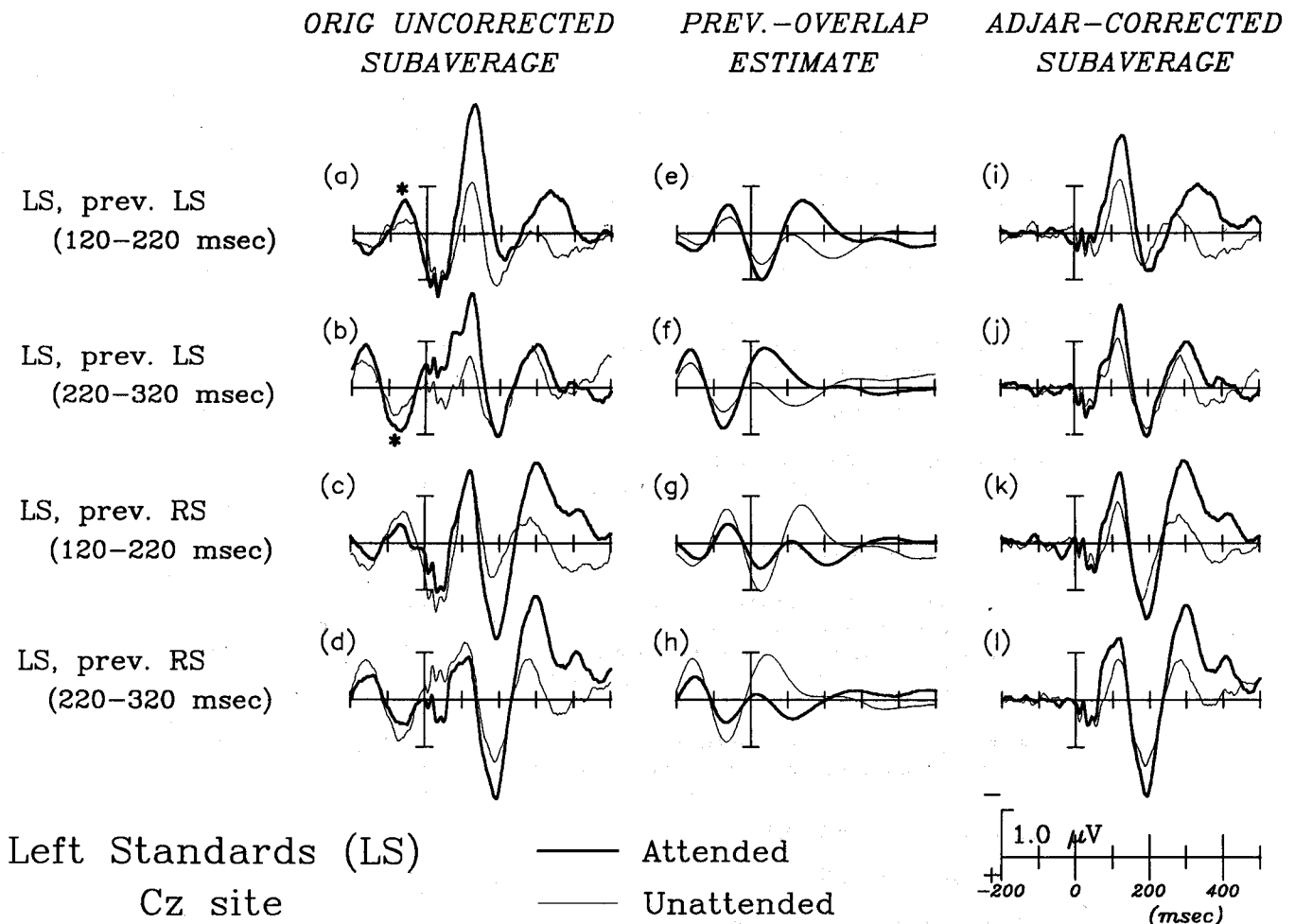
PREV.–OVERLAP
ESTIMATE

ADJAR–CORRECTED
SUBAVERAGE

Fig. 7. Removal of previous-response overlap from ERP subaverages (experiment 2). Left column shows the (grand averaged) ERP subaverages, before Adjar correction, for the attended and unattended left-ear standard tones, for each of 4 types of preceding events. Note the differential distortion from previous-response overlap. Middle column shows the estimates of the overlap, and the right column gives the corresponding corrected subaverages obtained by subtraction of these estimates. LS = left standard tone; RS = right standard tone.

10 and Table IV). For example, the Nd80 attention effect for preceded-by-opposite-ear tones was larger at the longer ISIs than at the shorter, whereas the Nd125 attention effect for preceded-by-same-ear tones was larger at the shorter ISIs than at the longer.

The Pd190 at central and posterior sites was larger for preceded-by-opposite-ear tones (Table IV and Fig. 9), as was the P190 itself (Figs. 7 and 8). At frontal sites the attention effects for both conditions were dominated by the long broad frontal negativity.

At central sites and at Pz, the Nd290 attention effect was also larger (i.e., more negative) for stimuli preceded in the opposite ear (Table IV and Fig. 9). The interaction of attention × previous type × ISI was significant at Fz, Pz, and central sites ($Ps < 0.002$), the pattern of effects being similar to that observed for the N80/Nd80 subcomponents.

Longer-latency sequential effects: temporal sites. At temporal sites, marked differences were observed in the ERP attention effects for stimuli preceded in the

opposite ear versus the same ear (Fig. 9 and Table V). The attention effect on ERPs to preceded-by-opposite-ear stimuli showed enhanced multiphasic activity that included the Pd100t and Nd135t peaks of the T complex, preceded by a smaller negative peak near 70 msec (Nd70t) and followed by the more widely distributed positivity at 190 msec (Pd190t) [5]. In contrast, the attention effect on the ERPs to preceded-by-same-ear tones was generally much smaller and nearly opposite in phase, consisting mainly of two broader negative waves in succession peaking at around 95 msec and 160 msec. In fact, the overall attention effect seen in the full averages at these sites was substantially attenuated because of mutual cancellation of these two different ERP patterns.

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[5] An attenuated version of the effect on the T complex was also picked up at the mastoids. This can be seen in inverted form in Fig. 9 at the site labeled Nc (non-cephalic referred to averaged mastoids).

TABLE IV

Sequential interactions: central and midline sites (experiment 2).

Component	Interaction	Site	Signif. level
N80	(attn)×(prev. stim. type)	Fpz	< 0.01
		Fz	< 0.01
	Meaning: attention effect negativity larger	Cz	n.s. (< 0.10)
	for preceded-by-opposite than for preceded-by-same.	Pz	n.s.
		C34	n.s.
	(attn)×(prev. stim. type)×(ISI)	Fpz	< 0.03
		Fz	< 0.001
	Meaning: attention effect negativity	Cz	< 0.008
	larger at longer ISIs for preceded-by-opposite, but	Pz	< 0.003
	larger at shorter ISIs for preceded-by-same.	C34	< 0.001
N125	(attn)×(prev. stim. type)	Fpz	< 0.001
		Fz	< 0.002
	Meaning: attention effect negativity larger	Cz	< 0.001
	for preceded-by-same than for preceded-by-opposite.	Pz	< 0.001
		C34	< 0.01
	(attn)×(prev. stim. type)×(ISI)	Fpz	n.s.
		Fz	n.s. (< 0.09)
	Meaning: attention effect negativity larger at	Cz	n.s. (< 0.10)
	shorter ISIs for preceded-by-same, but about equal	Pz	< 0.002
	at the two ISI subranges for preceded-by-opposite.	C34	< 0.003
P190	(attn)×(prev. stim. type)	Fpz	n.s.
		Fz	n.s. (< 0.06)
	Meaning: attention effect positivity larger	Cz	< 0.008
	for preceded-by-opposite than for preceded-by-same.	Pz	< 0.002
		C34	< 0.001
	(attn)×(prev. stim. type)×(ISI)	All sites	n.s.
N290	(attn)×(prev. stim. type)	Fpz	n.s.
		Fz	n.s. (< 0.06)
	Meaning: attention effect negativity larger	Cz	< 0.002
	for preceded-by-opposite than for preceded-by-same.	Pz	< 0.05
		C34	< 0.006
	(attn)×(prev. stim. type)×(ISI)	Fpz	n.s. (< 0.08)
		Fz	< 0.002
	Meaning: attention effect negativity	Cz	< 0.002
	larger at longer ISIs for preceded-by-opposite, but	Pz	< 0.002
	larger at shorter ISIs for preceded-by-same.	C34	< 0.001

As noted above, each of the attentional difference waves shown in Fig. 9 was derived in a way that controls for purely stimulus-specific refractory effects. However, since attention-related enhancement of the presumably exogenous T complex was only evident in the ERPs to preceded-by-opposite-ear stimuli, it was of interest to examine how refractoriness may have affected this complex. By taking the difference wave of the ERPs to attended tones preceded by a tone in the opposite ear minus the ERPs to attended tones preceded in the same ear, the stimulus-specific refractoriness of the attended responses could be examined (Fig. 11b). Note the strong similarity of this wave form to the *attentional* difference wave for preceded-by-opposite-ear stimuli (Fig. 11a). In contrast, the unattended ERPs were less sensitive to prior event type than the attended (see Fig. 8), and thus the analogous 'refractoriness' difference wave for the unattended ERPs showed little stimulus-specific refractoriness of the T complex (Fig. 11c).

A further breakdown of the refractory effects on the T complex of the attended responses can be seen in Fig. 12, which shows the difference waves calculated by subtracting the presumably most refractory attended response (preceded-by-same at short ISI) from progressively less refractory attended responses (preceded-by-same at long ISI, preceded-by-opposite at short ISI, preceded-by-opposite at long ISI). The T complex (along with the P190t) can be seen to increase in size with each successively less refractory response.

ATTENDED LEFT—EAR ERPs   UNATTENDED LEFT—EAR ERPs

C4

T4

−1 μV

−200   200   400

(msec)

··············· Prec'd by Left—Ear Tone (120—220 msec)
··············· Prec'd by Left—Ear Tone (220—320 msec)
———— Prec'd by Right—Ear Tone (120—220 msec)
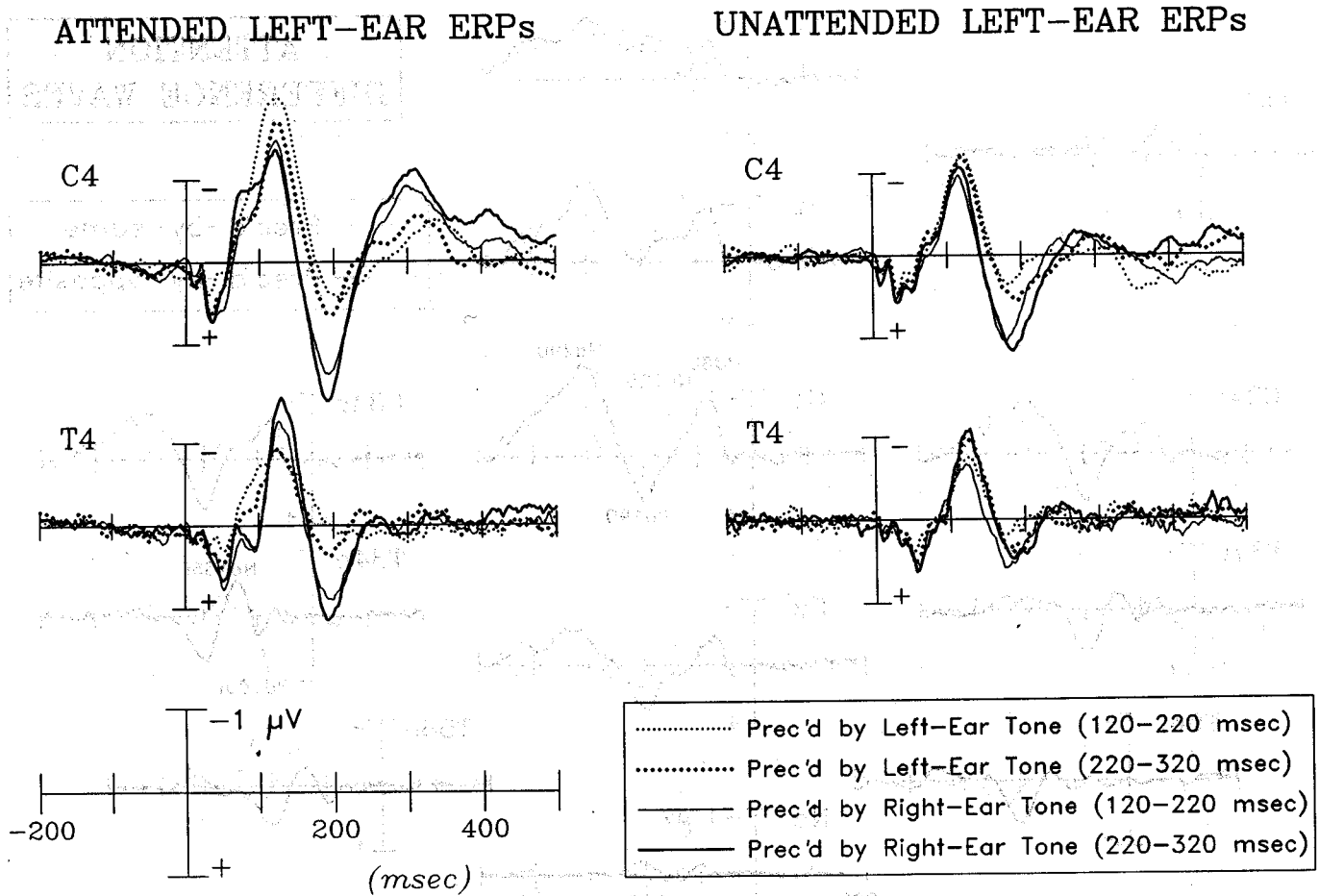———— Prec'd by Right—Ear Tone (220—320 msec)

Fig. 8. Adjar-corrected left-tone ERP subaverages as a function of previous stimulus type and ISI subrange. Superposition of the 4 attended and 4 unattended wave forms shows that the attended ERPs had considerably more variation as a function of sequence than did the unattended.

Target discrimination performance

Target discrimination accuracy (percentage correct) for both experiments 1 and 2 as a function of previous

stimulus type and ISI subrange is shown in Fig. 13. There was a strong effect of previous stimulus type, in that performance was less accurate for targets pre-

TABLE V

Sequential interactions: temporal sites (experiment 2).

| Component	Interaction	Site	Signif. level
P100t	(attn)×(prev. stim. type)	T3/T4	< 0.001
		T5/T6	< 0.001
	Meaning: attention effect is greater positivity for preceded-by-opposite but greater negativity for preceded-by-same.		
N135t	(attn)×(prev. stim. type)	T3/T4	< 0.001
		T5/T6	< 0.004
	Meaning: attention effect is greater negativity for preceded-by-opposite but is absent or slightly positive for preceded-by-same.		
P190t	(attn)×(prev. stim. type)	T3/T4	< 0.001
		T5/T6	< 0.001
	Meaning: attention effect positivity is larger for preceded-by-opposite than for preceded-by-same.		
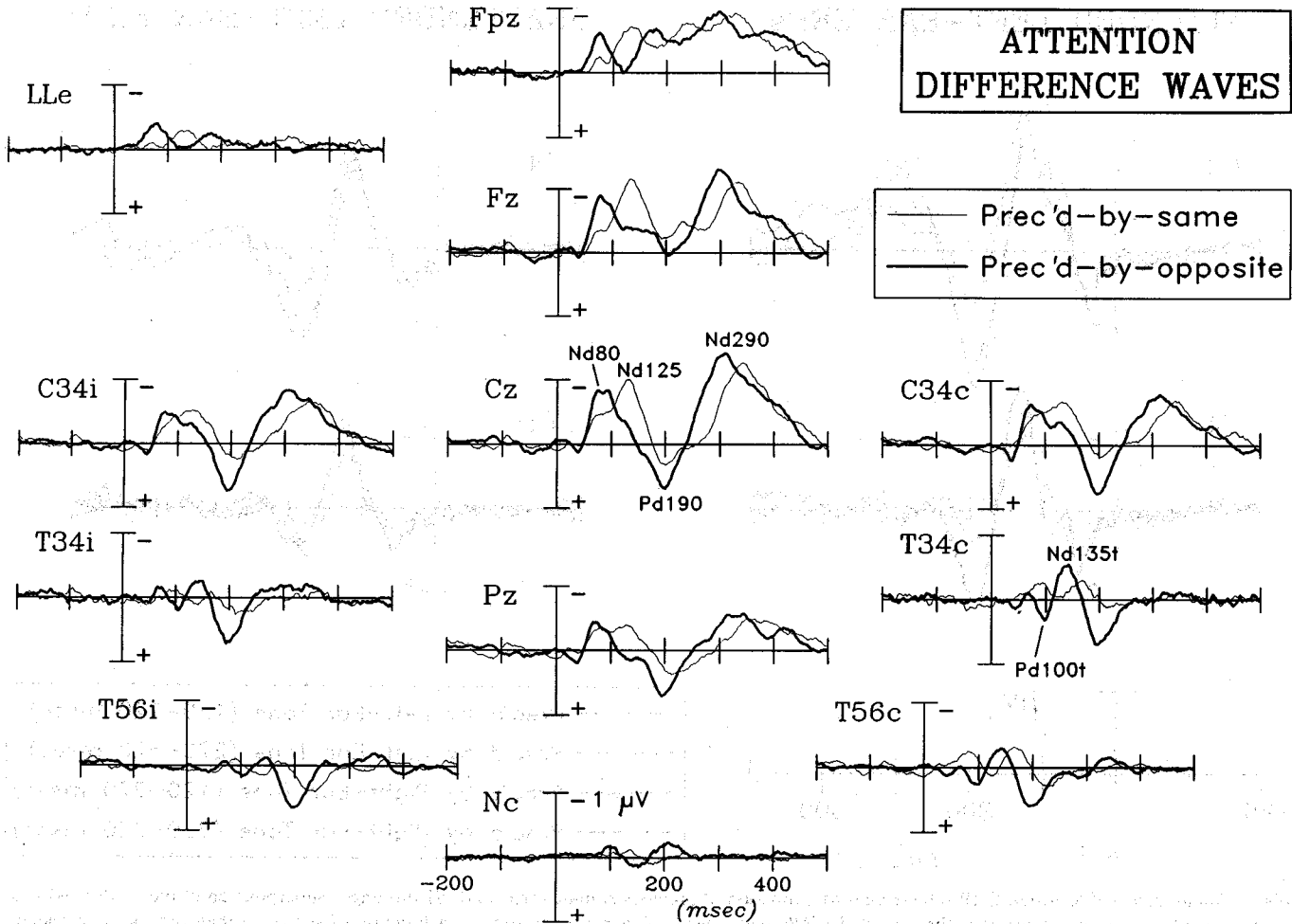
Fig. 9. Attentional difference waves (attended ERP minus unattended ERP) for tones preceded in the same ear versus preceded in the opposite ear, collapsed across ear of stimulation. For lateral sites, 'c' indicates the hemisphere contralateral to the stimulated ear, 'i' indicates the ipsilateral site. Reference for all sites is the algebraic average of the mastoids.

ceded by stimuli in the same ear than for those preceded by stimuli in the opposite ear ($P < 0.001$ in each experiment). There was also a main effect of previous

ISI, with reduced accuracy when the preceding stimuli were at the shorter ISIs ($P < 0.001$ in each experiment). There was an interaction in this, however, with most of
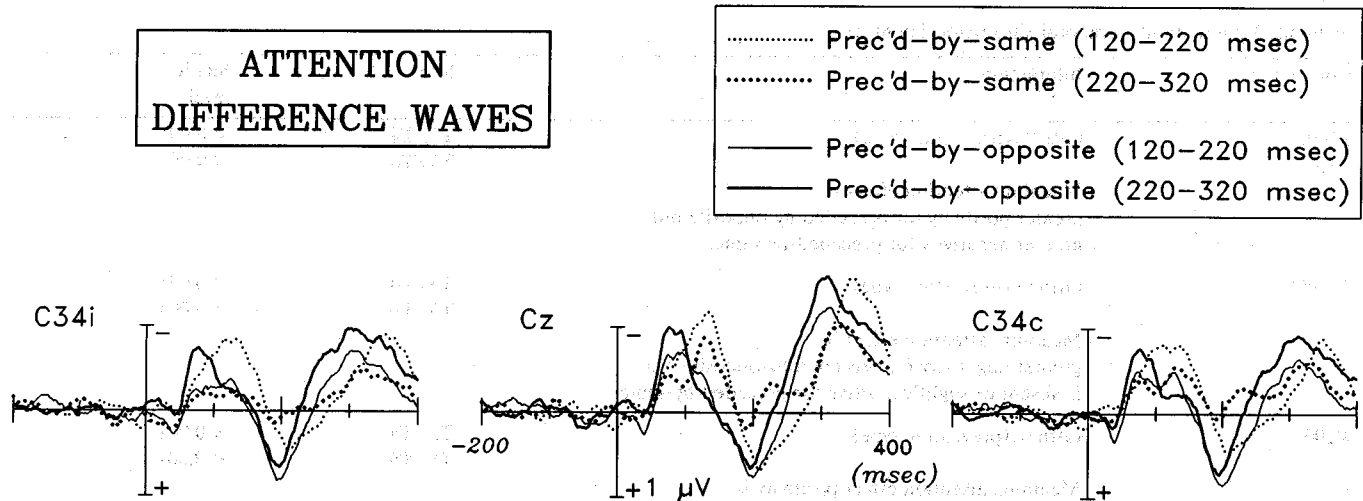

Fig. 10. Attentional difference waves at central sites as a function of both previous stimulus type and ISI subrange, collapsed across ear of stimulation. For the lateral sites, 'c' indicates the hemisphere contralateral to the ear of stimulation, and 'i' indicates ipsilateral.
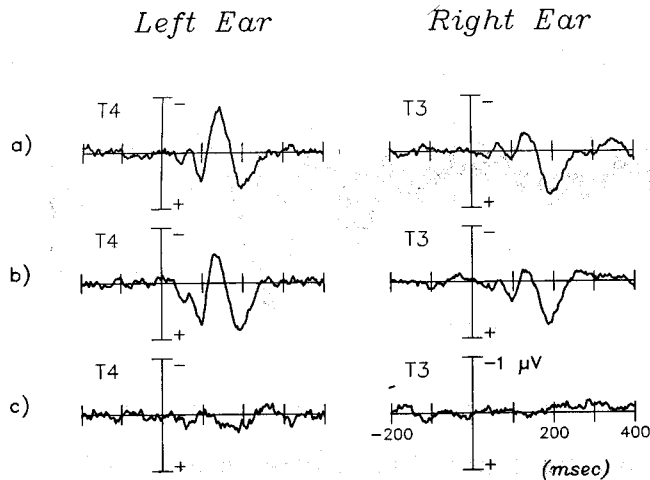
Fig. 11. Selected ERP difference waves from hemisphere contralateral to stimulated ear showing interaction of attention and refractoriness on the T complex. a: attentional difference waves (attended ERP minus unattended ERP) for preceded-by-opposite-ear tones, showing a large modulation of the T complex. b: 'refractoriness' difference waves for attended tones as a function of previous stimulus type (ERP to attended preceded-by-opposite-ear tones minus ERP to attended preceded-by-same-ear tones). Note the strong similarity to the wave forms in a. c: analogous 'refractoriness' difference waves for unattended tones as a function of previous stimulus type. Note that these show little stimulus-specific refractoriness of the T complex.

the ISI effect occurring for the preceded-by-same-ear targets. In fact, in the second experiment there was essentially no difference as a function of ISI for targets preceded in the opposite ear whereas targets preceded in the same ear had a large difference ($P < 0.001$ for the interaction) [6].

Reaction times showed relatively few effects of stimulus sequence, probably due to the instructions to the subjects having emphasized accuracy over speed. There was a small main effect of ISI in both experiments (experiment 1: $P < 0.01$; experiment 2: $P < 0.05$), with subjects responding slightly faster for the longer ISIs (experiment 1: 515 vs. 529 msec; experiment 2: 522 vs. 531 msec).

[6] The analysis of false alarm responses (see footnote 2) revealed no effect of prior event type or ISI upon the likelihood of making a false alarm to an attended standard tone. Thus, the variations in percent correct as a function of sequence were not due to an effect on response bias but rather can be interpreted as being due to sequential variations in perceptual discriminability.

Discussion

In the present experiments stimulus and task parameters were optimized to enhance the selective focusing of attention and facilitate the engagement of early stimulus selection. Under these conditions the effects of attention were found to be complex and involve multiple components of the auditory ERP.

Midlatency attention effects

The earliest attention effect observed in these experiments was a small enhancement of positivity (the P20-50) in the midlatency range for attended-channel stimuli. The present analysis ruled out the possibility that this early attention effect was an artifactual result of differential overlap from previous responses on the attended and unattended ERPs by showing that the P20-50 was still present after the residual overlap from preceding ERPs was removed.

Several other potential sources of artifact can also be ruled out. It is unlikely that the P20-50 was a result of myogenic contamination from the post-auricular muscle reflex (PAR) because: (1) subjects were pre-screened to reject those with appreciable background muscle activity or discernible evoked muscle responses, (2) the central scalp distribution and wave shape of the P20-50 were inconsistent with evoked PAR activity (Picton et al. 1974), and (3) a recent study by Hackley et al. (1987) using a very similar paradigm but with conditions optimized to elicit and record evoked PAR activity found no direct effect of attention on the PAR. The possibility that the P20-50 effect was a result of differential activation of the middle ear muscles (MEMs) can also be ruled out for two reasons: first, the BERs did not change with attention (Woldorff et al. 1987), and second, MEM contraction has limited effects on the tone pips in the frequency range used in these experiments (Møller 1974). Finally, since the attended and unattended stimuli were presented randomly, subjects had no information to help them predict what the next stimulus would be, thereby precluding differential phasic preparation for the two types of stimulus (Näätänen 1967, 1975). Therefore, the very early onset of this effect (20 msec) provides strong evidence for early selection theory (reviewed in Johnston and Dark 1982, 1986; Kahneman and Treisman 1984), which asserts that stimuli can be selected for further processing before full analysis and perception has occurred. This selective tuning or biasing is presumably accomplished by way of a tonically maintained pre-stimulus set.

The latency of the P20-50 effect was near that of the exogenous Pa component, a wave that is likely to reflect, at least in part, early activity in primary auditory cortex (see Introduction). Although the central/frontal distribution of the P20-50 effect bore some

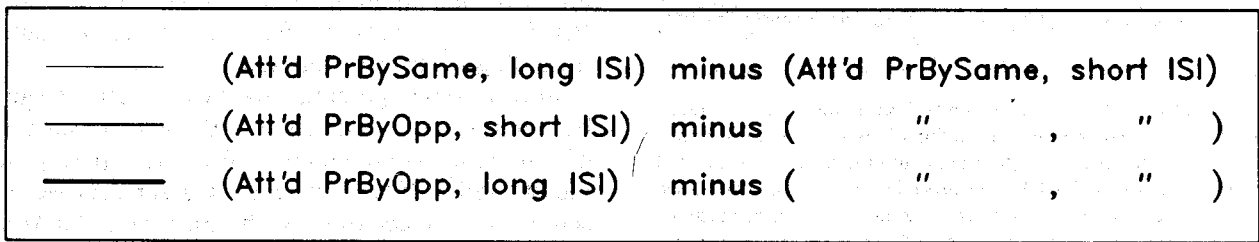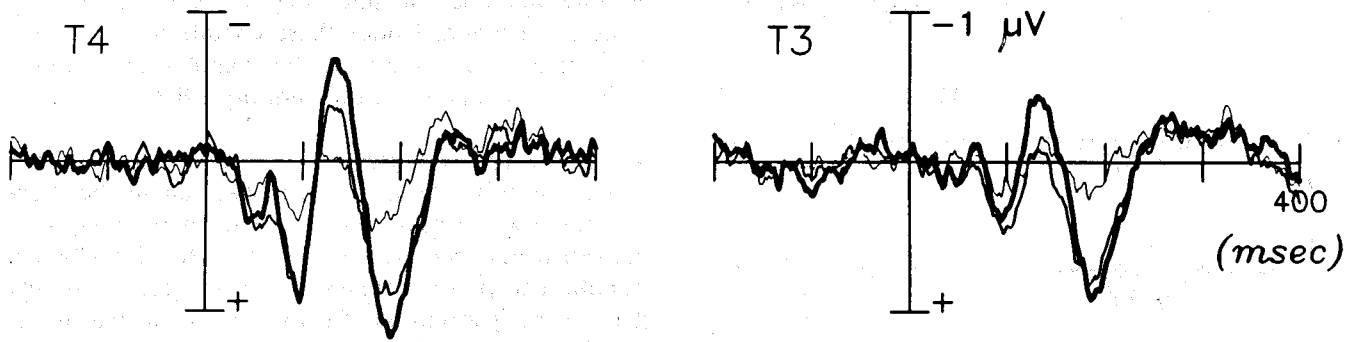# *Left Ear*   # *Right Ear*

Fig. 12. 'Refractoriness' difference waves for attended responses at temporal sites. These were calculated by subtracting the presumably most refractory attended ERP (that elicited by attended preceded-by-same-ear tones at short ISIs) from decreasingly less refractory attended responses. Note that the T complex and the P190t both increase in size in the successively less refractory ERPs.

similarity to that of the Pa wave itself, it is not clear whether this attention-related positivity included an actual enhancement of the Pa or not. Regardless, its onset at this latency strongly suggests that selective processing of attended versus unattended inputs in humans can begin by the level of primary or secondary auditory cortex. This would be consistent with monkey studies showing changes (with a latency as early as 20 msec) in the firing of single units in primary auditory

cortex as a function of selective attention to one ear during dichotic presentation of tones (Benson and Hienz 1978).

Subjects who showed larger P20-50 attention effects also produced enhanced attention effects in the N1 latency range. This relationship was unlikely to have resulted simply from individual differences in skull thickness, because neither the P190 nor the N290 nor the attention effects on these later components varied as a function of the size of the P20-50. This suggests 2 main possibilities: (1) those subjects with larger P20-50s were employing a more effective early selection, which was reflected in both the midlatency and N1 latency ranges, or (2) the P20-50 potential field happened to be manifested more distinctly on the scalp in certain subjects because of particular characteristics (e.g., orientation) of its neural generator(s), and these characteristics were shared by generators active in the N1/early Nd latency range. Regardless of which alternative may be correct, the correlation of the relatively small P20-50 wave with the more robust N1 attention effect reinforces the hypothesis that an early selection process can operate prior to 20 msec post stimulus.
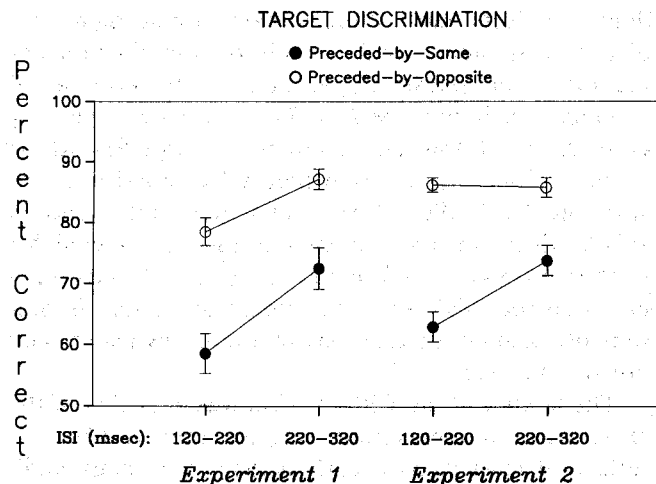

Fig. 13. Target discrimination accuracy as a function of previous stimulus type and ISI subrange.

Longer-latency attention effects

The attentional difference waves at frontal sites consisted mainly of a broad negativity lasting several

hundred milliseconds (Fig. 4). This prolonged wave seemed likely to be endogenous, bearing little resemblance to the more phasic waves seen in the unattended wave forms. In contrast, the attentional difference waves at central and parietal sites were distinctively triphasic, with the polarities and latencies of the 3 phases being highly similar to those of the original attended and unattended ERPs themselves (Figs. 2 and 3). It is conceivable that this triphasic attention effect was entirely endogenous as well, and that the wave shape similarity and close temporal correspondence with the N1, P2, and N2 components seen in the unattended wave forms were coincidental. However, a more plausible interpretation of this data pattern is that at least some of the exogenous components (or subcomponents) of the auditory evoked potential were modulated by the highly focused attentional conditions in these experiments.

Another important similarity at central sites between the exogenous waves and the attentional difference wave was that they were both larger contralaterally in the N1 latency range. A contralateral preponderance of the N1 itself has been widely reported (see Näätänen and Picton 1987), but the laterality of the early Nd has been little studied. Giard et al. (1988) found a small but significant contralateral preponderance for the early Nd, whereas Woods and Clayworth (1987) reported a small, non-significant, lateral asymmetry. In the current study, the lateral asymmetry of the early Nd (both the Nd80 and the Nd125) was more pronounced and highly significant. A more fine-grained correspondence between the attentional difference wave and the ERPs in the N1 latency range was also evident in the full average wave forms, in that they both included two subdeflections (at 80 and 125 msec) that lined up closely in time.

Topographical comparisons between attentional difference waves and the presumably exogenous waves of the original ERPs have been reported in previous studies (Hansen and Hillyard 1980; Alho et al 1986a; Woods and Clayworth 1987; Giard et al. 1988). In some of these cases, scalp distributional differences were used as evidence that the attention wave 'is caused by a separate, endogenous negativity' (Alho et al. 1986a). Such distributional differences must be interpreted cautiously, however, considering the substantial evidence that these longer-latency deflections (e.g., the N1, the early Nd) do not reflect unitary phenomena arising from a single source (e.g., see Näätänen and Picton 1987, and below). Thus, if some differences are observed between the distribution of an attentional difference wave and that of an original ERP wave to which it is being compared, one can correctly infer that the *entire set* of generators producing activity in the one wave form at the latency measured is not identical

to the entire set producing activity in the other wave form at that latency. It does not prove, however, that the two waves or deflections do not share any generators/subcomponents at all. For example, suppose that the ERP attention effect does indeed include an enhancement of one particular subcomponent of the exogenous N1 wave. To the degree that there is additional, concurrent activity from any other generators in either the attentional difference wave or the exogenous wave (which appears likely to be the case), the distributions of the two waves may differ.

In view of the complex ways that multiple sources may contribute to ERP distributions across the scalp at a particular latency, it may at times be advantageous to focus on the similarities between the distributions and wave form properties of ERPs, rather than just on the differences. For example, if two ERP deflections are similar in a number of characteristics, such as wave shape, lateral asymmetry, onset latencies, peak latencies, etc., either broadly or over a circumscribed scalp area, it is reasonable to consider the possibility that these similarities may arise from the sharing of one or more common generators. In the present study, for example, the close temporal overlap and other similarities at central sites between the attentional difference wave forms and the exogenous ERPs suggests that such similarity was not simply due to coincidence. Rather, we consider that a more plausible explanation may be that a substantial portion of the attention effects seen at these sites in this study reflects direct modulation of exogenous components by attention.

In contrast, those studies in which the attention-related ERPs appeared to be largely endogenous employed very different stimulus parameters from those used here. In particular, prolonged 'processing negativities' or Nds with predominantly fronto-central distributions have generally been found in experiments where the channels were less easily discriminated (such as two different frequencies presented binaurally) and/or where the rate of stimulus presentation was much slower (e.g., Näätänen et al. 1978, 1980; Hansen and Hillyard 1980, 1984). It has been proposed (Näätänen 1982; Alho et al. 1986b, 1987) that the processing negativity is an endogenous wave, the size and duration of which reflect the degree of matching of a stimulus to an attentionally controlled template. When stimulus and task parameters are not conducive to early selection between stimulus channels, a broad endogenous negativity of this type may be the principal attention effect elicited. The data from the present study suggest, however, that when parameters are optimized for the selective focusing of attention, the attention effect may include *both* a prolonged frontal endogenous negativity *and* a modulation of some of the major subcomponents of the exogenous waves.

The effects of stimulus sequence on the ERPs

The multicomponent nature of both the auditory evoked potentials and the attention effects became more apparent in the sequential analyses. The first point of interest was that the attended ERPs showed substantial variation as a function of sequence, whereas the unattended responses, which were considerably smaller, changed relatively little. Presumably, the changes in the attended ERPs reflected variations in stimulus processing that depended on the previous event. In contrast, a possible explanation for the unattended responses being smaller and less variable would be that they were tonically suppressed to a minimal level by a highly selective focusing of attention toward the attended stimuli at the expense of the unattended. Such an explanation would be consistent with subjects' reports that they had little awareness of the unattended stimuli and with the complete absence of P300 waves to the deviant stimuli on that side.

Overall, the attention effects on ERPs to preceded-by-opposite-ear tones tended to be larger than those for preceded-by-same-ear tones, especially for the earlier components. The most clear example of this was seen in the T complex, which was much larger in the attention effect for preceded-by-opposite tones. In addition, the initial phase of the early Nd (i.e., the Nd80) was larger for preceded-by-opposite tones, as was the Pd190, the Pd190t, and the Nd290, and the P20-50 tended to be so. The only attention-sensitive component that violated this pattern was the Nd125, which was larger for stimuli preceded by tones in the same ear.

In their detailed review, Näätänen and Picton (1987) considered the auditory N1 wave to be made up of several exogenous subcomponents (components 1-3), which they called 'true' N1 subcomponents, and several endogenous subcomponents that depend on the subject's state (components 4-6). It is unclear as to how the various central/midline N1 subcomponents observed in the present study (i.e., N80, Nd80, N125, Nd125) would fit into this classification scheme. Both the N80 and the N125 appeared to be exogenous subcomponents (being evident even in the unattended ERPs), whereas the temporally coincident Nd80 and Nd125 formed part of the attention effect; nonetheless, all four of these waves resembled Näätänen and Picton's component 1 in having fronto-central maxima with a contralateral predominance. One possible explanation for this might be that component 1 is itself made up of two subcomponents, both of which can be enhanced by attention, but which reflect different forms of processing and interact differently with stimulus sequence and ISI.

The specific ways in which these subcomponents were influenced by stimulus order may suggest something about their nature and function. The Nd80 was larger when the preceding stimulus was in the opposite ear than when it was in the same ear, and largest of all when the preceding stimulus was in the opposite ear at the longer ISIs. This suggests that refractory period effects may have played a role at these high rates of stimulation, despite the fact that in each case the Nd80 was part of an attentional difference wave formed by subtracting ERPs to two physically identical stimulus sequences. In particular, since the unattended responses changed relatively little in the N1 latency range, the variation in Nd80 activity as a function of sequence was due primarily to corresponding changes in the N80 of the attended responses. Thus, refractoriness could have played an interactive role in these effects by limiting the degree to which attention could enhance the N80 in the attended responses.

In contrast to the Nd80, the Nd125 variation as a function of sequence was opposite to what would be expected from refractory influences upon the attended responses, being larger for a stimulus preceded in the same ear than preceded in the opposite, and more so at the shorter ISIs. Such variations would appear to be correlated with the strength of the short-term sensory memory of the preceding attended stimulus. This suggests that the Nd125 might reflect an enhanced processing that is heavily influenced by the strength of the sensory representation of the attended-channel cues, perhaps resulting in improved channel selection by means of filtering or gating or by a more precise matching of the current stimulus to an attentionally controlled template (e.g., Näätänen 1982, 1988). An enhanced Nd (measured across 100-300 msec) for tones preceded in the same versus opposite ear was also observed by Hansen and Hillyard (1988), who interpreted the effect in a similar manner (also see Woods and Knight 1986).

At temporal sites, the influence of previous stimulus type upon the Pd100t/Nd135t attention effect was striking. The wave shape, latencies, and distribution of these components in the preceded-by-opposite attentional difference waves were strongly suggestive of the exogenous T complex described by Wolpaw and Penry (1975). They proposed that at temporal sites a biphasic wave consisting of positive peak at about 100 msec (Ta) followed by a negative peak at about 150 msec (Tb) was superimposed on an attenuated N1-P2 vertex response. They further proposed, based on properties such as contralateral predominance and localization to temporal sites, that the T complex resulted from activity in secondary auditory cortex in the superior temporal gyrus. Such a biphasic wave arising from a radially oriented dipole source in the lateral temporal lobe was also derived through dipole modeling by Scherg and Von Cramon (1986). Additional support for a lateral temporal source of this scalp activity comes from intracranial recordings by Celesia (1976) and McCallum

and Curry (1979, 1980). This complex was termed component 2 by Näätänen and Picton (1987).

In the present data, little or no T complex was discernible in the unattended wave forms, nor was it easily visualized even in the attended ones, because of its superposition with the larger, broadly distributed N1-P2 components. This complex was clearly evident only in the attentional difference waves for preceded-by-opposite stimuli and in the 'refractory difference waves' for attended responses (Figs. 11 and 12). Indeed, the striking similarity of this distinctive, multiphasic pattern of activity in the attentional and refractory difference wave forms suggests that attention and refractoriness were affecting the same exogenous components.

According to this view, the strong suppression of T complex activity to unattended-channel tones would be attributable to a combination of inattention to those stimuli plus a high degree of refractoriness at these high stimulus rates. Similarly, this complex may have been greatly reduced in response to the *attended* preceded-by-same-ear tones due to the T complex generators being too refractory to be enhanced because an identical stimulus in the attended channel had occurred so recently. Thus, as suggested above for the N80/Nd80, refractory effects may have limited the degree to which attention could enhance this presumably exogenous sensory-processing activity.

Effects of sequence on target discrimination performance

At first glance, the effects of stimulus sequence on target discrimination performance might seem unexpected. If the stimulus prior to a target tone was a standard tone in the same ear, one might expect that the perceptual 'template' for comparison would be stronger, and the target discrimination therefore more accurate, particularly at shorter ISIs. However, the results were just the opposite: discrimination performance for targets preceded in the same ear was significantly worse than for targets preceded in the opposite ear, and it was least accurate for targets preceded in the same ear at the shorter ISIs. This pattern of sequence effects suggests that the stimulus presentation within the attended channel may have sometimes been so rapid that the stimulus processors were too refractory to adequately perform the standard/target discrimination. Moreover, this sequential variation in performance paralleled that seen for the attention effects on several of the exogenous ERP components (e.g., T complex, N80, P190) which, as described above, also suggested that refractoriness limited stimulus processing within the attended channel.

In this framework, we propose the following account for the effects of stimulus sequence in these experiments. When the current and previous stimuli were in the same channel and the ISI between them was quite short, considerable refractoriness of processing resulted. If they were attended, this refractoriness limited the degree to which attention could boost the sensory processing of the current stimulus. This effect, which was reflected in limited enhancement of various of the exogenous ERP components, also resulted in impoverished information for the standard/target discrimination and thus in diminished task performance. The more recent the previous same-ear stimulus, the greater these effects. In contrast, when the current stimulus was attended and the previous stimulus had occurred in the opposite ear, the sensory processors were not so refractory and could be boosted by attention. This was reflected in larger exogenous components in the ERPs to the attended preceded-by-opposite stimuli and in better discrimination between the targets and standards for these stimuli.

An additional factor that may have accounted for some of the performance variation found in these experiments is the phenomenon of 'loudness enhancement' described by Elmasian and associates (Galambos et al. 1972; Elmasian and Galambos 1975; Elmasian et al. 1980). These researchers found that when one tone burst (S1) preceded another (S2) by a short ISI (typically 100 msec) the perceived loudness of S2 was enhanced if S1 was more intense and, to a lesser extent, decreased if it was less intense. These effects were seen at ISIs as long as 400 msec and were found to be greater if S1 and S2 were presented to the same ear and were similar in frequency content. In the present experiments, with ISIs of 120–320 msec, the target tones in each ear were identical to the standard tones in that ear except for having a lower intensity. Thus, when preceded by a standard tone in the same ear, targets may have been perceived as louder (i.e., closer to the standard), thereby making them more difficult to discriminate.

Note that the two explanations presented above for the effects of sequence on target discrimination are not mutually exclusive. Thus, when an attended target stimulus is preceded very recently by a standard tone in the same ear, not only may refractoriness limit the attentional enhancement of sensory-processing activity important for perceptual analysis of the target, but loudness enhancement may bias that analysis such that the target intensity is perceived as closer to that of the standard. Both of these effects would tend to reduce target discriminability.

In summary, the present study shows that selective auditory attention can affect what is generally considered exogenous sensory-processing activity and that these ERP modulations are paralleled by variations in perceptual discrimination accuracy. These relationships were evident under conditions where the differential processing of attended and unattended stimuli began by 20 msec post stimulus. Such a combination of

results provides strong support for the early selection hypothesis that attention can serve to selectively bias or gate stimulus processing before full perceptual analysis has occurred. Other attention-related components elicited in this selective listening task, however, appeared to be primarily endogenous. Further research is necessary to disentangle the exogenous and endogenous effects and to determine how they relate to each other and to perceptual processes.

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