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Cross-Modal Selective Attention Effects on Retinal, Myogenic, Brainstem, and Cerebral Evoked Potentials

STEVEN A. HACKLEY, MARTY WOLDORFF, AND STEVEN A. HILLYARD
Department of Neurosciences, University of California, San Diego

ABSTRACT

Short latency evoked potentials were recorded during a cross-modal selective attention task to evaluate recent proposals that sensory transmission in the peripheral auditory and visual pathways can be modified selectively by centrifugal mechanisms in humans. Twenty young adult subjects attended in turn to either left-ear tones or right-field flashes presented in a randomized sequence, in order to detect infrequent, lower-intensity targets. Attention-related enhancement of longer-latency components, including the visual P105 and the auditory N1/Nd waves and T-complex, showed that subjects were able to adopt a selective sensory set toward either modality. Neither the auditory evoked brainstem potentials nor the early visual components (electroretinogram, occipito-temporal N40, P50, N70 waves) were significantly affected by attention. Measures of retinal B-waves were significantly reduced in amplitude when attention was directed to the flashes, but concurrent recordings of eyelid electromyographic activity and the electro-oculogram indicated that this effect may have resulted from contamination of the retinal recordings by blink microreflex activity. A trend toward greater positivity in the 15–50 ms latency range for auditory evoked potentials to attended tones was observed. These results provide further evidence that the earliest levels of sensory transmission are unaffected by cross-modal selective attention, but that longer latency exogenous and endogenous potentials are enhanced to stimuli in the attended modality.

DESCRIPTORS: Event-related brain potentials, Intermodal selective attention, Brainstem evoked potentials, Startle-blink reflex, Electroretinogram.

The possibility that selective attention might influence sensory transmission at the most peripheral levels of the afferent pathways has intrigued researchers since the pioneering investigations of Hernández-Peón and colleagues (Hernández-Peón, Scherrer, & Jouvet, 1956). Although early studies that supported the idea of peripheral sensory gating were roundly criticized for lack of control over stimulus input and motivational factors (Worden, 1966; Näätänen, 1967), subsequent lines of investigation in animals have provided more credible evidence for stimulus-selective modulation of auditory input at the level of the eighth nerve (Oatman, 1976; Oatman & Anderson, 1977) and brainstem relay nuclei (Olesen, Ashe, & Weinberger, 1975; Gabriel, Saltwick, & Miller, 1975; Birt & Olds, 1982). Recordings of unit activity in the primary auditory cortex of cats and monkeys have also revealed a selective control over neural discharge patterns as a function of stimulus relevance (Hocherman, Benson, Goldstein, Heffner, & Hienz, 1976; Benson & Hienz, 1978; Weinberger & Diamond, 1987).

In humans, evidence for attentional modulation of sensory activity at or near the receptor level has been reported for both the auditory (Lukas, 1980, 1981; Brix, 1984) and visual (Eason, Oakley, & Flowers, 1983; Eason, 1984) modalities. However, the reliability of these findings has been called into question by subsequent failures to replicate both the visual (Mangun, Hansen, & Hillyard, 1986) and the auditory (Lukas, 1982; Picton, Stapells, & Campbell, 1981; Woldorff, Hansen, & Hillyard,

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S.A. Hackley is now at the Department of Psychology, 210 McAlester Hall, University of Missouri–Columbia, Columbia, MO 65211.

Address requests for reprints to: S.A. Hillyard, Department of Neurosciences, M-008, University of California–San Diego, La Jolla, CA 92093-0608.

1987) effects. Recent reports of alterations in mid-latency (20–50 ms) evoked potentials to auditory (McCallum, Curry, Cooper, Pocock, & Papakostopoulos, 1983; Woldorff et al., 1987) and visual (Oakley, Eason, Moore, & Conder, 1985; Oakley & Eason, 1987) stimuli raise the possibility that afferent transmission along subcortical or early cortical pathways might be altered by corticofugal mechanisms. This possibility is strengthened by observations that conduction through the sensory-specific circuitry of certain brainstem reflexes can be selectively modulated by attention (Anthony & Graham, 1983; DelPezzo & Hoffman, 1980; Hackley & Graham, 1987). The goal of the present study was to re-examine the peripheral gating hypothesis through concurrent recordings of retinal potentials and auditory brainstem potentials in a cross-modal selective attention task. In addition, mid- and long-latency evoked potentials were recorded to monitor attention effects on sensory processing at higher levels.

A cross-modal (auditory-visual) design was chosen in order to parallel prior studies in animals (e.g., Hernández-Peón et al., 1956; Oatman & Anderson, 1977) and humans (Lukas, 1980, 1981) that have reported attention effects on peripheral auditory transmission in the brainstem. Auditory and visual stimuli were delivered in random order, and attention was directed to each modality in turn on different runs. To maximize attentional selectivity, the stimuli were delivered at rapid rates, a difficult target discrimination task was required in each modality, and the auditory and visual stimuli were widely separated in spatial location. Although such a design may facilitate early stimulus selection, cross-modal attention studies of this type are difficult to control for nonselective influences on evoked potentials that may arise because of possible differences between the auditory and visual discrimination tasks. Hence, any early attention effects observed here would need to be substantiated in further studies with better control over general arousal and task difficulty variables.

In addition to evoked potentials, blink electromyograms (EMGs) were recorded to examine the possibility that myogenic contamination of the flash-evoked electroretinogram (ERG) might account for the discrepancy among previous reports as to whether visual-spatial attention does (Eason, 1984; Eason, Oakley, & Flowers, 1983) or does not (Mangun et al., 1986) have an effect on the ERG. In one study reporting such an effect (Eason, 1984), subjects attended to flashes of light 30° to the left or right of fixation in balanced blocks of trials. The ERG was recorded from electrodes at both the inner and the outer canthi of the right eye. Measures of both the positive-going B-wave and the negative after-potential at the inner canthus were enhanced when attention was directed to the evoking stimulus. Eason suggested that attention might modulate neuronal function in the retina by means of centrifugal fibers, which, although not yet positively identified in primates, have been shown to exist in other mammals (Itaya, 1980).

If blink EMG activity can contaminate recordings of retinal potentials, attention-related changes in the ERG such as those observed by Eason and coworkers might well be mediated by changes in flash-evoked myogenic potentials. Previous research has shown that selective attention can enhance visually evoked excitatory (Anthony & Graham, 1985) and inhibitory (DelPezzo & Hoffman, 1980) reflex responses by modulating transmission through sensory-specific portions of the reflex arc. Under this interpretation of Eason's results, modulation of visual afferent transmission would occur central to the retina (e.g., midbrain) and would be manifested in the peri-ocular region as enhanced myogenic activity when attention is directed toward the reflex-eliciting stimulus. Although Eason and coworkers have carefully examined the contribution of retinal and extraretinal generators to the peri-ocular ERG (Eason, Flowers, & Oakley, 1983), myogenic sources have not been directly evaluated. In order to assess the possibility of myogenic contamination of peri-ocular ERG recordings, electromyographic and retinal potentials were recorded concurrently in the present experiment.

Method

Subjects

Twenty normal young adults (7 males), aged 18–41 years, served as subjects. An additional 3 individuals were rejected because of either equipment problems (n=1) or failure to maintain adequate eye fixation (n=2). Subjects who normally wore glasses removed them during the experiment; normal acuity was not necessary given the diffuse nature of the visual task stimuli.

Stimuli

Flashes were generated by two Grass PS-2 photostimulators positioned so as to reflect off of a white rectangular screen located in the subject's upper right visual field. The strobe lamps were covered with translucent paper and produced 10-μs flashes of white light which diffusely illuminated the 30° high × 40° wide screen. The bottom edge of the screen extended about 5° below a fixation light, and the left edge was positioned 3° to the right of the vertical meridian defined by this light. The center of the screen was 150 cm distant from the subject. A black curtain occluded the left hemifield and extended across the vertical merid-

ian to the left edge of the screen; the green fixation light subtended 0.2° and was positioned immediately behind this curtain and shone through it.

Flash luminance was measured by setting the photostimulator at a constant flash rate of 18 Hz, and then comparing a source of known luminance (SEI Exposure Photometer) to the center of the screen. "Standard" flashes produced by one of the strobes were 37 millilamberts in intensity and constituted 28% of all experimental stimuli. "Rare" flashes from the other strobe were either 5.6 or 3.7 millilamberts, depending on the accuracy of the subject's performance during the visual practice runs, and occurred with a frequency of 5% relative to all other stimuli. Background illumination was 0.6 millilamberts at the center of the white screen. The strobe lamps were enclosed in a padded, plexiglass box to diminish the acoustic component of the flash discharge; continuous binaural presentation of background noise (about 30dB SPL) completely masked any remaining sound.

Acoustic stimulus waveforms were generated by a microcomputer and were delivered through TDH-49 earphones following appropriate amplification/attenuation. These stimuli were 4000-Hz tone pips of 1.5-ms duration with 0.5-ms rise/fall times, presented to the left ear. "Standard" tone pips were 65dB (SL) and made up 62% of the experimental stimuli. "Rare" tone pip intensity averaged 53dB (SL) and was varied across subjects and across runs to maintain performance at an intermediate level of difficulty. Rare tone pips occurred with a frequency of 5% and, therefore, roughly equalled the rare flashes in number. Standard tones and flashes were not presented in equal numbers because pilot work had shown that flicker fusion tended to occur when flashes were presented at the same rapid rate as tones. Interstimulus intervals varied at random between 120 and 320 ms (rectangular distribution); hence, the average presentation rate for tone pips was about 3.0 per second, and for flashes, about 1.5 per second. The sequential order of the four stimulus types was completely randomized.

Procedure

The experiment consisted of 24 runs, each lasting an average of 97 s and containing 440 stimuli. The subject, reclining in a lounge chair in a sound-attenuating chamber, was instructed prior to each run to attend to a specified modality and to make a speeded button press whenever a rare, lower intensity stimulus in that modality (a "target") was detected. The subject was told to maintain continuous fixation on the green light and to ignore stimuli in the other modality. The experimenter monitored the horizontal electro-oculogram and, if deviations in fixation were observed (these were rare), the subject was admonished to avoid eye movements in the future. Trials contaminated by brief eye movements were automatically rejected by the averaging program; in the few cases where slow eye movements contaminated many trials, the entire run was deleted and replaced on-line. For half of the subjects, task order for attending to the tones (T) and flashes (F) during the first 12 runs was TTFFFF-TTTTFF; this order was reversed for the second 12 runs. The other 10 subjects received identical scenarios of stimulation but had opposite task assignments for each run. Rest periods of approximately 2 min were given between runs, and a longer break was permitted at the midpoint of the session. After completing the entire 24-run session, subjects answered questions regarding relative task difficulty and stimulus intensity.

Recording

Event-related brain potentials (ERPs) were recorded using 15-mm Ag-AgCl electrodes positioned at C_Z, midway between T_3 and T_5 (hereafter designated T_3'), midway between T_4 and T_6 (T_4'), midway between T_5 and O_1 (O_1'), and midway between T_6 and O_2 (O_2'). These electrode sites were referenced to the right mastoid (RM) during acquisition of the electroencephalographic signals. The right mastoid site was also recorded against a noncephalic lead (Nc) consisting of a potentiometrically balanced pair of electrodes placed over the upper sternum and dorsal base of the neck, to permit off-line re-referencing of the averaged responses against the noncephalic lead. Such re-referenced averages are shown in most of the figures in order to portray topographical distributions more accurately. However, these averages were noisier than the original mastoid derivations and, hence, were not used in tabular or statistical analysis of the results.

Recording bandpass was 1–300 Hz for the above sites. C_Z/RM and RM/Nc were also recorded at 0.01–60 Hz to visualize slow potential changes. A left earlobe (A_1) reference was used for vertex recordings of auditory brainstem responses. The bandpass for this C_Z/A_1 channel was 30–3000 Hz (6dB down).

The electroretinogram (ERG) and electro-oculogram (EOG) were recorded (bandpass 0.01–60 Hz) from 10-mm electrodes positioned 1.5 cm lateral to the left and right outer canthi (LOC and ROC), from a 10-mm electrode just above the left supra-orbital ridge (Sup), and from a 3-mm electrode (Silverstein & Graham, 1978) placed above the left infra-orbital ridge about 1.5 cm below the upper edge of the lower eyelid (Inf). The superior, inferior, and left outer canthus electrodes were referenced to the right mastoid during data acquisition; the horizontal EOG was recorded from a bipolar derivation of the outer canthal sites, ROC versus LOC. The electromyogram (EMG) was recorded using a bipolar derivation of the inferior electrode versus an adjacent 3-mm electrode (Adj) positioned 1 cm medially along the orbital (slow-twitch) portion of the left lower eyelid. The electromyogram was full-wave rectified following amplification (bandpass 10–1000 Hz).

Electrophysiological data were recorded by two parallel systems. In the main system, all of the channels described above were converted from analog to digital at 512 Hz by a minicomputer and written to magnetic tape. Overlapping epochs beginning 200 ms prior to stimulus onset and continuing for 800 ms poststimulus were then extracted from this continuous recording. Following artifact rejection for blinks, eye movements,

and amplifier blocking, these epochs were then averaged according to stimulus type and attention direction. In addition, to record high frequency evoked activity more faithfully, channels C_Z/A_1, LOC/RM, T_3'/RM, and O_1'/RM were digitized at 3200 Hz and averaged on-line over an epoch beginning 7 ms before and lasting 75 ms after each standard stimulus; no artifact rejection was used. The canthal-, temporal-, and occipital-site recordings provided information that was redundant with the 512-Hz data, and will not be reported.

Analyses

The different components of retinal, neural, and reflexogenic potentials were measured by computer in terms of mean amplitude over a specified window, relative to a 100-ms baseline period. The measurement window for each component encompassed its peak in the grand average waveform and varied in width from 20 ms to 80 ms, depending on the duration of the deflection (see Tables 1–3). The boundaries for these windows were chosen so as to maximize inclusion of the selected peak while minimizing intrusion of adjacent peaks. Although most of the figures illustrate waveforms that have been re-referenced to the noncephalic site (in order to more accurately portray scalp distributions), the mean amplitudes shown in Tables 1–3 are based on waveforms referenced to mastoid. Consequently, there may be small differences between tables and figures in the apparent size of the attention effects. Auditory brainstem potentials were measured from positive peak to subsequent negative peak.

The amplitude measurements for each component were entered into separate repeated-measures analyses of variance (ANOVA) for each electrode site or, in the case of temporal and occipital sites, for each bilateral electrode pair. In addition, these averages were subjected to a newly developed procedure (the "ADJAR filter," Woldorff, 1988) for estimating and removing the distortion due to overlapping responses from previous and subsequent stimuli in experiments using rapid presentation rates. The corrected waveforms were evaluated statistically, and only effects confirmed by both analyses are reported. No correction of degrees of freedom (e.g., Geisser & Greenhouse, 1958) was necessary because no factor in the ANOVAs contained more than two levels.

Results

Electroretinogram and Reflex Electromyogram

Standard flashes evoked a negative-positive-negative series of potentials in the peri-ocular channels (see Inf, Sup, and ROC/LOC of Figure 1 and Table 1), which corresponded in latency and polarity to the A-wave, B-wave, and after-potential (A.P.) commonly observed with corneal-scleral recordings of the electroretinogram (Armington, 1974). Past research (Hoeppner, Bergen, & Farrow, 1981) has shown that such peri-ocular potentials closely reflect the waveform of the corneal electroretinogram.

Separate one-way ANOVAs assessed attention-related variation in mean amplitude for these components. Neither the A-wave (peak latency, 30 ms) nor the initial peak of the negative after-potential (116 ms) was affected by attention at any of the peri-ocular sites. Likewise, the B-wave as recorded at the superior orbit and at the outer canthi (ROC/LOC) did not differ as a function of attention instructions, but at the inferior orbit the B-wave measure (38–98 ms) was significantly smaller when subjects attended to the flashes ($F(1/19)=9.95$, $p<.01$).

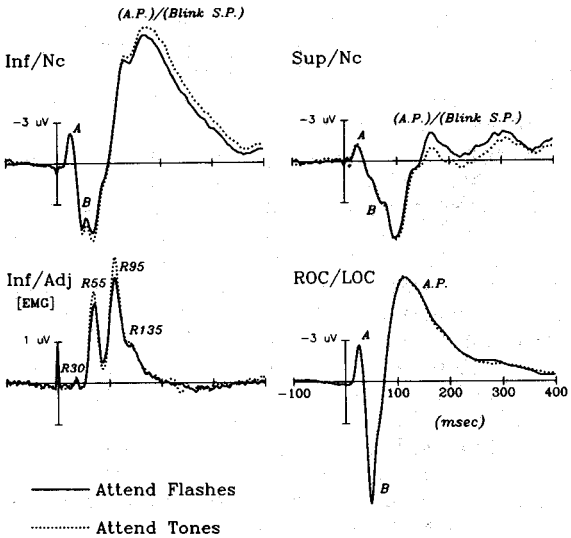

Figure 1. Evoked potentials to flashes recorded from peri-orbital sites during attend flash (solid tracings) and attend tone (dotted tracings) conditions. Grand average waveforms over 20 subjects. Electrode placements are at inferior orbit (Inf), superior orbit (Sup), a site adjacent to inferior orbital placement (Adj), right outer canthus (ROC), and left outer canthus (LOC). Inferior and superior recordings are referred to the noncephalic (Nc) site. Waveform components include A-wave (A), B-wave (B), after-potential (A.P.), and blink slow potential (S.P.). Note that components of the evoked EMG response are labelled according to onset latency rather than peak latency.

Eyeblinks were manifested in two distinct electrophysiological signals: First, action potentials in the *orbicularis oculi* muscle produced a high frequency evoked electromyograph (EMG) signal. Second, a slower deflection, which was positive at electrodes above the orbit and negative below, occurred after a latency imposed by the excitation-contraction delay and the inertial properties of the lid. This blink slow potential is primarily due to a shunting of current from the corneal-retinal dipole through the upper lid as it slides over the sclera (Matsuo, Peters, & Reilly, 1975; Antervo, Hari, Katila, Ryhanen, & Seppanen, 1985). Despite artifact rejection of trials containing well-defined blinks (i.e., trials with blink potentials at least 20–25% of the amplitude of the typical spontaneous blink), both

Table 1

Visual event-related potential amplitudes at selected peri-ocular sites as a function of attention direction

Component	Peak Latency (ms)	Measurement Window (ms)	Recording Site	Mean Amplitude (μV) Attend Flash	Attend Tone
A Wave	30	18–38	ROC/LOC	−1.46	−1.44
B Wave	50	38–98	Inf/RM	3.38	3.83**
		38–83	Sup/RM	1.56	1.55
		38–78	ROC/LOC	4.19	3.96
After Potential	116	78–158	ROC/LOC	−5.86	−5.90
Blink Slow Potential	168	153–193	Sup/RM	−1.53	−0.61*
		143–203	Inf/RM	−8.30	−8.94*

Note. These data were recorded with a bandpass of .01–60 Hz. Electrode sites are abbreviated as follows: Inf—inferior orbit, LOC—left outer canthus, RM—right mastoid, ROC—right outer canthus, and Sup—superior orbit.
* $p<.05$, ** $p<.01$, *** $p<.001$.

of these signals were evident in the present recordings due to microreflexive activation of the lid musculature by the flashes (see Blackburn, Trejo, & Lewis, 1985). Figure 1 illustrates both the rectified myogenic responses (see EMG tracings) and the blink slow potential (peaking negatively at 160–180 ms in the Inf/Nc trace). The slow component is not visible in the ROC/LOC recordings because lid movement produces a vertically oriented dipole that does not appear in the horizontal EOG derivation. The blink slow potential is positive above the orbit and is almost entirely cancelled out by the concurrent negative after-potential in the Sup/Nc recording. The percentage of trials rejected for blink activity (spontaneous, reflexive, or voluntary) or vertical eye movements was 9.9% in the visual task and 14.8% in the auditory task ($F(1/19)=10.87$, $p<.01$).

Visual stimuli evoked four discrete bursts of EMG activity in the inferior lid, with *onset* latencies of 30, 55, 95, and 135 ms (see Figure 1). These are labelled R30, R55, R95, and R135, respectively, rather than by peak latencies, because neurologists and reflex physiologists have traditionally been more concerned with onset latencies than with peak latencies of reflexes. Not every subject showed all four components: R30 was seen in 40% of the participants[1], R55 in 95%, R95 in 85%, and R135 (which merges with R95 in the grand average waveforms) in 65%. Mean amplitudes of R30, R95, and R135 did not vary reliably with attention, but R55 (measured at 58–88 ms) was significantly smaller when attention was directed toward the flashes ($F(1/19)=7.37$, $p<.02$), as was the B-wave of the electroretinogram (see above) at a similar latency (38–98 ms).

Auditory stimuli evoked a one-component EMG response (onset latency 30 ms) in the inferior orbital bipolar recording (Inf/Adj) in 85% of the subjects (see Figure 2). Like the visual R55, this component

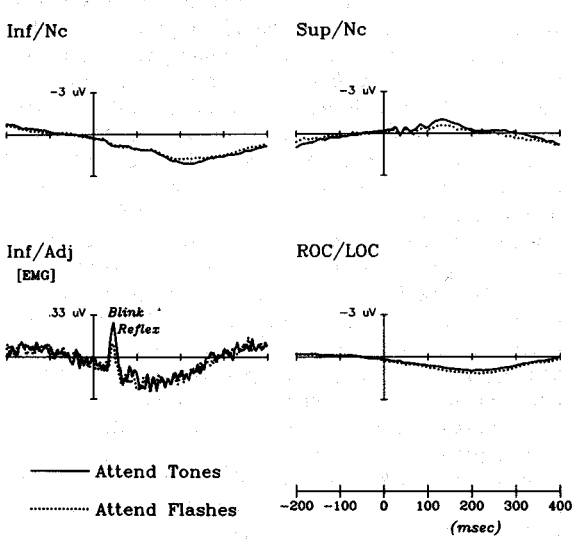

Figure 2. Grand average (N=20) evoked potentials to tones recorded from the same peri-orbital sites as in Figure 1. Inf/Adj (EMG) recording shows tone-evoked microreflex response in lower eyelid musculature. Slow drift potentials in Inf and Sup recordings that begin before tone onset represent evoked activity to preceding flash stimuli which was not completely removed by the computer algorithm applied to these data to correct for such waveform overlap.

[1]A component of the visual blink reflex with such a short onset latency has not been previously described in the literature, to our knowledge. Because 30 ms is equal to or shorter than the time required for conduction along the geniculo-striate pathway to cortex (Wilson, Babb, Halgren, & Crandall, 1983) and, *a fortiori*, is too brief a time for retinal-cortical-orbital transmission, this component is presumed to be mediated solely by brainstem pathways (see Yasuhara & Naito, 1982). Hence, this reflex may offer researchers and clinicians an electrophysiological measure of retino-pretectal function.

was smaller when attention was directed toward the visual modality ($F(1/19)=9.67$, $p<.01$). Thus, the attentional manipulations had a nonselective effect on reflex amplitude in that both the auditory and visual microreflexes were smaller during the attend-flash conditions.[2]

A similar pattern of results was obtained for the blink slow potential. Analysis of mean amplitude in the window 153–193 ms revealed a decrease in positivity at the superior orbit ($F(1/19)=6.95$, $p<.02$), and an increase in positivity at the inferior orbit ($F(1/19)=6.85$, $p<.02$), when subjects attended to the flashes (see Figure 1); the interaction of site (Sup/Inf, an index of vertical EOG) and attention direction was also significant ($F(1/19)=13.85$, $p<.001$). Thus, the blink slow potential was smaller during the attend-flash task than during the attend-tone task, an effect parallel to that described above for the blink electromyogram. In contrast, the after-potential of the electroretinogram, which was superimposed upon the blink slow potential, did not vary across tasks (Table 1). The invariance of this retinal potential is best seen in the horizontal derivation (ROC/LOC, Figure 1) where it is not obscured by the vertically oriented blink slow potential.

[2]This contrasts with prior reports (e.g., Anthony & Graham, 1983) of stimulus-selective effects of cross-modal attention on startle-blink amplitude, such that visually-evoked blinks were larger when attention was directed to the visual modality relative to conditions where attention was directed toward the auditory modality, with a reverse pattern seen for auditory-evoked blinks. Another recurrent finding in the literature (reviewed by Hackley & Graham, 1987) is that reflexive blinks are faster when attention is directed toward the evoking stimuli. To test whether such stimulus-selective modulation occurred for the microreflexes recorded in this study, separate two-way ANOVAs were performed, with evoking stimulus modality and attention direction (i.e., attend tones versus attend flashes) as factors. One ANOVA assessed effects on mean amplitude, and the other, effects on onset latency (20% fractional peak latency), for auditory and visual (R55) blink microreflexes for the 15 subjects who showed both responses. If attention selectively modulates activity in the modality-specific portion of the auditory and visual (R55) reflex arc, then an interaction should be observed such that blinks are faster and larger when attention is directed to the evoking stimulus relative to when it is directed away. No such interaction was observed for either latency or amplitude, however. Congruent with the analysis described above for all subjects, a nonselective effect of the attention manipulation was found such that the amplitudes of both auditory and visual blinks were decreased during the attend-flash conditions ($F(1/14)=4.87$, $p<.05$).

Visual ERPs

The diffuse flashes in the right visual field evoked a series of alternating negative (N) and positive (P) waves at contralateral occipital and temporal sites with the following peak latencies (rounded to the nearest 5 ms): N40, P50, N70, P105, N160, P220, and N285 ms; this componentry is similar to that observed by previous investigators (e.g., Allison, Matsumiya, Goff, & Goff, 1977; Ciganek, 1961). Waves P50, N70, P105, and P220 showed significant differences in amplitude between the left and right sides of the head (see Figure 3 and Table 2). Both the P50 and the N70 waves appeared to exhibit polarity inversions between the hemispheres at temporal and occipital sites. Left-right comparisons of mean amplitudes confirmed this inversion for the P50 at temporal and occipital sites ($F(1/19) = 9.07$ and 29.35, $p < .01$ and $.001$, respectively) and similarly for the N70 ($F(1/19) = 23.7$ and 30.5, both p's $< .001$). Neither of these waves nor the earlier N40 was significantly affected by attention at either temporal or occipital sites.

Longer-latency visual ERPs did vary as a function of modality attended. The P105 component,

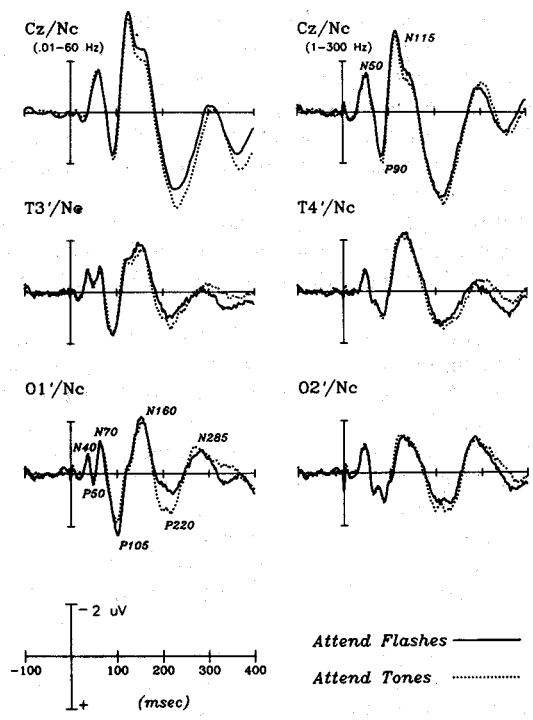

Figure 3. Grand average (N=20) event-related potentials to flashes recorded during attend flash (solid tracings) and attend tone (dotted tracings) conditions. Vertex (C_Z) recordings were taken at two bandpasses: .01–60 Hz, left; and 1–300 Hz, right. Left and right temporal (T_3', T_4') and occipital (O_1', O_2') recordings were made with the 1–300 Hz bandpass, all referred to the noncephalic (Nc) site.

Table 2

Visual event-related potential amplitudes at selected scalp sites as a function of attention direction

Component	Peak Latency (ms)	Measurement Window (ms)	Recording Site	Mean Amplitude (μV) Attend Flash	Attend Tone	
N40	39	35–45	O_1'/RM	−0.46	−0.48	
P50	50	45–55	O_1'/RM	0.39	0.40	
N70	68	62–74	O_1'/RM	−0.97	−0.94	
P105	104	78–123	T_3'/RM	0.96	0.76	**
			T_4'/RM	0.79	0.70	
			O_1'/RM	1.26	0.99	**
			O_2'/RM	0.26	0.15	
N160	160	123–178	O_1'/RM	−0.80	−0.70	
			O_2'/RM	−0.43	−0.49	
P220	223	183–243	O_1'/RM	0.25	0.81	***
			O_2'/RM	0.77	0.99	
N285	284	253–313	O_1'/RM	−0.52	−0.75	
N50	51	33–73	C_Z/RM	−0.68	−0.57	
P90	89	68–108	C_Z/RM	0.43	0.63	
N115	117	88–148	C_Z/RM	−1.01	−0.65	**

Note. All channels recorded with bandpass 1–300 Hz. Brackets indicate significant levels based on data from combined left and right electrode sites.
*$p<.05$, **$p<.01$, ***$p<.001$.

larger over the scalp contralateral to the stimulus, was enhanced by attention within the 78–123 ms measurement window at both the temporal and occipital sites ($F(1/19) = 10.85$ and 11.29, respectively, both p's $< .01$); for the O_1' and O_2' recordings this enhancement was greater at the contralateral site ($F(1/19)=8.58$, $p<.01$). The posterior N160 deflection was not significantly modulated by attention, but the vertex negativity over the range 88–148 ms (N115) was enhanced when flashes were attended ($F(1/19)=9.39$, $p<.01$). No earlier component in the C_Z/RM recording (e.g., N50 or P90) showed an attention effect. The posterior P220 and the N285 deflections were actually reduced in amplitude when attention was directed toward the evoking flashes (for P220 at O_1'/RM and O_2'/RM, $F(1/19)=15.01$, $p<.001$); this attention effect interacted with hemisphere of recording, being larger at the O_1' (contralateral) site ($F(1/19)=10.75$, $p<.01$). The N285 amplitude also tended to be reduced with attention and showed a similar interaction between modality attended and hemisphere of recording ($F(1/19)=10.02$, $p<.005$).

Auditory ERPs

Waves I, II, III, and V of the brainstem auditory ERP were scored for peak latency and peak-to-peak amplitude. None of these measures were affected by attention (see Figure 4 and Table 3). Mean amplitude over the range of 20–50 ms was also analyzed in light of prior findings (Woldorff et al., 1987) that attend-ear tones elicit enhanced positivity in this midlatency range in a dichotic listening task. The grand average waveforms at C_Z (1–300 Hz) are suggestive of such an effect (Figure 5), but the 20–50 ms measure thereof only approached significance ($F(1/19)=3.70$, $p<.07$) for waveforms corrected for overlap from adjacent responses. With

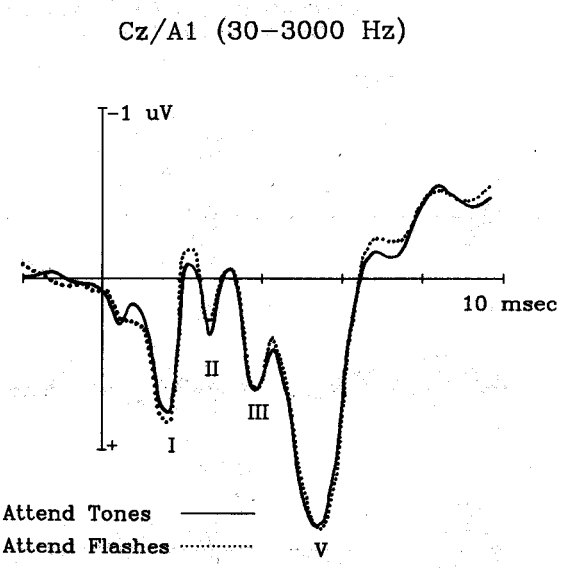

Figure 4. Grand average (N=20) brainstem evoked potential to tones recorded from vertex (C_Z) to left (ipsilateral) earlobe.

Table 3

Auditory event-related potentials at selected scalp sites as a function of attention direction

Component	Peak Latency (ms)	Measurement Window (ms)	Recording Site	Mean Amplitude (μV) Attend Flash	Attend Tone
Wave I	1.6	0.8–2.8	C_z/A_1	1.39	1.40
Wave II	2.6	2.0–3.6	C_z/A_1	0.46	0.42
Wave III	4.0	3.3–5.0	C_z/A_1	0.28	0.31
Wave V	5.5	4.3–7.4	C_z/A_1	1.93	1.91
P15–50	36	15–50	C_z/RM	0.04	0.14 *
P1	52	40–60	C_z/RM	0.20	0.22
N1/Nd	120	90–150	C_z/RM	−0.12	−0.41 ***
P2	186	160–220	C_z/RM	−0.28	0.28 ***
N2/Late ND	283	260–320	C_z/RM	−0.26	−0.71***
N70	67	48–72	T_3'/RM	−0.09	−0.19 *
			T_4'/RM	−0.02	−0.03
			O_1'/RM	−0.20	−0.37 *
			O_2'/RM	−0.12	−0.18
P100	102	80–110	T_3'/RM	−0.01	0.01
			T_4'/RM	0.03	−0.02
N130	132	120–160	T_3'/RM	0.02	−0.19 ***
			T_4'/RM	0.14	−0.02 ***

Note. Waves I–V recorded with bandpass 30–3000 Hz and measured peak-to-peak; all other ERPs recorded at 1–300 Hz and measured as mean voltage over specified window. The P15–50 attention effect was significant only for overlap-corrected waveforms.
*$p<.05$, **$p<.01$, ***$p<.001$.

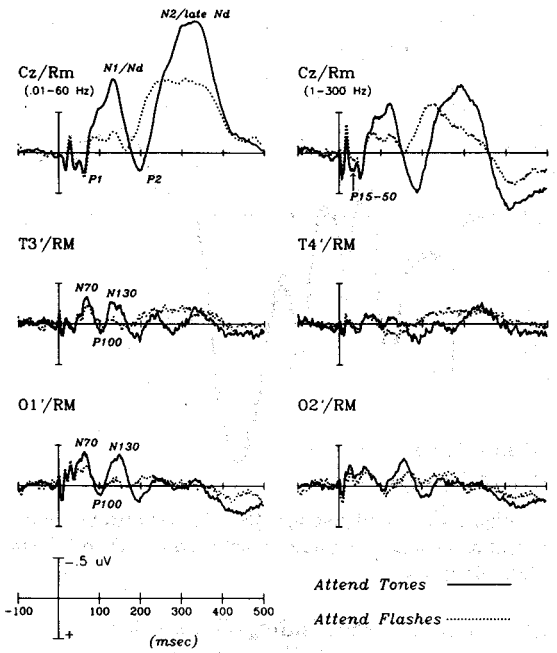

Figure 5. Grand average (N=20) event-related potentials to tones recorded from same sites as in Figure 3 but referred to the right mastoid (RM).

post hoc adjustment of the scoring window to 15–50 ms to correspond with the observed waveform difference, the attention effect became slightly more reliable, ($F(1/19)=4.60$, $p<.05$).

The long-latency components at the vertex consisted of a series of components with peaks at 52 ms (P1), 120 ms (N1/Nd), 186 ms (P2), and 283 ms (N2/late Nd); measures of the latter three components were markedly enhanced by attention (see Table 3 and Figure 5; $F(1/19) = 20.03$, 36.59, and 41.99, respectively, all p's $<$. 001).

At temporal and occipital sites a "T complex" (Wolpaw & Penry, 1975) was observed, which consisted of P100 and N130 deflections preceded by an N70 peak. The asymmetrical scalp distribution of these subcomponents, with larger responses *ipsilateral* to the left-ear tones, resulted from the right mastoid reference picking up activity common to the T_4' and O_2' electrodes. (Re-referencing to the noncephalic lead was not feasible because reflexogenic potentials in the neck region contaminated the Nc/RM recordings in many subjects.) Of the three components visible at posterior lateral sites—N70, P100, and N130—only the N130 mean amplitude showed an overall increase when attention was directed to the tones ($F(1/19) = 21.99$ and 7.03, $p<.001$ and $p<.02$, for temporal and occipital sites, respectively). However, at ipsilateral recording sites, the N70 wave was also significantly enhanced by attention (at T_3, $F(1/19)=4.76$, and at O_1, $F(1/19)=4.82$, both p's $<$ .05). The P2 attention effect mentioned above for the vertex recording was also evident at the temporal sites ($F(1/19)=19.42$, $p<$ .001).

Performance and Subjective Report

In evaluating task performance, hits were defined as button presses within 250–1250 ms following an attended target; presses at other times were considered false alarms. Misses were defined as failures to respond to targets in the attended modality, and correct rejections were counted as the number of attended-modality standards less the number of false alarms. From these response categories, values of d', Beta, and reaction time for hits were calculated for each subject. Reaction times for target flashes and tones averaged 566 and 544 ms, respectively, a nonsignificant difference. Similarly, the criterion measure did not differ between modalities; the values for Beta were 16.7 and 26.7 for flashes and tones, respectively. The sensitivity measure (d') did differ between modalities, however, suggesting that a slight imbalance in task difficulty may have been present. Sensitivity was greater for the auditory task (2.70) than for the visual task (2.29) ($F(1/19)=5.81$, $p<.05$). If an imbalance was present, it was not strong enough to affect subjects' evaluation of task difficulty: Of the 19 subjects asked about task difficulty after the session, 10 said that the visual task was more difficult, 7 said the auditory task was harder, and 2 reported that they could discern no difference (not significant by the binomial test). Subjective report of standard stimulus intensity also did not vary significantly: Of the 19 subjects who were asked, 12 said the flashes were "more intense" than the tones, 6 said the tones were more intense, and 1 found no difference.

Discussion

The present results do not support the hypothesis that attending selectively to inputs in the auditory or visual modality produces a modulation of afferent transmission in the peripheral sensory pathways. Neither the auditory brainstem evoked potentials nor short-latency flash-evoked activity in the retina (A-wave, B-wave, after-potential) or in the visual pathways (N40, P50, N70) showed reliable changes as a function of direction of attention. The earliest consistent effects of attention on auditory transmission were evident in the centrally recorded N1/Nd complex (onset about 70 ms) and in the N70 component of the T-complex (onset around 45 ms), although effects approaching significance were also seen in the central P15–50 deflection. The posterior P105 wave was the earliest visual evoked component to show clear enhancement when the flashes were attended. Thus, cross-modal selective attention did not appear to affect evoked activity in either modality at more peripheral levels than those described in numerous intramodal attention studies (e.g., Woldorff et al., 1987; Mangun & Hillyard, 1987; reviewed in Harter & Aine, 1984, and Hillyard & Picton, 1987).

The present results did not confirm the reports of Lukas (1980, 1981) and Brix (1984) that waves I and V of the brainstem evoked potentials could be enhanced in amplitude and/or shortened in latency by directing attention toward the evoking tones and away from a visual task. Two other cross-modal studies (Lukas, 1982; Picton et al., 1981) and a recent intramodal dichotic listening study (Woldorff et al., 1987) similarly reported an invariance of the brainstem evoked potentials during attentional manipulations. Taking another approach to the question of efferent control of brainstem auditory transmission, we recently tested the sensitivity of the post-auricular muscle reflex (onset latency 8–12 ms) to selective attention in a dichotic listening task (Hackley, Woldorff, & Hillyard, 1987). The tri-synaptic reflex arc for the rat homolog of this response, the pinna-flexion reflex, branches off from ascending auditory pathways within the brainstem; therefore, if attention were to alter sensory transmission in the cochlea via the olivo-cochlear bundle as proposed by Lukas (1980, 1981), it might be expected that directing attention toward or away from the evoking sounds would influence the amplitude or latency of the post-auricular reflex. However, no evidence for an attention effect on the afferent limb of this reflex was found. Thus, studies in humans to date have not confirmed the attention-related changes in early brainstem evoked activity that have been reported in cats (Oatman, 1976; Oatman & Anderson, 1977).

Cross-modal attention had a strong effect on the auditory N1/Nd components over the central scalp during the latency range 70–170 ms. This attention-related negativity is probably a composite of enhanced exogenous (N1) and endogenous (Nd) activity (Näätänen & Picton, 1987; Woldorff et al., 1987) arising primarily from cortical generators (Sams et al., 1985). Enlarged N1/Nd components have been observed following attended-channel auditory stimuli in numerous intramodal (e.g., Okita, 1987; Hansen & Hillyard, 1983, 1984) and cross-modal (Hillyard & Picton, 1979; Desmedt & Debecker, 1979; Hillyard, Simpson, Woods, Van Voorhis, & Münte, 1984; Parasuraman, 1985) studies. Attended tones also elicited an enhanced central P2 component, an effect that has been seen previously during intramodal selective attention at high rates of stimulation (Woldorff et al., 1987; Hackley et al., 1987) and to probe tones superimposed on attended speech messages (Hink & Hillyard, 1976; Woods, Hillyard, & Hansen, 1984). In the same latency range, attending to tones produced a marked enlargement of the N130 component of the temporal-occipital T-complex and a lesser enhance-

ment of the N70 deflection; the T-complex is most likely an exogenous response dissociable from the fronto-centrally distributed N1 wave (Näätänen & Picton, 1987; Wolpaw & Penry, 1975).

Attended tones also elicited a marginally significant greater positivity than unattended tones over the latency range 15–50 ms. This small effect might have escaped notice except for a prior report of comparable changes in midlatency auditory evoked components during intramodal selective attention (Woldorff et al., 1987). There is evidence that evoked positivity in this latency range arises in or near auditory cortex (Kraus, Özdamar, Hier, & Stein, 1982; Lee et al., 1984). An attention effect at this level in humans would thus be congruent with the results of studies in lower primates (Benson & Hienz, 1978; Hocherman et al., 1976) showing modulation of evoked auditory cortex activity by selective attention manipulations.

Early visual-evoked activity, including the B-wave of the electroretinogram recorded from lateral canthal and superior orbital sites, was invariant as a function of direction of attention. The B-wave measure (over 38–98 ms) recorded from the inferior orbit, however, did vary with task assignment, being *less* positive (i.e., reduced in amplitude) when attention was directed toward the evoking flashes. This effect is in the opposite direction from that reported by Eason and coworkers (Eason, 1984; Eason et al., 1983) and is contrary to the straightforward prediction that efferent control of retinal activity (if such exists) should produce enhanced B-wave activity to attended visual stimuli. Given the polarity and infra-orbital localization of this attention effect, we suggest that its most likely mechanism would be a task-related influence on the motor pathways of the blink reflex, which may contaminate peri-orbital recordings of retinal potentials.[3] Presumably the inferior orbital electrode, situated in closest proximity to the eyelid, would be more susceptible to such contamination than the canthal or superior orbital electrodes. According to this interpretation, the efferent limb of the eyeblink reflex would have been inhibited during the visual task because subjects suppressed spontaneous blinking to a greater extent while watching the flashes than while listening to the tones.[4]

Analysis of blink microreflex activity in the 30–85 ms range supported this interpretation. Mean reflex amplitude was smaller in the visual attention condition, whether the myogenic activity was evoked by flashes or tones. Moreover, of the four component bursts making up the visual microreflex, the one most strongly inhibited during visual attention (R55) happened to correspond in time with the prominent B-wave of the electroretinogram (ERG), as shown in Figure 1. Thus, contamination of the inferior orbital recording of the retinal B-wave by myogenic potentials in the same latency range might well account for the observed reduction in this measure during the visual task.

This analysis raises the possibility that the reported modulation of ERG activity by selective attention (Eason, 1984; Eason et al., 1983) might also be ascribed to myogenic potentials. The findings of Eason's group differed from the present results, however, in that B-wave amplitude was enhanced when attention was directed toward the evoking flash relative to when attention was directed toward other locations. A similar relationship has been demonstrated for the blink reflex (Anthony & Graham, 1983, 1985; Balaban, Anthony, & Graham, 1985; DelPezzo & Hoffman, 1980). According to the present account, the earliest point at which attention would influence visual afferent activity would not be at the retina but either in midbrain or cortical visual centers that provide rapid feedback onto the brainstem pathways mediating the startle-blink. Because stronger stimuli produce faster, larger reflexes (Ljubin, Licul, & Ljubin, 1981; Sherrington, 1906), visual afferent signals enhanced by attentional processes would also tend to produce faster, larger blink reflexes. Because the R55 component of the blink microreflex overlaps in time with the retinal B-wave, attention-related enhancement of myogenic potentials might have contaminated the peri-ocular recordings of the B-wave made by Eason and associates. Thus, modulation of activity in the afferent limb of the blink reflex by selective attention might well account for the apparent effects of attention on retinal potentials that have been previously reported. It should be noted, though, that the particular ERG derivation used in the present study that was most similar to Eason and coworkers' (the bipolar canthal record-

[3]It is well known that evoked microreflex activity in unrectified averages may be associated with slow field potentials that have a similar waveform to short-latency evoked brain and retinal potentials (e.g., Bickford, 1972). Inspection of individual subjects' data in the present study revealed a close correspondence between morphological variations in the rectified EMG waveform (e.g., the relative amplitudes of the four reflex components) and the averaged ERG at the inferior orbit site.

[4]Comments by the subjects further support this interpretation. For example, one subject spontaneously commented after the experiment that "The flashes come so fast that you don't even want to blink for fear of missing a target."

ing) was the least susceptible to myogenic contamination.

In a previous attempt to replicate the B-wave effect, Mangun et al. (1986) adhered more closely to the methods used by Eason and coworkers, yet they also observed no modulation of the B-wave. One of the major differences in methods relative to the Eason et al. studies was that Mangun and coworkers recorded retinal activity using a gold-foil electrode placed in direct contact with the corneal-scleral surface, as well as with peri-ocular electrodes placed at the canthi. With this more sensitive electrode, the authors obtained B-wave amplitudes nearly an order of magnitude larger than those recorded with peri-ocular electrodes. Thus, the failure of Mangun et al. to observe modulation of B-wave amplitudes during visual-spatial attention may have been because their recordings were proportionately more sensitive to retinal than to myogenic potentials. In addition, the longer interstimulus intervals used by Eason (800–2000 ms) would have resulted in less refractory and thus larger blink microreflexes than in the Mangun et al. experiment (300–700 ms).

Subsequent to the B-wave, a negative peak at about 130 ms in the peri-orbital recordings was reported by both the Mangun and Eason groups to be enlarged by attention. Rather than an enhanced retinal after-potential, Mangun and co-authors suggested that this negativity might be volume conducted activity from the brain, specifically, enhancement of an anterior N150 component. In the present experiment, a similar pattern of enhanced negativity above the orbit and greater positivity below the orbit was observed in this latency range when attention was directed toward the flash. Although this effect might represent a more anterior manifestation of the attention-related negativity seen at the vertex (starting at about 90 ms), an alternative interpretation is that the slow component of the reflex blink, produced by a slight excursion of the upper lid across the sclera, was smaller during the visual task when blinking was more suppressed.[5]

The apparently nonselective effect of the attentional manipulation on the blink reflex contrasts with prior findings. Previous work has identified a reliable effect of attention that is stimulus-selective and localizable to sensory-specific portions of the blink reflex arc (reviewed by Anthony, 1985, and by Hackley & Graham, 1987). This attention effect has been obtained for visual evoked blinks (Anthony & Graham, 1983, 1985; Balaban et al., 1985), cutaneous evoked blinks (Hackley & Graham, 1983), and auditory evoked blinks (Anthony & Graham, 1983, 1985; Hackley & Graham, 1983, 1987), as well as for an inhibitory midbrain reflex (DelPezzo & Hoffman, 1980; Hackley & Graham, 1987). These earlier investigations all employed discrete-trial paradigms with long intertrial intervals, in contrast with the rapid, sequential stimulus presentation used in the present study. This difference, though, is unlikely to explain the present failure to obtain a selective attention effect on reflexes, in light of recent evidence that attentional modulation of an inhibitory reflex may be obtained using the staccato style of stimulus delivery common to many ERP experiments (Hackley et al., 1987). More likely, the present negative result may be related to task differences in suppression of spontaneous blinks. For example, if blink microreflexes were minimal in amplitude during the visual task because of greater suppression of spontaneous blinks and because of reflex refractoriness due to rapid stimulus presentation, then a floor effect could have obscured any selective modulation of the afferent limb of the reflex arc.

The earliest reliable attention effect on the visual evoked potentials was an enhanced P105 wave over the occipital scalp contralateral to the stimulus. This finding is consonant with prior studies of visual-spatial attention (e.g., Eason, 1981; Mangun & Hillyard, 1987; Neville & Lawson, 1987) and with the interpretation that the P105 is an exogenous potential generated in visual cortex, which is subject to modulation by selective attention (Hillyard & Mangun, 1987; Mangun & Hillyard, 1988). The visual N70 component was also largest at occipital sites and was of opposite polarity at contralateral and ipsilateral sites. This distribution is compatible with the suggestion of Kraut, Arezzo, and Vaughan (1985), based on studies of a putative homolog of the N70 in monkeys, that this potential may reflect activation of striate cortex. Although the grand average waveforms are suggestive of an attentional effect on the N70 peak, no statistical confirmation was obtained. The earlier deflections, N40 and P50, were also invariant with attention. Visual evoked components in this latency range have been attributed both to subcortical (Harding & Rubinstein, 1980) and early cortical (Pratt, Bleich, & Berliner, 1982; Ducati, Fava, & Motti, 1988; Whittaker & Siegfried, 1983) activity (but note that single unit responses with latencies as short as 31 ms have been recorded from visual cortex in humans, Wilson,

[5]Latency and topographical analyses of the blink slow potential recorded in a pilot study, in which conditions were optimized for the elicitation of large blink reflexes, support the latter interpretation.

Babb, Halgren, & Crandall, 1983). Thus, the present results lend no support to hypotheses of subcortical modulation of visual transmission (e.g. at the thalamic level, Skinner & Yingling, 1977; Hughes & Mullikin, 1984) as a mechanism of cross-modal selective attention.

In conclusion, the present findings argue that the earliest levels of sensory analysis, indexed by the electroretinogram, the visual N40/P50 waves and the auditory brainstem components, are both obligatory and invariant as a function of cross-modal selective attention. Longer latency exogenous components (e.g., visual P105, auditory T-complex), which probably originate in modality-specific sensory cortices, however, are subject to attentional modification. Prior reports that peripheral sensory-evoked activity can be modulated by attention may have been influenced by contamination by microreflex activity, in the case of retinal potentials, or may have resulted from Type I error, in the case of auditory brainstem potentials. It cannot be ruled out, of course, that selective attention may affect sensory processing at a more peripheral level under a different set of task demands or stimulus conditions from those used in the present and closely related studies.

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Announcement

Research Associate

The Medical College of Pennsylvania has a doctoral-level position which is funded for four years, with annual extensions dependent upon mutual satisfaction. The project is a collaborative effort among psychophysiologists, mathematicians, and physicists that involves research to evaluate the effectiveness of measures of brain electrical activity in the detection of deception. The successful applicant must have strong quantitative skills, a thorough graduate training experience in cognitive psychophysiology, and the interpersonal skills essential to working as part of a research team. The starting salary is $30,000 plus excellent fringe benefits and annual cost of living raises. Interested applicants should send a current curriculum vitae, reprints and/or preprints, and three letters of recommendation to Dr. Theodore R. Bashore, The Medical College of Pennsylvania at EPPI, 3200 Henry Avenue, Philadelphia, PA 19129. The Medical College of Pennsylvania is an Affirmative Action/Equal Opportunity Employer.