Combined Use of Microreflexes and Event-Related Brain Potentials as Measures of Auditory Selective Attention

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ABSTRACT

Two versions of a selective listening experiment were conducted in an attempt to specify the level of the nervous system at which selective attention first influences auditory information processing. Post-auricular reflexes (PARs), prepulse inhibition of reflexes, and the N1 component of the event-related potential (ERP) were measured concurrently to assess auditory processing in the hindbrain, midbrain, and forebrain, respectively. Sequences of intense, reflex-eliciting tones were presented to the two ears in random order and at a rapid rate as subjects listened to a designated ear to detect rare tones of slightly lower intensity. The ERPs showed the typical enhancement of early and late negativity (Nd) to attended ear tones, with the early Nd overlapping the evoked N1 component. Although there was an overall effect of attention direction on the efferent limb of the post-auricular reflex, no effect of selective attention on the afferent limb was observed. A selective sensory attentional effect was found for prepulse inhibition of the post-auricular reflex: Inhibition of PAR amplitude was enhanced when the immediately preceding tone was in the attended ear relative to when it was in the unattended ear. These results, together with findings from prior studies of reflexes and ERPs, indicate that evoked auditory activity in the lower brainstem is obligatory and invariant with attention, whereas later activity mediated in the upper brainstem can be modulated by attention.

DESCRIPTORS: Selective attention, Automaticity, ERPs, Auditory brainstem reflexes.

There has been a long-standing controversy about how early in auditory processing selective attention first exerts an influence (reviewed in Johnston & Dark, 1986; Hillyard & Kutas, 1983). This has been debated both on psychological levels (e.g., early vs. late selection) and on neurophysiological levels (peripheral vs. central gating). Neurophysiological studies in humans have generally found that auditory transmission through the brainstem, as indexed by the brainstem evoked potentials, is unaffected by attention (Picton & Hillyard, 1974; Picton, Campbell, Baribeau-Braun, & Proulx, 1978;

Woods & Hillyard, 1978; Woldorff, Hansen, & Hillyard, in press). Although there have been some reports of attentional modulation of these early evoked potentials (Lukas, 1980, 1981), these have not been consistently replicated (Picton, Stapells, & Campbell, 1981; Lukas, 1982). In contrast, studies of neuromuscular reflexes have provided more consistent evidence for attentional effects on early auditory processing. For example, paying attention to reflex-eliciting sounds resulted in shortening of the latency of the startle eyeblink (ca. 40 ms), a reflex requiring only brainstem structures (Hackley & Graham, 1983, 1987; reviewed by Anthony, 1985). A second mode of reflex activity mediated in the brainstem, the "prepulse inhibition" of a reflex by a prior stimulus, can also be modulated by selective attention directed toward or away from the prior stimulus (Balaban, Anthony, & Graham, 1985; DelPezzo & Hoffman, 1980; Hackley & Graham, 1987).

Recordings of longer latency event-related brain potentials (ERPs) show a variety of attention effects on auditory processing, including an enhanced negativity that onsets as early as 50–60 ms, overlaps the evoked N1 component, and may extend for hundreds of milliseconds (for reviews see Donald, 1983; Hillyard & Kutas, 1983). This attention-re-

lated negativity (termed "processing negativity" or "Nd") is generally attributed to cortical sources, although there is controversy over whether the Nd consists in part of an amplitude modulation of the N1 wave or is a completely separate, endogenous component (Hillyard, 1981; Kaufman, Curtis, Luber, & Williamson, 1986; Näätänen, 1982, 1985). More recently, evidence for modulation of auditory mid-latency components in the range of 20–50 ms has been obtained (McCallum, Curry, Cooper, Pocock, & Papakostopoulos, 1983; Woldorff et al., in press). At least some of these components also appear to be of cortical origin, with likely generators in or near primary auditory cortex (Celesia, 1976; Kileny, Paccioretti, & Wilson, 1987; Kraus, Özdamar, Hier, & Stein, 1982). Thus, while brainstem ERP recordings indicate stability of processing through wave V (6 ms), mid- and long-latency ERP recordings indicate attentional modulation of processing by 20–50 ms. The reflex data further indicate that some forms of attentional modulation prior to 40–50 ms may take place subcortically, presumably by means of a bias in afferent pathways preset in advance of stimulus arrival by higher centers exerting centrifugal control (see below). These various levels of auditory processing are illustrated schematically in Figure 1.

The present study combines recordings of auditory evoked reflex activity and ERPs within the same dichotic selective listening task, with the major aim of further delineating the anatomical/physiological level at which attention first operates in auditory processing. The principal reflex to be evaluated is the post-auricular reflex (PAR), which is shorter in latency (onset at 10–12 ms) than the startle blink reflex and is mediated by a different pathway. Direct modulation of the post-auricular reflex by selective attention would implicate centrifugal influences on auditory processing prior to the midbrain. The paradigm also allowed investigation of reflex modulation by prior stimuli that may represent a form of prepulse inhibition, a phenomenon that does not depend upon structures higher than the midbrain (Davis & Gendelman, 1977).

### Direct Modulation of Reflexes by Attention

Studies of direct reflex modulation by selective attention exploit the fact that some reflexes have multiple afferent limbs converging on a common central-efferent limb. By comparing the effects of attending to or away from reflex-eliciting stimuli for reflexes with different afferent limbs, any modulatory effects can be localized to a pre-convergence segment of the reflex arc (Anthony & Graham, 1983, 1985; Balaban, Anthony, & Graham, 1985; Cohen, Cranney, & Hoffman, 1983; Hackley & Graham,

1983, 1987). This method was employed in a recent experiment by Hackley and Graham (1987). On each trial, subjects received an intense, blink-eliciting tone pip 1–4 s after a visual warning stimulus. The tones were presented unpredictably to either the left ear, right ear, or to both ears simultaneously (perceived at the midline) and differed in pitch at the three locations. Tone durations were 50 ms on a random half of the trials and 75 ms on the other trials. Subjects made an unspeeded duration judgment of tones in the designated location-pitch "channel" and ignored the other channels. In accordance with predictions that attention can produce a preset bias in selected auditory pathways, the latency of the blink (ca. 50 ms) was speeded when attention was directed to the reflex-eliciting tone channel relative to when it was directed away; this reflex facilitation averaged 1.6 ms and was replicated in two additional groups. A tendency toward magnitude facilitation was also observed. These effects held only for lateral stimuli.

Attentional Modulation of Prepulse Inhibition

Prepulse inhibition of reflex magnitude is a phenomenon in which a prestimulus, which may itself be too weak to elicit a reflex, inhibits the magnitude of the response to a subsequent eliciting stimulus occurring after an appropriate interval, 30–400 ms in the case of blink. The effect does not involve conditioning, masking, or middle-ear muscle contraction, does not require that prepulse and eliciting stimuli be in the same modality, and, like startle itself, requires only brainstem structures (see Hoffman & Ison, 1980, for a review). A more intense prestimulus produces greater inhibition than does a weak prestimulus (Sanes & Ison, 1979). Insofar as attention acts to increase the effective stimulus intensity, it might be expected that an attended prestimulus would produce greater inhibition of the reflex elicited by a subsequent stimulus than would an ignored prestimulus. This is the pattern of results that has been generally observed (Balaban et al., 1985; DelPezzo & Hoffman, 1980; Hackley & Graham, 1987; Ison & Ashkenazi, 1980).

A second experiment by Hackley and Graham (in press) used this method in a design similar to that described above. Subjects again made unspeeded judgments of the duration of tones presented at the designated location and ignored the other two positions. However, in this experiment the tones were too weak to elicit a blink themselves and were followed after 63 ms by a task-irrelevant, blink-eliciting airpuff to the right orbital region. Comparison with trials on which no prepulse was presented allowed assessment of the overall amount of inhibition generated. It was predicted that if attention
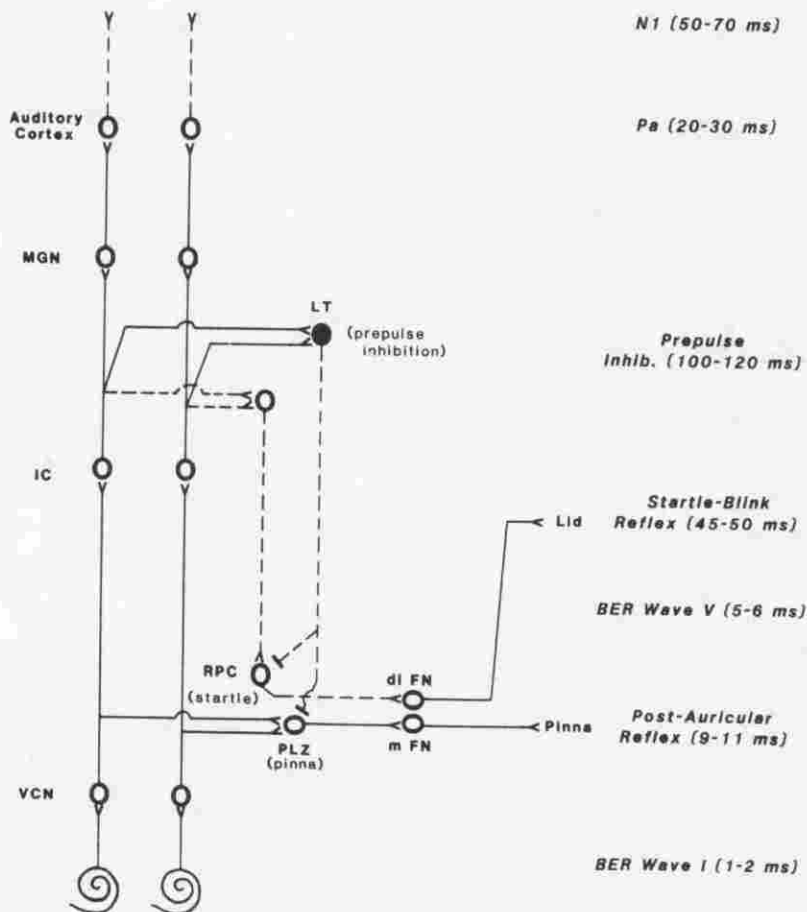
Figure 1. A schematized account of likely substrates for neurogenic and myogenic potentials discussed in the text. "Dashed axons" represent pathways with unknown loci and numbers of neurons. Open circles represent cells having net excitatory effects, while the filled circle in the prepulse inhibition "center" represents an inhibitory influence. Vertical positions of the response labels are ordered by approximate anatomical level, not by onset latency.

BER wave I of the brainstem auditory evoked potential is generally agreed to reflect transmission in the distal portion of the VIIIth cranial nerve (Jewett & Williston, 1971; Møller & Jannetta, 1986). The circuit for the *post-auricular reflex* is based on lesion (Cassella & Davis, 1986b) and anatomical (Henkel, 1981; Henkel & Edwards, 1978) data for the pinna reflex in rat and cat, and an intra-cranial recording study in man (Fialkowska, Janczewski, Kukwa, Kochanek, & Dobrzynski, 1981). The first central synapse is at the ventral cochlear nucleus (VCN). Convergence of left- and right-ear afferent limbs is probably at the second synapse, the paralemniscal zone (PLZ) near the nucleus of the lateral lemniscus. From the PLZ, the pathway continues to the medial division of the contralateral facial nucleus (mFN) and thence to the post-auricular muscle. Recent intra-cerebral recording data (Møller & Jannetta, 1986) indicate that *BER wave V* probably originates in the rostral portion of the lateral lemniscus near the inferior colliculus (IC). The exact branch point of the human *blink reflex* is uncertain, but lesion studies of whole-body startle (of which blink is a component) in rat are compatible with a midbrain site, at least when relatively long-latency components are measured (reviewed in Davis, Gendelman, Tischler, & Gendelman, 1982; Willott & DeMuth, 1986). Final convergence of left- and right-ear pathways for startle blink must occur prior to or at the final site of elaboration for startle, the nucleus reticularis pontis caudalis (RPC) (Leitner, Powers, & Hoffman, 1980). The efferent limb ultimately branches to innervate both the left and right orbicularis oculi muscles via the left and right dorsolateral facial nuclei (dl FN). The exact circuit for *prepulse inhibition* is also uncertain, but like startle, the phenomenon does not require structures (e.g., the medial geniculate of the thalamus, MGN) higher than midbrain (Davis & Gendelman, 1977). Nuclei or fibers-of-passage in the lateral tegmentum (LT) of the midbrain (Leitner, Powers, & Hoffman, 1979) are essential for prepulse inhibition by visual or auditory prestimuli but not for startle itself. The *Pa wave* probably originates in or near auditory cortex of the supratemporal plane (Celesia, 1976; Kileny, Paccioretti, & Wilson, 1987; Kraus, Özdamar, Hier, & Stein, 1982). It also appears that at least one of the generators of the *N1* component also lies in or near auditory cortex (Hari, Kaila, Katila, Tuomista, & Varpula, 1982; Scherg & Von Cramon, 1985; Vaughan & Arezzo, in press).

selectively facilitates transmission through auditory brainstem pathways that engage the prepulse inhibition circuitry, then inhibition of blink magnitude to the cutaneous eliciting stimulus should be greater when the tones in the prestimulus channel were attended. In line with these predictions, blink magnitude was relatively smaller when the preceding tone was in the attended channel, but again, this effect held only for the lateral auditory stimuli.

Combined Use of ERPs and Reflexes to Study Attention

Studies of attention using ERPs have typically used short interstimulus intervals (ISIs), high stimulus loads, and weak or moderate intensities in order to optimize the selectivity of attention (Hillyard & Picton, 1979; Hillyard & Hansen, 1986). These features were incorporated in an experiment by Woldorff et al. (in press), after which the present study was patterned. In this study, early brainstem, mid-latency, and late potentials were recorded in response to high- and low-pitch tone pips presented in rapid sequence (ISIs of 120–320 ms) to the left and right ears, respectively. The task was to attend to tones in one ear at a time and press a button whenever a rare, weaker-intensity target on that side was detected. It was found that direction of attention had no effect on the auditory brainstem evoked potentials. A small but significant modulation was observed in the mid-latency range, however, with attended-ear tones eliciting an enhanced positivity that overlapped in time with the Pa component (20–50 ms). Among the longer-latency waves, amplitudes of both the N1 (ca. 110 ms) and the subsequent P2 (ca. 190 ms) were also enhanced to attended-ear stimuli relative to unattended-ear stimuli.

In order to study reflexes concurrently with ERPs in this paradigm, it was necessary to use a reflex with a shorter refractory period and lower threshold than the blink reflex. The post-auricular reflex has a temporal recovery period of around 100 ms and can be elicited by stimuli of less than 20dB(SL) (Yoshie & Okudaira, 1969). The post-auricular reflex is commonly seen in ERP recordings as a biphasic response at the mastoid, with negative and positive peaks at about 12–14 and 17–25 ms, respectively (e.g., Picton, Hillyard, Krausz, & Galambos, 1974). As with the acoustic blink reflex, the VIIIth and VIIth cranial nerves comprise the most peripheral portions of the afferent and efferent limbs, respectively, of the post-auricular reflex arc (Bickford, 1972; Bochenek & Bochenek, 1976). Given the short onset latency of the post-auricular reflex, the central portion can have but a few synapses. For the rat homolog of the PAR, the pinna-flexion reflex, a trisynaptic pathway has been identified,

with synapses at the ventral cochlear nucleus, the paralemniscal zone, and the medial division of the facial motor nucleus (Cassella & Davis, 1986b; M. Davis, personal communication, November 1986). In humans, the post-auricular reflex has been termed a "microreflex" (Bickford, 1972; Cody & Bickford, 1969) because it normally can only be observed with response averaging techniques and/or with high levels of background agonist muscle activity. It seems to be purely vestigial in humans, because no physical movement of the pinna occurs with even high amplitude EMG responses.

Although weak eliciting stimuli are usually employed as the prestimuli in studies of prepulse inhibition, the effect can also be observed when one intense, reflex-eliciting stimulus precedes a second (e.g., Ison & Krauter, 1974). In the present study, sequences of moderately loud (90dB) tone pips were presented at ISIs appropriate for prepulse inhibition. Thus each tone, in addition to evoking a post-auricular reflex and brain potentials, served as a prepulse to partially inhibit the post-auricular reflex to the subsequent tone. Following the rationale described above for prepulse inhibition of reflexive blink, it was predicted that, if attention modulates activity in afferent pathways overlapping with the prepulse inhibition circuitry, an interaction of attention direction with ear of preceding stimulus should occur. Specifically, reflex magnitude should be smaller when attention direction and ear of prestimulus coincide relative to when they differ. On the other hand, direct effects of attention on the post-auricular reflex would be predicted if attention alters transmission in auditory pathways that overlap with the afferent limb of the PAR circuit itself. An interaction of attention direction and ear of eliciting stimulus should be observed, with reflex latency and magnitude facilitated for attended-ear stimuli. Other outcomes would be indicative of either nonselective or nonsensory factors; for example, if lateralized muscle contractions were to accompany attending to one side, an interaction between recording site and attention direction might be obtained.

The best available estimates of the neural substrates for the post-auricular reflex, prepulse inhibition, and the N1/Nd attention-related negativity suggest that these measures are mediated, respectively, in the hindbrain (Cassella & Davis, 1986b), the midbrain (Leitner, Powers, & Hoffman, 1979), and the forebrain (Hari, Kaila, Katila, Tuomista, & Varpula, 1982; Kaufman et al., 1986). Concurrent recordings of these three classes of responses may, therefore, permit a hierarchical assessment of attention effects, as schematized in Figure 1. For example, if attending to one ear produces a preset bias in afferent pathways at the receptor or at one

of the first few synapses, all three measures might show modulation. Similarly, if attention alters afferent transmission at a point subsequent to where the PAR circuit branches off but prior to the level that mediates prepulse inhibition, then only modulation of prepulse inhibition and N1/Nd should be observed. Finally, if selective attention modifies only activity rostral to the mesencephalon (e.g., at the thalamic nuclei, Skinner & Yingling, 1977), then only ERPs such as N1/Nd (and possibly Pa) should show effects of attention.

EXPERIMENT 1

Method

Subjects

Fourteen paid volunteers (aged 16–31 yrs, 6 female) comprised the final sample of subjects in Experiment 1. An additional 6 were rejected due to either poor hearing (n=1) or failure to meet a criterion of reliable elicitation of the reflex from the post-auricular muscle on at least one side by tones to either ear (n=5). Subjects were recruited through advertisements, and preference was given to individuals who could make voluntary pinna movements (n=9).

Apparatus and Procedure

The subject was seated upright in a lounge chair in a sound-attenuating chamber and wore a headband attached by means of a cord and pulley to a weight (about 3 kg) behind the chair. During runs, the subject flexed his or her neck to pull forward against this weight, thereby increasing the background electromyographic (EMG) activity and enhancing microreflex responses (Bickford, 1972).

Waveforms of the acoustic stimuli were generated by a microcomputer and, following suitable amplification/attenuation, were transduced by TDH-49 earphones. Sounds were delivered through plastic tubes terminating at the headphones. All reported latency values are corrected for the 1.8-ms delay introduced by the sound tubes.

The experiment was composed of 24 runs of 220 stimuli each. "Standard" stimuli occurred with a probability of .90 per ear and were 10-ms duration, 90dB(SL) tone pips with a 1-ms rise/fall time. (A preliminary study using 80, 90, and 100 dB tones showed that 90dB stimuli produce post-auricular reflexes that are of intermediate amplitude, i.e., neither at ceiling nor floor.) "Rare" stimuli had probabilities of .10 per ear and differed from standards delivered to the same ear only with regard to intensity (see below). Left- and right-ear tones were 2000 Hz and 4000 Hz, respectively, and order of presentation was randomized, as were the time intervals between successive tone onsets. Interstimulus intervals (ISIs) ranged from 120 to 320 ms with a rectangular distribution.

The subject's task on each run was to attend to stimuli in a designated ear and to make a speeded button press whenever a lower intensity tone (target) was detected. In addition, the subject was instructed to maintain eye fixation on a point in the foreground and to pull his or her head forward against the weight throughout the run. For half of the subjects, task order for attending to left- and right-ear tones during the first 12 runs was LLRRRRLLLLRR and the reverse order for the second 12 runs. The other half of the subjects received identical scenarios of stimulation but had opposite task assignments for each run. Task difficulty was set to an intermediate level for each subject by adjusting rare stimulus intensity; left- and right-ear rare stimuli averaged 82 and 79 dB, respectively, over the group. Feedback regarding task performance was provided in the 3–4-min interval between runs, during which time the weight was released. Runs were deleted and replaced if the subject reported difficulty in concentrating. After completing the entire 24-run session, subjects answered forced-choice questions about task difficulty, relative loudness of left- and right-ear tones, and their general state of arousal.

Recording System

Event-related potentials were recorded using 15-mm Ag-AgCl electrodes at sites F_Z, C_Z, P_Z, and positions 2 cm above T_3 and T_4, hereafter designated T_3' and T_4'. All ERP recordings were referred to a noncephalic lead, N_C, consisting of a potentiometrically balanced pair of electrodes, one over the upper sternum and one at the dorsal base of the neck. Brain potentials were amplified by Grass 7P511 amplifiers (bandpass 0.1–300 Hz), digitized at 500 Hz by a PDP-11/34 computer, and stored on magnetic tape for subsequent averaging. Blink and vertical eye movements were recorded through the same system from a bipolar pair of electrodes taped just above and just below the right orbit.

Bipolar recordings of compound action potentials from the post-auricular muscle were obtained through two 3-mm Ag-AgCl surface electrodes (Silverstein & Graham, 1978) taped to the glabrous skin behind each ear with a 15-mm separation. If the muscle could be located by palpation while the subject wiggled his or her ears, the two electrodes were placed directly over the muscle with the anterior lead abutting the wall of the pinna and the other situated posteriorly along the longitudinal axis. If the muscle could not be felt, placement was guided by the presumed location according to Gray's Anatomy (1974).

The bipolar EMG signals were amplified with a bandpass of 3–1000 Hz and were then sent to both the PDP-11/34 and to a high-speed special purpose averaging computer. The high-speed system digitized EMG activity on-line at 25,000 Hz per channel and averaged the EMG waveforms for each run over an epoch beginning 7 ms before and lasting 75 ms after each standard stimulus. A monopolar derivation was also recorded (posterior mastoid to N_C) but provided information largely redundant with the bipolar channel, and its analyses will not be reported.

Data Analysis

Microreflex activity recorded at 25,000 Hz was averaged across runs separately for each post-auricular

muscle according to attention direction (L/R) and eliciting stimulus (left- or right-ear standards); this will be referred to as the "short time-base" analysis. The averaged responses were scored for maximum peak-to-peak (p–p) amplitude within 9–30 ms poststimulus onset, and for maximum base-to-peak (b–p) amplitude within 9–23 ms relative to average prestimulus baseline. Three measures of latency were used: Peak latency was measured to the largest peak within the window 9–23 ms identified by the scoring program (usually negative); quintile peak latency was defined as the point at which the waveform first exceeded 20% of base-to-peak amplitude; and extrapolated latency within the window 4.5–18.5 ms was measured as the intercept of a line drawn along the 20th and 50th fractional peak latency values with a line defined by the mean prestimulus baseline activity.

The amplitude and latency scores were analyzed in 2×2 repeated measures analyses of variance (ANOVA-R), with eliciting stimulus and attention direction as factors, separately for each mastoid. All subjects were included in the analyses of response amplitude, but latency analyses were restricted to only those subjects and recording sites (mastoids) from which scorable, non-zero responses to stimuli at both ears were obtained. This subject-selection decision was based on inspection of the averaged waveforms digitized at 500 Hz, which were of such low temporal resolution that any effect of attention on latency was not discernible; hence, this selection was effectively unbiased as to possible attention effects.

Electromyograms digitized at the slower rate, the "long time-base data," were subjected to additional amplitude analyses. The data from all subjects were averaged separately for each mastoid and according to attention direction, eliciting stimulus, and previous stimulus (prior left- or right-ear standard). Peak-to-peak and base-to-peak amplitude scores were analyzed

according to a 2×2×2×2 ANOVA-R with the above factors.

Brain potentials digitized at 500 Hz were averaged, with artifact rejection, according to attention direction, evoking stimulus (left- or right-ear standards), previous stimulus, and scalp site. Potentials at the midline sites were measured for mean amplitude within the windows of 60–160 ms (early Nd), 160–260 ms, and 260–360 ms (late Nd). Values at each epoch were analyzed in separate ANOVA-Rs.

Button presses within the interval of 140 to 1200 ms after the onset of each target were considered as hits, while presses at other times were considered false alarms. Misses were defined as the remaining number of attended-ear rare stimuli, and correct rejections as the number of attended ear standards less the number of false alarms. From these values d′ and beta were calculated for each subject, as were mean reaction times, for left- and right-ear tones.

Results and Discussion

Direct Reflex Modulation

The averaged EMG waveform in the short time-base recordings consisted of a negative-positive diphasic potential with peaks at about 13 and 24 ms, respectively (Figure 2). In a few cases, later peaks and polarity inversion for the first two peaks were observed. These variations might be due to differences in electrode placement relative to the underlying muscle across subjects or to variations in motor unit recruitment across conditions for a given subject. In contradistinction to the blink reflex (Hackley & Graham, 1987), responses tended to be larger at the recording site *contralateral* to the eliciting stimulus; due to large inter-subject variability, however, this effect did not reach significance.
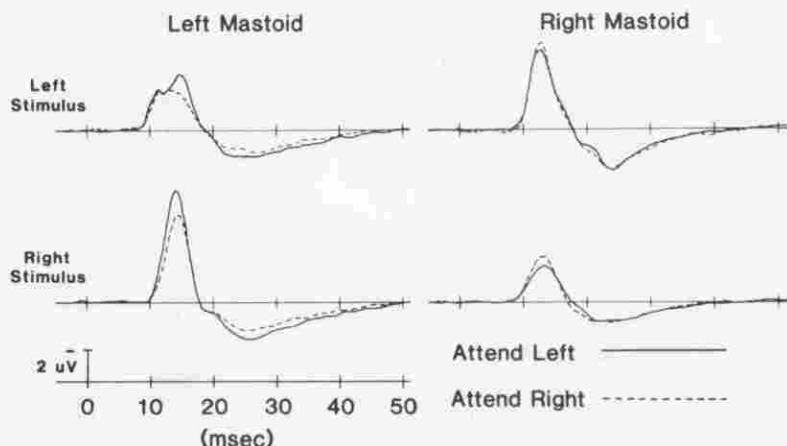

Figure 2. Post-auricular reflexes from left and right mastoids as a function of ear of eliciting stimulus and attention direction (Left/Right), for Experiment 1. Attend-to vs. attend-away differences, had they been obtained, would be seen in these waveforms by comparing conditions in which attention direction and ear of eliciting stimulus coincide with those in which they differ.

Table 1

Microreflex measures as a function of attention direction (to or away), collapsed over right and left ears

	Mean Values (SDs in Parentheses)					
	Experiment 1		Experiment 2			
Microreflex Measures	Unrectified		Unrectified		Rectified	
Short Time-Base						
	Attention re Eliciting Stimulus		Attention re Eliciting Stimulus		Attention re Eliciting Stimulus	
	To	Away	To	Away	To	Away
Extrapolated Latency (ms)	9.4 (1.6)	9.7 (1.7)	9.2 (1.7)	9.0 (1.2)	9.4 (1.3)	9.7 (2.1)
Quintile Peak Latency (ms)	10.3 (1.5)	10.4 (1.6)	10.0 (1.5)	9.9 (1.2)	10.6 (1.3)	10.9 (2.0)
Peak Latency (ms)	14.0 (2.2)	13.8 (2.0)	13.7 (2.3)	13.8 (2.1)	15.9 (3.0)	16.0 (3.0)
Base–Peak Amplitude (μV)	5.7 (7.5)	5.8 (7.4)	4.9 (6.5)	4.6 (6.0)	4.1 (5.2)	4.0 (5.0)
Peak–Peak Amplitude (μV)	8.8 (10.6)	9.0 (10.7)	7.9 (10.1)	7.3 (9.0)	4.7 (5.5)	4.5 (5.2)
Long Time-Base						
	Attention re Prestimulus		Attention re Prestimulus		Attention re Prestimulus	
	To	Away	To	Away	To	Away
Base–Peak Amplitude (μV)	5.8 (7.7)	6.4 (8.7)*	4.6 (6.9)	4.9 (7.4)**	4.1 (5.9)	4.4 (6.4)**
Peak–Peak Amplitude (μV)	9.2 (11.4)	10.1 (12.6)*	7.5 (10.5)	8.0 (11.0)***	4.9 (6.4)	5.2 (6.8)**

*$p<.05$, **$p<.01$, ***$p<.001$.

Contrary to the aforementioned studies of the blink reflex, neither latency nor magnitude of the post-auricular reflex was facilitated when attention was directed to the eliciting stimuli relative to when it was directed to stimuli in the opposite ear (see Figure 2 and Table 1). In the attention direction × eliciting stimulus analyses of the short time-base data, no interaction approached significance for either the left or right mastoid for any of the amplitude or latency measures. The long time-base analysis confirmed that no attention direction × eliciting stimulus interaction was significant.

There were no main effects for latency, but for amplitude the main effects for attention direction showed that the reflex was consistently enhanced on the side to which attention was directed (see Figure 2). This indicates an effect on the motor limb of the reflex arc. This effect can be seen in the short time-base, left mastoid analysis as a larger response for attend-left relative to attend-right conditions, b–p $F(1/13)=12.74$, p–p $F(1/13)=12.58$, both p's< .01. Similarly, attending to the right produced larger responses at the right mastoid: p–p $F(1/13)=5.27$, $p<.05$. In the long time-base analysis, this effect was manifested in a significant mastoid × attention direction interaction, p–p $F(1/13)=12.06$, and b–p $F(1/13)=12.48$, both p's<.01. No analogous finding has been reported in blink studies; therefore, it is possible that this effect may be either specific to the post-auricular reflex or tied to the use of the neck-tensing procedure (e.g., while flexing their necks, subjects may have inclined slightly toward the direction they were attending rather than straight ahead as instructed).

Prepulse Inhibition

Congruent with past research on the blink reflex, reflexes were smaller in size when attention was directed toward rather than away from the immediately preceding stimulus (see Table 1 and Figure 3). In the long time-base analysis, this enhancement of prepulse inhibition by attention was revealed in significant attention direction × prestimulus interactions, p–p $F(1/13)=8.76$, $p<.05$, b–p $F(1/13)= 6.88$, $p<.05$. Other amplitude effects included three that were marginally significant[1] and did not replicate in the second experiment.

Event-Related Potentials

Attended-ear tones elicited an enhanced negativity similar in latency and in scalp distribution to the early and late Nd components described in previous reports (e.g., Hansen & Hillyard, 1980; Wol-

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[1]Among these marginal effects were the following: Peak-to-peak reflex amplitudes were larger in the attend left condition, p–p $F(1/13)=5.66$, $p<.05$; amplitudes were larger when the preceding stimulus was in the right ear (high pitched), p–p $F(1/13)=5.74$, b–p $F(1/13)=6.10$, p's< .05; and b–p amplitudes recorded from the mastoid ipsilateral to the prestimulus were larger than those recorded from the contralateral side, $F(1/13)=5.22$, $p<.05$.
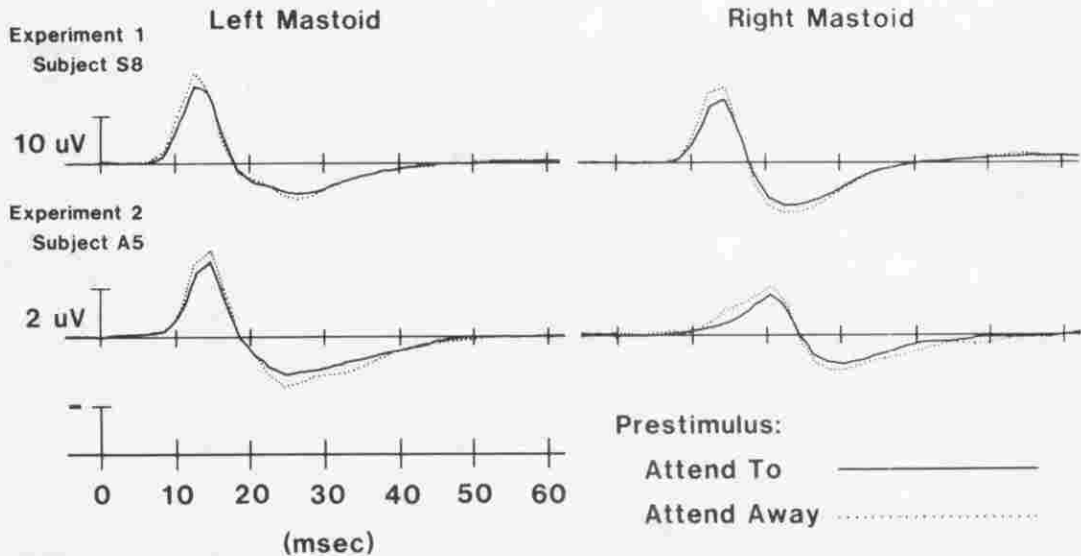
Figure 3. Post-auricular reflexes for one representative subject from Experiment 1 and one from Experiment 2 as a function of recording site (mastoid) and attention direction relative to the prestimulus that preceded the evoking stimulus. Smaller response amplitudes in the "attend to" conditions are attributed to enhancement of prepulse inhibition by attention.

dorff et al., in press). For the 60–160 and the 260–360 ms epochs, selective attention produced enhanced negativity at midline electrodes in attend-to relative to attend-away conditions, yielding significant attention direction × evoking stimulus interactions, $F(1/13) = 39.28$ and 46.78, both p's < .001 (Table 2). A three-way interaction of recording site, attention direction, and ear of evoking stimulus, reflected a larger Nd effect at frontal and central sites during both the 60–160 and 260–360 ms epochs, $F(2/26) = 11.35$ and 12.65, respectively, p's < .001. In the EOG, there was a prolonged enhancement of negativity to attended-ear tones at the forehead, significant over all three scoring epochs (see Figure 5, in the **Results** of Experiment 2, and Table 2).

Performance and Subjective Report

Sensitivity (d') and criterion (beta) measures of target detection performance were subjected to one-way ANOVA-Rs with attention direction as the factor. For attended left-ear tones, the mean values of d' and beta were 3.16 and 29, respectively; for right-ear tones, the corresponding values were 3.11 and 14. Neither measure showed a significant inter-aural difference. Mean reaction times averaged over the session for left- and right-ear stimuli were 484 and 490 ms, a nonsignificant difference. Thus, the attend-left and attend-right conditions seemed to be well matched in difficulty. Similarly, no difference was found between left- and right-ear tones for subjective reports of loudness or of difficulty in performing the target discrimination.

Table 2

Event-related potential amplitudes to tones as a function of direction of attention (to or away), collapsed over right and left ears

	Mean Amplitudes (μV) (SDs in Parentheses)			
	Experiment 1		Experiment 2	
ERP Measures	To[a]	Away[a]	To[a]	Away[a]
Early Nd at midline	−.69　(.63)	−.16　(.50)***	−.25 (.38)	.08 (.34)***
Early Nd at V-EOG	−.68 (1.06)	−.44　(.84)*	.03 (.32)	.16 (.34)
160–260 ms at midline	.41　(.67)	.34　(.59)	.24 (.41)	.13 (.32)
160–260 ms at V-EOG	−.74 (1.27)	−.44 (1.16)*	.22 (.46)	.38 (.58)
Late Nd at midline	−.40　(.68)	.47　(.54)***	−.26 (.47)	.43 (.37)***
Late Nd at V-EOG	−.98 (1.49)	−.56 (1.44)***	−.26 (.76)	.65 (.78)*

[a]Attention re eliciting stimulus.
*p < .05, **p < .01, ***p < .001.

EXPERIMENT 2

Experiment 2 was basically a replication of the first experiment, but with shortened interstimulus intervals and larger pitch separations between the two channels, as well as improved recording techniques designed to optimize the possibility of obtaining attention effects on the post-auricular reflex.

Methods

Subjects

Subjects in Experiment 2 were 9 women and 3 men (aged 18–29 yrs) selected from the same population but without regard for ability to wiggle the ears (3 could). Three additional subjects were rejected for failure to meet the criterion of adequate reflex responsivity.

Procedure

To increase information load during the task, interstimulus intervals were shortened to 65–205 ms (mean of 135 ms) and, to equate run length with the first experiment, the number of stimuli per run was increased from 220 to 360. Standard and rare stimuli occurred with probabilities of .94 and .06, respectively, and rare stimulus intensity averaged 72 and 67 dB for left- and right-ear tones. For half of the subjects, the left-ear tones were 2000 Hz and the right-ear tones were 6000 Hz; for the other 6 subjects, this ear-pitch correspondence was reversed.

Recording System and Data Analysis

A more reliable method for locating the post-auricular muscle was employed in Experiment 2. The ear-flap was gently pulled outward and forward at different points until a wedge-shaped protrusion at the juncture of the pinna wall and mastoid process, corresponding to the tendon of insertion, was found. One 3-mm electrode was taped to the skin 5 mm from the pinna wall over the muscle and a 15-mm electrode was glued 30 mm posteriorly along the axis of the muscle.

A full-wave rectifier was interposed between the amplifiers and computers in parallel with the direct connection so that both rectified and unrectified EMG channels were processed by both the short and long time-base systems. Averages based on unrectified EMG can reveal only potentials which are time-locked to stimulus onset and have a consistent polarity-latency waveform (i.e., potentials arising from synchronously recruited motor units). The rectified channel, on the other hand, should pick up any time-locked changes in muscle activity relative to the constant background level produced by the neck-tensing maneuver, regardless of polarity.

Measurement of microreflex activity was the same as in Experiment 1, except that the window for peak-to-peak amplitude of the rectified data was extended from 30 to 50 ms in order to include the inhibition of background EMG (the PAR silent period—Meier-Ewert, Gleitsmann, & Reiter, 1974).

Results and Discussion

Direct Reflex Modulation

Reflex responses were similar to those described for Experiment 1, but the rectified recordings revealed that the response may be divided into an initial 20-ms excitatory phase followed by a 40–50 ms period of inhibition of background activity (see Figure 4). The onset of the excitatory phase differed
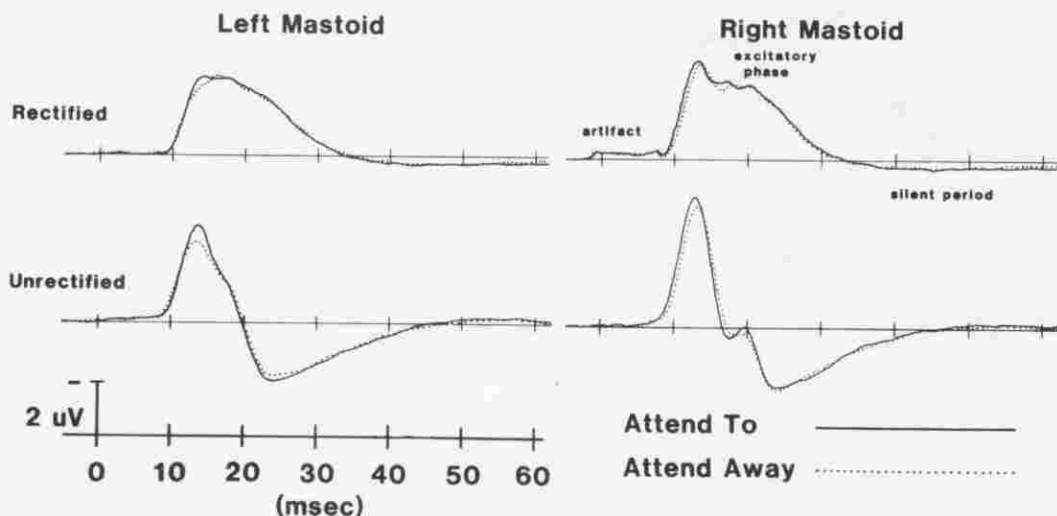

Figure 4. Post-auricular reflexes from Experiment 2 as a function of mastoid, attention direction (To/Away), and rectification averaged over left and right ear standard tones. The stimulus artifact visible in the top right waveforms begins prior to the origin of the abscissa because of the 1.8-ms delay time imposed by the delivery tubes.

little between the rectified and unrectified recordings, suggesting an initial recruitment of a fixed population of motor units on each trial followed by a more variable pattern of recruitment for the remainder of the excitatory phase.

As in Experiment 1, no direct effect of attention on the post-auricular reflex was found (see Figure 4 and Table 1). The attention direction $\times$ eliciting stimulus interaction failed to reach significance for either latency or amplitude measures for short time-base data from either mastoid. This interaction was also nonsignificant for the long time-base analysis. However, a three-way interaction between attention direction, prestimulus, and eliciting stimulus was obtained for the rectified EMG data, $F(1/11) = 5.67$ and 5.87, p's $<.05$, for base-to-peak and peak-to-peak measures, respectively; this interaction was not significant for the unrectified responses.[2]

The efferent-limb effect observed in Experiment 1 was replicated in Experiment 2, in that reflexes were enhanced on the side to which attention was directed; for the long time-base analysis, mastoid $\times$ attention direction interaction, $F(1/11) = 8.70$ and 6.59, p's $<.05$, for the rectified and unrectified p–p data, respectively, and $F(1/11) = 10.41$ and 5.27, p's $<.01$ and .05, for rectified and unrectified

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[2]Such an interaction was observed in a previous experiment (Balaban, Anthony, & Graham, 1985) in which the direct effects of attention on a reflex (blink) and modulation of the prepulse inhibition pathway by attention were measured concurrently. Note that the direction of these two attention effects on response amplitude is opposite: Attending to a prestimulus results in smaller reflexes, whereas attending to an eliciting stimulus results in larger reflexes. Thus, when prestimulus and eliciting stimulus are in separate channels the effects of attention would be expected to summate, but when prestimulus and eliciting stimulus are in the same channel, the effects of attention should tend to cancel. Means from the present Experiment 2 are compatible with this interpretation, thus implying a possible direct effect of attention on the post-auricular reflex. However, the means are also compatible with an interpretation based on refractory period effects. When prestimulus and eliciting stimulus are in the same ear, refractory effects would be expected to be greater, resulting in smaller responses. If response amplitude is thereby reduced to near its floor, then the attention-induced enhancement of prepulse inhibition may be prevented. Absence of this 3-way interaction in Experiment 1, where a slower ISI would result in less refractory interaction, is compatible with this interpretation. Because the interaction was only marginally significant for the rectified data and was nonsignificant for the unrectified data, type I error is also a strong possibility.
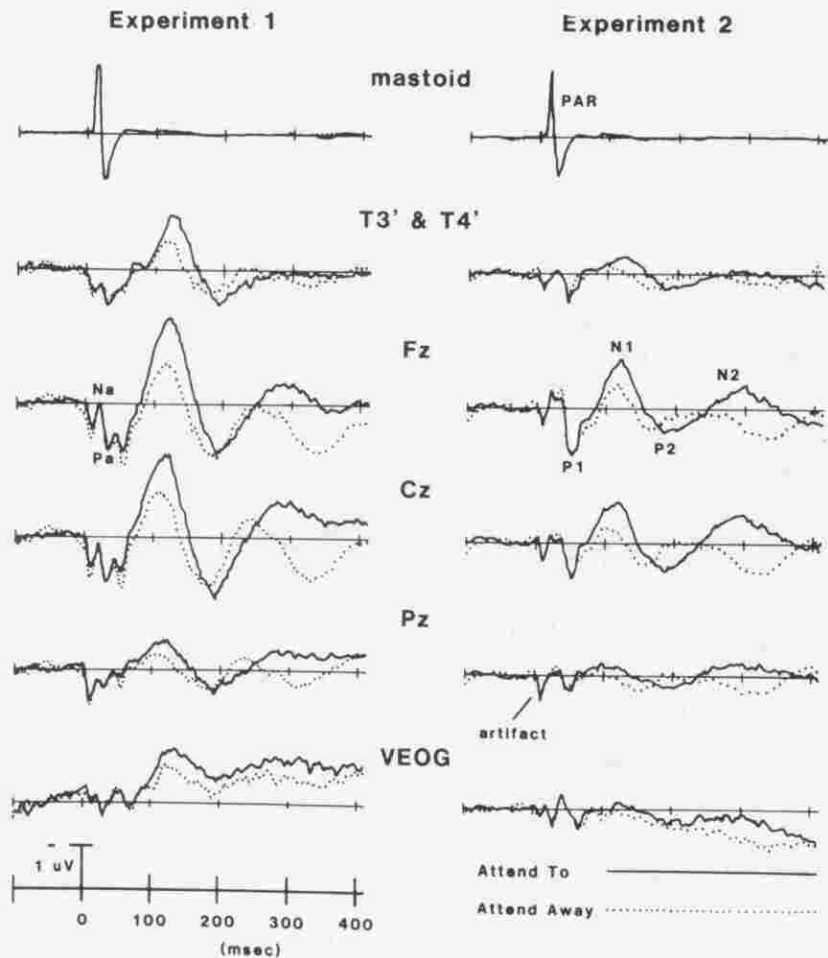
b–p data. Amplitude effects in the short time-base analysis confirmed the long time-base results.

Prepulse Inhibition

The effect of selective attention on prepulse inhibition of the post-auricular reflex that was observed in Experiment 1 was confirmed in the second experiment (see Table 1 and Figure 3). Microreflex amplitudes were relatively inhibited when attention was directed toward the previous stimulus vs. directed away from it. The attention direction $\times$ prestimulus interaction was significant for p–p measures for both the rectified, $F(1/11) = 16.05$, $p < .01$, and the unrectified long time-base data, $F(1/11) = 31.00$, $p < .001$; significance was also obtained for b–p measures of both rectified, $F(1/11) = 10.02$, and unrectified EMG, $F(1/11) = 16.65$, p's $< .01$.

Sequential and Refractory Effects

The shorter ISIs in Experiment 2 apparently led to a stimulus-specific refractory effect, such that reflexes to stimuli in a given ear were smaller when preceded by a tone in the same ear relative to when the prestimulus was in the other ear. This effect was revealed in an interaction of prestimulus with eliciting stimulus, for p–p measures of rectified EMG, $F(1/11) = 12.23$, and of unrectified EMG, $F(1/11) = 11.60$, p's $< .01$; for b–p measures, $F(1/11) = 10.54$ and 9.98, p's $< .01$, for rectified and unrectified data, respectively. Analogous F values in Experiment 1 were nonsignificant.

To test this interpretation of the prestimulus $\times$ eliciting stimulus interaction, the long time-base data were reaveraged with short/long prior ISI as a factor. For Experiment 1, the short and long prior ISIs were 120–220 and 220–320 ms, and for Experiment 2, 65–135 and 135–205 ms. A separate analysis of variance of the peak-to-peak amplitudes from the unrectified, long time-base responses for each mastoid (with factors of attention direction $\times$ ISI $\times$ prestimulus $\times$ eliciting stimulus) showed main effects for ISI in both Experiment 1, $F(1/13) = 5.49$ and 6.87, p's $< .05$, for left and right mastoids, respectively, and in Experiment 2 for the left mastoid, $F(1/11) = 7.89$, $p < .05$. Three-way interactions demonstrated that the eliciting stimulus $\times$ prestimulus effect was stronger at shorter ISIs; for Experiment 1, $F(1/13) = 6.62$, $p < .05$, for the right mastoid, and for Experiment 2, $F(1/11) = 6.07$ and 8.84, p's $< .05$, for the left and right mastoids, respectively.

Event-Related Potentials

The pattern of attention effects on the ERPs was similar to that observed in Experiment 1 (see Figure

Figure 5. Event-related potentials from Experiments 1 and 2 as a function of attending to or away from the evoking stimulus.

5 and Table 2). Again, a biphasic Nd was observed at the scalp leads, and a prolonged negativity is visible in the EOG recording. The Nd at the midline sites yielded significant attention direction × evoking stimulus interactions for both the 60–160 and the 260–360 ms epochs, $F(1/11) = 25.71$ and 21.84, p's<.001, respectively. The attention direction × evoking stimulus interaction did not reach significance for the 160–260 ms epoch, but when the apparent enhancement of P2 by attention was tested by an analysis of mean amplitude at C_z between 180 and 240 ms, the interaction did reach significance, $F(1/11)=6.03$, $p<.05$. The Nd effect was larger at frontal and central than at parietal sites for both the first- and third-epoch analysis, as reflected in three-way interactions of attention direction, eliciting stimulus, and site, $F(2/22) = 10.52$ and 12.91, p's<.001, for the early and late Nd, respectively.

Performance and Subjective Report

As in Experiment 1, no behavioral measure distinguished left- and right-ear attention direction or stimulus conditions, thus indicating that the two tasks were approximately equal in difficulty and in associated states of arousal. The left- and right-ear values were, respectively, 3.11 and 3.04 for d', 33 and 18 for beta, and 471 and 482 ms for reaction time. Number of subjects rating left and right tones as relatively more loud did not differ significantly, nor did the number of subjects reporting that the left or right target discrimination was relatively more difficult.

GENERAL DISCUSSION

In a single experimental design, selective attention effects were shown for long-latency ERPs and for prepulse inhibition of reflex magnitude, but no

direct effect of attention was obtained for the post-auricular reflex. The presence of attention effects for the first two measures implies that the absence of an effect for the post-auricular reflex was not due to a failure of the instructional manipulation to produce a selective attentional set. Although cross-paradigm comparisons must be made with caution, studies that have employed both the prepulse inhibition and direct reflex modulation paradigms (Balaban et al., 1985; Hackley & Graham, 1987) suggest that the latter is as sensitive to attention as the former, and perhaps more so. Thus, the finding of prepulse inhibition but not direct modulatory effects on the post-auricular reflex is probably not due to lack of measure sensitivity. Instead, the absence of a direct effect on the post-auricular reflex is likely to result from stability in the processing of auditory information up to and including the point at which the reflex circuit branches off from the ascending auditory pathways. Assuming that the post-auricular reflex and the rat pinna-flexion response have essentially the same circuitry, this branching occurs at the paralemniscal zone, near the nuclei of the lateral lemniscus (Cassella & Davis, 1986b; M. Davis, personal communication, November, 1986). Until this branch point, the PAR circuit overlaps with that of the auditory afferents mediating the brainstem ERPs. This overlap is exemplified by the finding (Robinson & Rudge, 1982) that in a group of 40 patients with multiple sclerosis, virtually all (98%) who showed abnormalities of the post-auricular reflex also demonstrated some abnormality in the brainstem auditory evoked potentials; by comparison, the proportion of patients with deviant post-auricular reflexes who showed abnormalities in the somatosensory evoked potential (measured at 36 ms) was only 41% (Clifford-Jones, Clarke, & Mayles, 1979). Thus the present negative results for attention effects on the post-auricular reflex are in accord with the repeated finding that brainstem auditory evoked potentials are invariant in the face of changes in the direction of attention (e.g., Picton et al., 1981; Woldorff et al., in press).

In contrast with the post-auricular reflexes and the brainstem ERPs, the eyeblink component of startle has been reported to show reliable effects of selective attention (reviewed by Anthony, 1985; Hackley & Graham, 1987). Knowledge of the circuitry underlying the acoustic startle-blink in man is limited, but it is known to persist after neocortical death (Keane, 1979). Similarly, whole body startle in the rat, of which the blink reflex is a component (Davis, 1984), survives section of the brain above the mesencephalon (Davis & Gendelman, 1977). For a short-latency (8 ms) component of startle,

Davis and colleagues (Davis, Gendelman, Tischler, & Gendelman, 1982) have identified an oligosynaptic pathway that branches off prior to the inferior colliculus, but these authors noted previous evidence suggesting that longer latency components of startle may involve midbrain structures. Anthony (1985) observed that the human blink reflex appears to be too slow (latency 25–50 ms) to be mediated by the rapid, oligosynaptic pathway delineated by Davis, and suggested that a longer, polysynaptic pathway including the inferior colliculus was more probable. (See Willott & DeMuth, 1986, for a discussion of the role of the inferior colliculus in startle.)

In the case of prepulse inhibition, the data are consistent with a mediation through the midbrain and, thus, at a level intermediate between that of the post-auricular reflex and that of the N1/Nd (see Figure 1). Only infra-thalamic structures are required for this effect (Davis & Gendelman, 1977), and destruction of the lateral tegmentum of the midbrain eliminates prepulse inhibition by visual or auditory prepulses while leaving whole-body startle itself intact (Leitner et al., 1979; Leitner, Powers, Stitt, & Hoffman, 1981). Furthermore, the inferior colliculus has been specifically implicated in the production of inhibition by acoustic prestimuli (Leitner & Cohen, 1985), thus suggesting that the prepulse inhibition circuit may branch-off from the main ascending auditory pathways at this level.

A substantial body of research (reviewed by Anthony, 1985; Hackley & Graham, 1987) indicates that both prepulse inhibition and the startle blink reflex can be modulated by selective attention, thus implying that the first point at which selective attention influences auditory processing is prior to the branch points for these responses but rostral to the lower brainstem pathways which mediate the post-auricular reflex and the brainstem ERPs. However, auditory information reaches the cortex as early as 15 ms following stimulus onset (Celesia, 1976). It would be theoretically possible, therefore, that the earliest point at which selective attention influences auditory processing is at the cortex, and that rapid feedback from the cortex onto the startle and prepulse inhibition circuits would produce the observed selective modulation.

Evidence for modulation of prepulse inhibition in the present study is less direct than in prior studies specifically designed to examine this process. The paradigm used here was different in that each stimulus served as the inhibitory prepulse for the subsequent stimulus. Further, since no baseline trials in which the prepulse was omitted could be included, it cannot be stated with certainty that the

modulatory process that was altered by attention was inhibitory in nature.[3] Prepulse inhibition of the post-auricular reflex has not previously been reported in humans, although it appears that reflex modulation by a prepulse is a pervasive phenomenon, found in many species and for a variety of reflexes (Hoffman & Ison, 1980). Cassella and Davis (1986a) have reported prepulse inhibition for the rat pinna-flexion response and, as in the present study, their prepulse was in the same modality as the eliciting stimulus (auditory); in their study, however, possible contributions from refractory or middle-ear muscle effects were not ruled out.

The attention direction × prestimulus interactions we observed on the post-auricular reflex are not likely to have been mediated by either refractory or middle-ear muscle effects. Stimulus-specific refractory effects were identified by a prestimulus × eliciting stimulus interaction that was stronger for shorter ISIs, and this interaction did not vary with attention direction. Middle-ear muscle contractions are known to attenuate predominantly sounds below 1000–2000 Hz (Møller, 1974), such that little effect would be produced on the stimuli used in the present study, or perhaps an effect only on the 2000 Hz tones. Thus, if the attention direction × prestimulus interaction were produced by enhancement of middle-ear reflexes to attended-ear prestimuli that resulted in weaker post-auricular reflexes to the subsequent eliciting stimuli, this effect should have been greater for eliciting stimuli of 2000 Hz than of 4000 or 6000 Hz. However, specific comparisons revealed that the attention direction

× prestimulus interaction was not larger for the 2000 Hz tones than for the higher frequency tones, for either Experiment 1 or Experiment 2.

The present ERP findings replicated those of Woldorff et al. (in press) in demonstrating a close temporal overlap of the early Nd attention effect with the evoked N1 component. This observation fits with the original proposal of Hillyard, Hink, Schwent, and Picton (1973) that the evoked N1 wave to auditory stimuli is enhanced when task demands promote a "stimulus set" mode of selective attention. A contrasting interpretation of this auditory attention effect was suggested by Näätänen and Michie (1979). According to this view, the obligatory (evoked) potentials are not modified by attention, but rather the apparent enhancement of the N1 component by attention is due to the superposition upon it of a slow endogenous negativity associated with stimulus-selective processing. While slow, long-lasting negativities (Nd) have been observed in a number of auditory studies (e.g., Hansen & Hillyard, 1980, 1984), findings of nearly perfect overlap in time between the early attention-related negativity and the exogenous N1 suggest that at least part of the early Nd effect consists of a modulation of the N1 wave itself.

We were not able to assess the possibility of attention effects on the brainstem or mid-latency evoked potentials because responses in this latency range were obscured by myogenic activity. The neck-tensing maneuver produced high levels of background EMG in all ERP channels, and reflexogenic potentials further contaminated the early ERPs. However, considering the present failure to obtain a direct effect of attention on the post-auricular reflex, it seems unlikely that the mid-latency attention effects (20–40 ms) observed by Woldorff and colleagues (in press) in a highly similar experiment were due to modulation of evoked myogenic activity.

The exogenous/endogenous classification that is often applied to ERP components may also be extended to reflex activity. The post-auricular reflex (Picton et al., 1974), as well as the blink reflex and prepulse inhibition (Silverstein, Graham, & Calloway, 1980), are present during sleep and occur to ignored as well as attended stimuli. Their absence may provide evidence for neurological deficit (e.g., Halliday, 1982). Therefore, according to the definition offered by Donchin, Ritter, and McCallum (1978), these three physiological processes may be classified as exogenous (obligatory). In contrast, the transcortical stretch reflex (Hammond, 1956) and the evoked saccade may be considered as more endogenous. These rapid responses are stimulus-controlled and are stereotyped and ballistic in nature,

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[3] Alternative mechanisms of reflex inhibition may also be considered. An anonymous reviewer pointed out that "reactive head micromovements" might mimic or influence a prepulse inhibition effect. Suppose, for example, that attended stimuli preferentially elicited movements such as small head rotations or saccades. If the post-auricular reflex evoked by the subsequent stimulus were suppressed by these movements, the observed pattern of results could have been produced. However, if such a movement were systematically lateralized (e.g., a brief eye movement toward the attended tone), it might be expected that the effect would be greater for the post-auricular reflex recorded on the ipsilateral side; since the prestimulus × attention direction effect did not interact with mastoid, such an explanation appears less likely. Similarly, the absence of an interaction of prestimulus × attention direction with ISI suggests that the selective attention effect was too rapid to be secondary to any discriminative voluntary movement. In Experiment 2, for example, the effect was somewhat larger (0.55 μV) when the prepulse-eliciting stimulus interval was 65–135 ms than when the interval was 135–205 ms (0.31 μV).

but their elicitation is dependent on state and task variables.

Among exogenous responses, a further distinction may be made between those that are affected by attention and those that are not. This classification is concordant with Kahneman and Treisman's (1984) expansion of the widely accepted distinction between automatic and controlled processes (Posner, 1978; Shiffrin & Schneider, 1977). According to Kahneman and Treisman, a perceptual process is *strongly automatic* if it is neither facilitated by focusing attention on a stimulus, nor impaired by diverting attention from it. In contrast, a process is said to be *partially automatic* if it can be speeded or facilitated by attention, but is normally completed even when attention is diverted from the stimulus. The present data as well as previous findings support the hypothesis that the earliest sensory processes, as reflected in the post-auricular reflex and brainstem ERPs, are both obligatory and independent of attention (strongly automatic), while later sensory processes, beginning perhaps as early as the midbrain (i.e., those indexed by the blink reflex and prepulse inhibition), are obligatory but subject to attentional influences (partially automatic).

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