

Electrophysiological analysis of cortical mechanisms of selective attention to high and low spatial frequencies

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Abstract

Objectives: This study investigated whether short-latency (<100 ms) event-related potential (ERP) components were modulated during attention to spatial frequency (SF) cues.

Methods: Sinusoidally modulated checkerboard stimuli having high (5 cycles per degree (cpd)) or low (0.8 cpd) SF content were presented in random order at intervals of 400–650 ms. Subjects attended to either the high or low SF stimuli, with the task of detecting targets of slightly higher or lower SF, respectively, than the above standards. ERPs were recorded from 42 scalp sites during task performance and spatio-temporal analyses were carried out on sensory-evoked and attention-related components.

Results: Attended high SF stimuli elicited an early negative difference potential (ND120) starting at about 100 ms, whereas attended low SF stimuli elicited a positivity (PD130) in the same latency range. The neural sources of both effects were estimated with dipole modeling to lie in dorsal, extrastriate occipital areas. Earlier evoked components evoked at 60–100 ms that were modeled with striate and extrastriate cortical sources were not affected by attention to SF. Starting at 150 ms, attended stimuli of both SFs elicited a broad selection negativity (SN) that was localized to ventral extrastriate visual cortex. The SN was larger over the left/right cerebral hemisphere for attended stimuli of high/low SF.

Conclusions: These results support the view that attention to SF does not involve a mechanism of amplitude modulation of early-evoked components prior to 100 ms. Attention to high and low SF information involves qualitatively different and hemispherically specialized neural processing operations. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

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1. Introduction

An important cue for visual selective attention is the size or spatial scale of a stimulus. For example, attention can be directed to emphasize perception of the parts ('trees') or the wholes ('forest') of a scene, both of which may occur in common regions of the visual field but at different spatial scales. One way to account for the attentional selection of parts and wholes is in terms of the selective enhancement of different spatial frequencies (SFs). There is abundant evidence suggesting that early in visual processing, retinal images are filtered by parallel SF selective channels (Cornsweet, 1970; De Valois and De Valois, 1990), and that attending selectively to gratings of a particular SF improves their detection and discrimination (Davis and Graham, 1981; Watson and Robson, 1981; Graham et al., 1985).

Experiments using hierarchical stimuli comprised of a global figure made up of local elements have also provided evidence that high or low SFs (associated with the local and global levels, respectively) may be attended selectively (Shulman et al., 1986; Robertson, 1999). Accordingly, it has been proposed that the ability to selectively attend to high or low SFs is critical for visual object recognition (Ivry and Robertson, 1998).

The visual-cortical mechanisms underlying attention to SF have been studied by recordings of event-related potentials (ERPs). In the first such study, Harter and Previc (1978) recorded ERPs while presenting randomized sequences of checkerboards having 6 different check sizes as subjects attended to one check size at a time. Differences in the ERP waveforms elicited by attended vs. unattended stimuli were observed beginning at a latency of 160 ms in the form of an enlarged selection negativity (SN) to stimuli having the attended check size. Similar results were obtained in a series of studies in which gratings of high and low SF were

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presented in random order, with one of the frequencies being attended on any given run (Previc and Harter, 1982; Kenemans et al., 1993; Heslenfeld et al., 1997). Although ERPs to high and low SFs differed markedly in early-evoked components in the 60–140 ms range, selective attention did not reliably modulate these early components.

In the studies reviewed above, the earliest consistent effects of attention to SF cues were manifest as a broad SN over occipito-temporal scalp sites that onset in the 160–220 ms range accompanied by a frontal selection positivity (SP) beginning at 150–200 ms. Recently, however, Zani and Proverbio (1995) reported modulations of early, stimulus-evoked ERPs as a function of attention to SF. In their study, random sequences of 6 different checkerboards varying in SF (from 0.5 to 6 cycles per degree (cpd)) were presented. On different runs, subjects selectively attended to checkerboards of a single SF and ignored the remaining 5. The ERPs elicited by each checkerboard when it was task-relevant were compared to the averaged waveforms elicited by the same stimulus when it was task-irrelevant. Specifically, attended checkerboards yielded significantly enhanced amplitudes for a positive component peaking at 90 ms post-stimulus (termed P1 or P90). This component was largest at lateral occipital scalp sites and was also present in the unattended waveforms. Attended high SF checkerboards additionally elicited a significantly larger negativity with a medial occipital distribution peaking at 115 ms (N115). An SN with a peak latency of 270 ms was elicited by both high and low frequency patterns when attended.

The attention effects on these short-latency P90 and N115 components were interpreted by Zani and Proverbio (1995) as evidence that attention to SF involves an amplitude modulation of early-evoked cortical ERP components. They proposed that these attention effects reflected a modulation of sensory information flowing into SF channels and further that the enhanced N115 component might reflect attentional selection of SF information in the primary visual (striate) cortex, whereas the P90 modulation may originate in extrastriate visual cortex.

The findings of Zani and Proverbio (1995) stand in contrast with a number of previous studies, which concluded that early visual ERP components are only modulated during selective attention to location and not by attention to other stimulus features such as SF or color (reviewed in Mangun, 1995; Heslenfeld et al., 1997; Wijers et al., 1997; Hillyard and Anllo-Vento, 1998; Martínez et al., 2001). In these studies, stimuli at attended locations were found to elicit a characteristic ERP pattern that included an amplitude enhancement of the P1 (latency 80–120 ms) and N1 (140–200 ms) components relative to when the same stimuli were outside the ‘spotlight’ of spatial attention. Based on these findings, several authors have proposed that spatial attention acts by a sensory gain control mechanism reflected in P1/N1 amplitude modulations, which operates at an earlier stage of visual processing than does attention to non-spatial attributes (Hillyard and Munte, 1984; Heslenfeld et al., 1997; Wijers et

al., 1997; Hillyard et al., 1998). Source localization studies have indicated that this enhancement of early P1/N1 activity during spatial attention takes place in extrastriate visual areas rather than in the primary visual cortex (Heinze et al., 1994; Clark and Hillyard, 1996; Gratton, 1997; Mangun et al., 1997; Woldorff et al., 1997; Martínez et al., 1999).

The findings reported by Zani and Proverbio (1995, 1997) call into question the proposed uniqueness of spatial attention in exerting a gain control over sensory-evoked activity at the earliest levels of the visual pathways. To investigate this question further, the present experiment carried out multi-channel recordings and source localization of ERPs elicited during attention to sinusoidal gratings differing in SF. The task was designed to produce a state of highly focused attention to SF by presenting stimuli at a rapid rate and by requiring subjects to make a difficult discrimination of targets. The aim was to see whether early-evoked sensory activity is modulated by attention to SF in a manner resembling spatial attention effects.

A secondary aim of the present study was to obtain ERP evidence bearing on the hypothesis of hemispheric specialization for the processing of SF information (Christman et al., 1991; Kitterle et al., 1992). Behavioral studies using unilateral hemifield presentations have shown that when attention is selectively engaged in the right visual field (RVF) high SF stimuli are discriminated more readily than those of low SF content, and vice versa when attention is directed to the left visual field (LVF) (reviewed in Ivry and Robertson, 1998). Electrophysiological studies of attention to hierarchical letter stimuli have reported that selection of global targets is associated with a negative component (N2) having a greater amplitude over the right hemisphere (Heinze and Munte, 1993; Heinze et al., 1998); in contrast, the N2 was larger over the left hemisphere for local-level targets. The present study aimed to determine whether ERPs elicited during attention to sinusoidally modulated gratings of high and low SF are differentially distributed over the left and right hemispheres and to ascertain whether such asymmetries occur at early or late stages of processing (Ivry and Robertson, 1998).

2. Methods

2.1. Subjects

Twelve subjects (7 females, age range 19–33 years) participated as paid volunteers in the experiment. All subjects were right-handed as assessed by a brief questionnaire and had normal or corrected-to-normal vision. Each subject gave informed consent to participate in this experimental protocol, which was approved by the UCSD committee on human subject investigations.

2.2. Stimuli and task

Stimuli were sinusoidally modulated black and white checkerboard patterns, circular in overall form, presented

on a high-resolution video monitor. At a viewing distance of 70 cm, the checkerboards had a SF of either 0.8 cpd (low frequency standards) or 5 cpd (high frequency standards). The checks were aligned with the horizontal and vertical axes of the screen. Each circular stimulus subtended 6.5° of visual angle from the center to its outer edge. The stimuli were presented against a gray field of 25 cd/m² that was isoluminant with the mean luminance of the checkerboards, which had a light/dark contrast of 70%. Target stimuli consisted of infrequent ($P = 0.2$) checkerboards having a slightly higher (6 cpd, high frequency targets) or slightly lower (0.5 cpd, low frequency standards) SF than their respective standards ($P = 0.8$). All checkerboards were presented at the center of gaze with 100 ms durations and stimulus onset asynchronies (SOAs) varying randomly between 400 and 650 ms. Subjects were instructed to maintain eye fixation on a central point, which was visible on the screen at all times.

Subjects were seated in a sound-attenuated, electrically shielded, and dimly illuminated recording chamber facing the video monitor. Two attention conditions (attend-high SF and attend-low SF) were administered in separate runs. Each run lasted 4 min (with two 20 s breaks interspersed after 1.5 and 3 min). At the start of each run, subjects were instructed as to which SF was task-relevant (high or low). The subjects' task was to respond with a button press to target checkerboards, which deviated slightly from the attended standard frequency. Reaction times (RT) and false alarm rates were monitored and recorded. Each subject performed 5 attend-low and 5 attend-high frequency runs presented in counterbalanced order. This resulted in a total of 875 presentations of each SF standard when attended and unattended.

The standard and target stimuli were closer together in SF (0.26 octave apart for the high SF stimuli, 0.68 octave apart for the low SF) than the bandwidths generally estimated for peripheral SF channels based on psychophysical procedures of adaptation and masking, which range from 1 to 2 octaves (Ginsburg, 1986; Olzak and Thomas, 1986). Moreover, estimates of attentional tuning to SF based on ERP recordings obtained by Harter and Previc (1978) ranged from 1.9 to 2.7 octaves at 160–200 ms post-stimulus, with progressively sharper tuning at longer latencies. Since the components of major interest here occurred well before 160 ms, it would follow that early attentional tuning to SF should be broad enough to encompass both standards and targets with little difference in extent of processing.

2.3. ERP recordings and data analysis

ERPs were recorded from 42 scalp locations including the principal sites of the 10-20 system (Fz, F3, F4, F7, F8, Cz, C3, C4, Pz, P3, P4, O1, O2, T3, T4, T5, T6 and the left mastoid) and 24 additional scalp sites (IPz, INz, IN3, IN4, IN5, IN6, PO1, PO2, TO1, TO2, CP1, CP2, CT5, CT6, FP1, FP2, FC1, FC2, FC5, FC6, C1, C2, C5, C6) (see Anllo-Vento et al., 1998). All scalp channels were referenced to

an electrode placed on the right mastoid. Bipolar recordings of the horizontal electro-oculogram (EOG) were made from two electrodes placed on the left and right outer canthi to record horizontal eye movements. Blinks were recorded from an electrode below the left eye, also referenced to the right mastoid. The electroencephalogram (EEG) data from each recording site was digitized at 250 Hz with an amplifier bandpass of 0.01–80 Hz.

Due to the short SOAs used in this study, the ERP waveforms elicited by successive stimuli overlapped in time, leading to distortions in the ERP averages. The ADJAR procedure (Woldorff, 1993) was used to remove the estimated overlap of preceding stimuli from the ERP waveforms. The absence of significant ERP activity in the baseline prior to stimulus presentation is indicative of successful overlap removal.

ERPs from each electrode site were averaged separately for standard and target stimuli of each SF under each attention condition (attend-high SF or attend-low SF). To avoid hemispheric biases, the ERP waveforms were algebraically re-referenced to the average of the left and right mastoids prior to data analyses. Artifact rejection was also performed prior to averaging in order to eliminate trials contaminated with eye movements, blinks, excessive muscular activity, or amplifier blocking. Additionally, ERPs elicited by stimuli that were preceded by a target stimulus within 1000 ms or followed by a target stimulus within 200 ms were removed from the average in order to reduce contamination by large ERPs related to target detection and/or motor responses. On an average, 11% of the trials were rejected on one or more of these grounds.

Mean amplitude measures of ERP components and attention effects were taken within specified time windows with respect to the mean baseline voltage over 100 ms preceding stimulus onset. Attentional difference waves (i.e. waveforms resulting from the subtraction of ERPs elicited by unattended stimuli from the waveforms elicited by the same stimuli when attended) were calculated and analyzed separately for each SF because the early attention effects were qualitatively different for high and low SF stimuli. ERPs to standards and targets of each SF were also analyzed separately. The presence of SF-related attention effects was examined by testing the mean amplitude of each difference wave within successive 40 ms intervals against the mean voltage of the preceding 100 ms baseline period in a repeated measures analysis of variance (ANOVA) with factors of attention and electrode site. To simplify the analyses, ANOVAs were performed on 12 posterior electrode sites (O1, O2, TO1, TO2, PO1, PO2, IPz, INz, IN3, IN4, IN5, and IN6) where the early attention effects were maximal. A separate analysis was carried out on ERPs from 10 anterior sites (Fp1, Fp2, F3, F4, F7, F8, Fz, C3, C4 and Cz) to examine the SP. For tests of lateral asymmetry, hemisphere (right vs. left) and lateral electrode sites (5 in each hemisphere) were included as factors in the ANOVA, with the midline sites omitted. All statistical analyses including more than two electrode loca-

tions employed the Greenhouse–Geisser sphericity correction (Vasey and Thayer, 1987).

In addition, for comparing the scalp distributions of different posterior ERP components, the raw amplitudes were scaled to a common mean value across electrode locations within each condition prior to ANOVA according to the method described by McCarthy and Wood (1985). These comparisons also included hemisphere as factor and were based on the 5 lateral posterior sites in each hemisphere as noted above.

Attention effects were tested statistically for both standard and target ERPs, but major emphasis was given to the standard ERPs in the spatio-temporal analyses of the early components. This was done because the more frequent standard ERPs had a higher signal/noise ratio, resulting in more reliable comparisons of component scalp distributions and estimates of source locations (as well as more powerful tests of attention effects). This emphasis on the standard ERPs was based on our finding of virtually identical early attention effects for standard and target stimuli (see Section 3) as well as on considerations of the bandwidth of SF channels (discussed above).

2.4. Modeling of ERP sources

A Polhemus Isotrak digitizer was used to record the 3-dimensional (3D) position of each electrode site and 3 fiducial landmarks (the nasion, and left and right preauricular points) for each individual subject. The digitized coordinates were used to calculate a best-fit sphere that encompassed the locations of all recording electrodes. These spherical coordinates were used for modeling the dipolar sources of the major ERP components and attention effects using the brain electrical source analysis (BESA) algorithm (Scherg, 1990; Miltner et al., 1994). The general approach was to fit symmetrical pairs of dipoles that were mirror-constrained in location but not in orientation over restricted time intervals corresponding to the components of interest, as described in Section 3. The dipole models obtained were little affected by using different symmetry constraints or different starting locations in the dipole fitting.

To relate the estimated dipole locations to brain anatomy, high-resolution anatomical magnetic resonance imagings (MRIs) were obtained for 7 of the subjects in this experiment using a 1.5 T Siemens Vision MR scanner, equipped with a quadrature head-coil. Two hundred and twenty coronal slices (1 mm thick) were acquired using a 3D magnetization prepared rapid gradient echo sequence (TR = 11.4 ms, TE = 4.4 ms, flip angle = 10°, matrix = 256 × 256). This protocol covered the entire brain and provided equal resolution in all 3 planes. The acquired coronal images were used to compute a 3D volume package that was transformed into the standard coordinate system of Talairach and Tournoux (1988) using the AFNI software package (Cox, 1996). For each subject, the cranial fiducial landmarks (nasion, left and right preauricular points) were identified on their respective

MRIs, which enabled co-registration of the BESA sphere with the MRI images. The locations of each dipole in the group-average BESA models were projected on each subject's MRI scan, converted into Talairach coordinates and averaged across all subjects (see Anllo-Vento et al., 1998 for details of this co-registration procedure). In this way, the average anatomical position of each dipole could be estimated, subject to the well-known limitations of the inverse dipole modeling (Scherg, 1990; Miltner et al., 1994).

3. Results

3.1. Behavioral performance

Responses to target stimuli of the attended SF made between 200 and 1200 ms following stimulus onset were considered 'hits'. On an average, subjects correctly detected 85% of the high SF targets and 84% of the low SF targets. The mean RTs for detection of high and low SF targets were 533 and 545 ms, respectively. False alarms were calculated as the percentage of standard stimuli (of either the attended or unattended SF) that were followed by a response. The mean false alarm rate during the attend-high SF condition was 5% and during the attend-low SF runs was 3%. Neither hit rates, RTs nor false alarm rates differed significantly for high vs. low SFs.

3.2. Event-related potentials

As seen in the grand-averaged ERP waveforms (Fig. 1, top), the earliest component evoked by high SF stimuli was a posterior midline negativity onsetting at 50–60 ms and peaking at 90–100 ms. This component was termed C1 following Jeffreys and Axford (1972). A positive component onsetting at approximately 70 ms (P1) was elicited over lateral occipito-temporal recording sites. Neither C1 nor P1 amplitude was affected by attention (measured in the window 60–100 ms) for either the standard or target stimuli, as is evident in the attentional difference waves (attended minus unattended ERPs) to high SF stimuli shown in Fig. 2. Neither the C1 nor the P1 showed significant hemispheric asymmetry.

The significance levels of the attention effects in the standard and target difference waves over the 12 posterior sites are given in Table 1. Also shown in Table 1 are the significance levels for the attention × electrode site interaction, indicating the extent to which the attention effects differed among the scalp sites. Table 2 provides attended and unattended ERP amplitudes at medial and lateral occipital sites and averaged over all posterior sites for the key early time windows.

The first significant effect of attention to high SF stimuli was an increased negativity over the latency range of 100–140 ms in both standard and target ERPs. This early attention effect (labeled ND120) peaked at about 120 ms and was maximally negative over medial occipital scalp sites. The

onset latency and scalp distribution of the ND120 differed from those of the C1 component. Fig. 3 compares the sequential scalp topographies of the ERP elicited by unattended high SF standard stimuli (top row) with those of the high SF stan-

dard attentional difference wave (bottom row). The unattended C1 component had its onset in the latency range 60–80 ms and peaked in amplitude between 80 and 100 ms over ventro-medial occipital sites. The ND120, on the other hand,

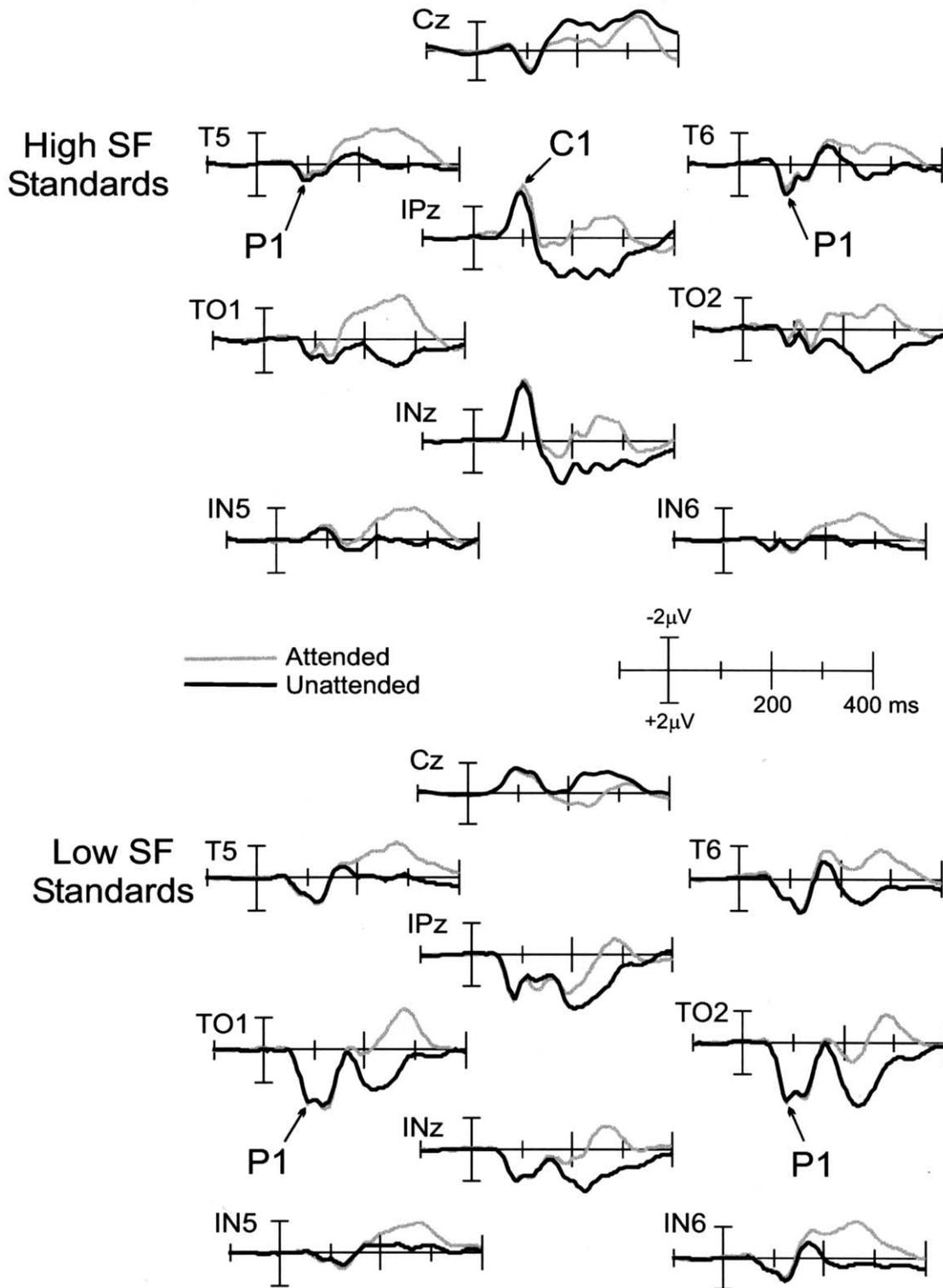


Fig. 1. ERPs elicited by high and low SF standards. Grand-averaged ERPs to high SF (top) and low SF standard stimuli (bottom) are shown for 8 posterior electrode sites. Black tracings depict ERPs to attended stimuli and gray tracings show the ERPs elicited by the same stimuli when unattended.

did not appear until 100–120 ms and was distributed more broadly and dorsally over the occipital scalp. The scalp topographies of these two components differed significantly over the posterior electrode array; this was tested by comparing

the distribution of the C1 in the interval of 60–100 ms with that of the ND120 in the interval of 100–140 ms: $F(4, 44) = 3.98$, $P < 0.01$, for interaction of component (standard ND120 vs. standard C1) \times electrode site (5 in

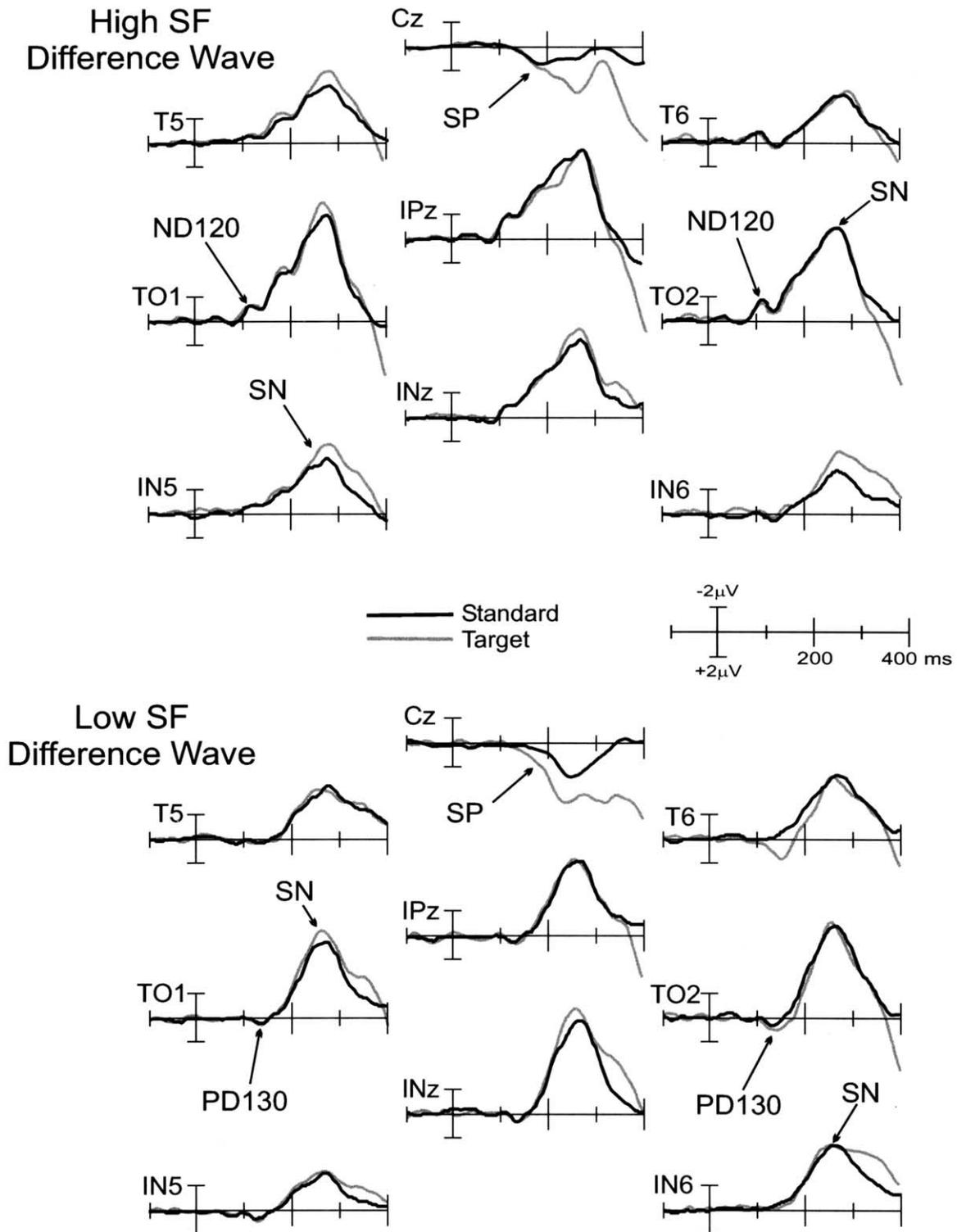


Fig. 2. Attentional difference waves. The grand-averaged difference waves for high (top) and low (bottom) SF standards (black line) and targets (gray line) were formed by subtracting the ERPs elicited by standard or target stimuli when they were unattended from those elicited by the same stimuli when they were attended.

Table 1

Significance levels (*P* values) of the attention effects and attention × electrode site interactions (in parenthesis) for ERPs to standard and target stimuli at successive latency intervals

Time interval		d.f.	60–100 ms	100–140 ms	140–180 ms	180–220 ms	220–260 ms	260–300 ms
<i>Posterior electrodes</i>								
High SF	Standards	1,11	N.S.	< 0.05	< 0.05	< 0.01	< 0.01	< 0.01
		11,121	(N.S.)	(<0.005)	(<0.001)	(<0.001)	(<0.001)	(<0.001)
	Targets	1,11	N.S.	< 0.05	< 0.01	< 0.005	< 0.001	< 0.005
		11,121	(N.S.)	(<0.01)	(N.S.)	(N.S.)	(N.S.)	(N.S.)
Low SF	Standards	1,11	N.S.	< 0.05	N.S.	< 0.05	< 0.05	< 0.01
		11,121	(N.S.)	(<0.05)	(N.S.)	(<0.05)	(N.S.)	(<0.05)
	Targets	1,11	N.S.	< 0.05	< 0.05	< 0.05	< 0.01	< 0.005
		11,121	(N.S.)	(<0.05)	(<0.005)	(N.S.)	(N.S.)	(N.S.)
<i>Anterior electrodes</i>								
High SF	Standards	1,11	N.S.	N.S.	< 0.05	< 0.05	< 0.05	< 0.05
		9,99	(N.S.)	(N.S.)	(N.S.)	(N.S.)	(N.S.)	(N.S.)
	Targets	1,11	N.S.	N.S.	< 0.05	< 0.05	< 0.005	< 0.01
		9,99	(N.S.)	(N.S.)	(N.S.)	(N.S.)	(N.S.)	(N.S.)
Low SF	Standards	1,11	N.S.	N.S.	N.S.	< 0.05	< 0.01	< 0.05
		9,99	(N.S.)	(N.S.)	(N.S.)	(N.S.)	(N.S.)	(N.S.)
	Targets	1,11	N.S.	N.S.	< 0.05	< 0.05	< 0.001	< 0.001
		9,99	(N.S.)	(N.S.)	(<0.05)	(N.S.)	(N.S.)	(N.S.)

each hemisphere). This interaction was also significant during the interval 80–120 ms ($F(4, 44) = 3.45, P < 0.05$), which encompassed the peaks of both components.

The most prominent ERP effect produced during attention to high SF was a broad SN that was bilaterally distributed over ventro-lateral scalp sites beginning at approximately 140 ms and persisting for 200 ms or more (Fig. 2). The SN amplitude was significant in the high SF

difference waves for all intervals between 140 and 300 ms (see Table 1), with the targets generally producing more significant effects than standards at posterior sites. The scalp distribution of the high frequency standard SN showed bilateral occipital maxima and differed markedly from the mid-occipital distribution of the shorter-latency ND120 attention effect (Fig. 4). The posterior scalp distribution of the ND120 at 100–140 ms differed significantly from that of

Table 2

Mean amplitude values for attended and unattended ERPs in early time windows at medial (O1, O2) and lateral (TO1, TO2) scalp sites and overall posterior sites

			High SF					Low SF					
			O1	O2	TO1	TO2	All posterior sites	O1	O2	TO1	TO2	All posterior sites	
<i>Standards</i>	60–100 ms	Attended	-1.46	-1.78	0.32	0.23	-0.68	1.89	1.91	2.10	2.18	1.44	
		SE	0.20	0.31	0.14	0.10	0.15	0.32	0.33	0.33	0.37	0.24	
		Unattended	Attended	-1.66	-1.90	0.39	0.28	-0.79	1.91	1.86	2.09	2.06	1.40
			SE	0.17	0.27	0.17	0.17	0.15	0.32	0.34	0.34	0.36	0.24
	100–140 ms	Attended	-1.33	-2.35	0.59	0.38	-0.87	2.02	1.67	3.21	2.98	1.99	
		SE	0.34	0.46	0.09	0.20	0.26	0.24	0.15	0.29	0.19	0.17	
Unattended		-0.82	-1.81	0.96	0.48	-0.30	1.82	1.45	2.79	2.57	1.67		
SE		0.37	0.48	0.17	0.14	0.26	0.15	0.18	0.28	0.20	0.16		
<i>Targets</i>	60–100 ms	Attended	-1.49	-1.81	0.40	0.31	-0.72	1.87	1.95	2.29	2.22	1.62	
		SE	0.18	0.17	0.18	0.21	0.22	0.18	0.16	0.39	0.29	0.22	
		Unattended	Attended	-1.70	-1.77	0.58	0.34	-0.86	1.95	1.82	2.11	2.13	1.56
			SE	0.11	0.18	0.19	0.10	0.18	0.28	0.26	0.17	0.22	0.22
	100–140 ms	Attended	-1.49	-2.51	0.64	0.35	-0.98	2.25	1.86	3.64	3.17	2.31	
		SE	0.27	0.33	0.15	0.12	0.24	0.27	0.13	0.35	0.22	0.12	
Unattended		-0.81	-1.79	1.05	0.58	-0.32	1.94	1.51	3.01	2.48	1.69		
SE		0.27	0.19	0.19	0.18	0.15	0.17	0.15	0.27	0.28	0.15		

SE, standard error.

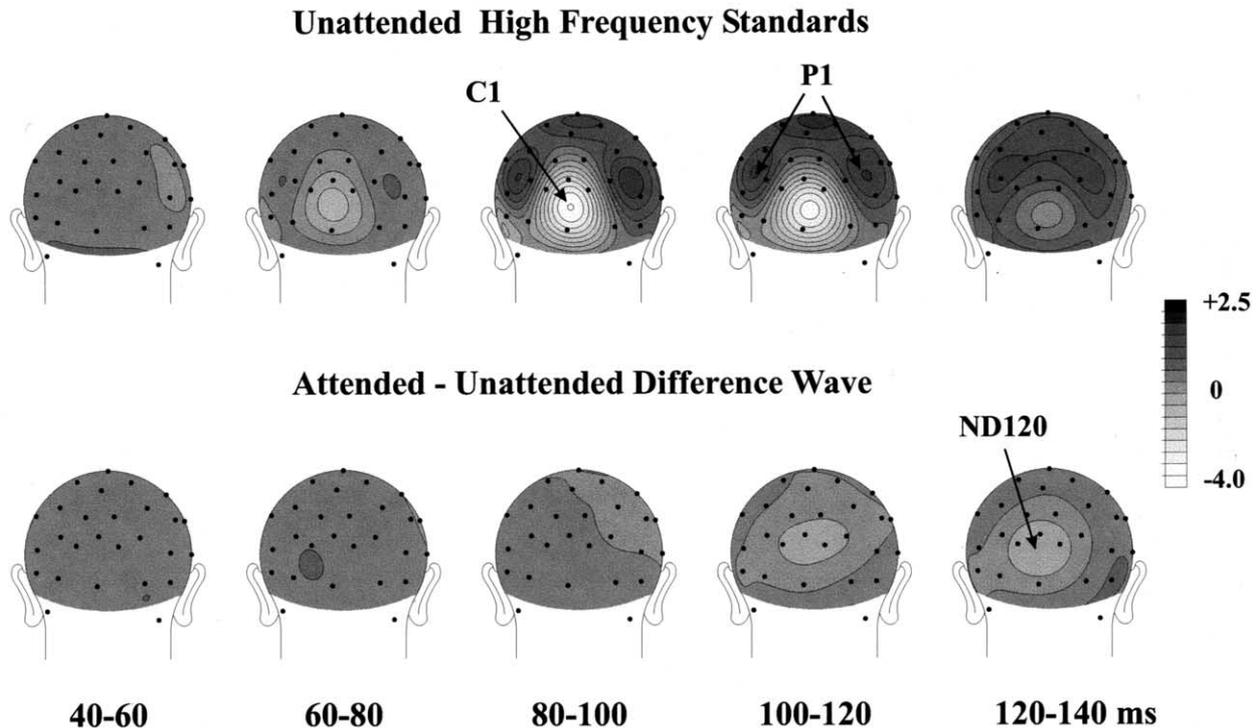


Fig. 3. Topographical distributions of ERPs to unattended high SF standards (top) compared with the early phase of the attentional difference wave for standards (bottom). Voltage topography maps at 20 ms intervals depict the differences in onset latency and distribution of the unattended C1 and P1 components (top) and the ND120 attention effect (bottom). Gray scale depicts positive and negative voltage in microvolts in this and subsequent figures.

the SN over the interval of 220–260 ms: $F(4, 44) = 5.65$, $P < 0.01$, for interaction of component (standard ND120 vs. standard SN) and electrode site (5 in each hemisphere).

The ND120 in the interval 100–140 ms also showed a significant interaction between the factors of attention, electrode sites, and hemisphere ($F(4, 44) = 6.13$, $P < 0.001$). Post hoc analyses (Tukey HSD) revealed that the lateral asymmetry was significant ($P < 0.05$) at the ventro-lateral electrode pair (IN3 / IN4), with greater negative amplitude over the left hemisphere. The 3-way interaction was also significant for the SN in the intervals of 220–260 ms ($F(4, 44) = 2.83$, $P < 0.05$) and 260–300 ms ($F(4, 44) = 5.66$, $P < 0.01$). Like the ND120, the SN showed significantly greater negativity over the left hemisphere at ventro-lateral scalp sites (IN3 > IN4 and IN5 > IN6, both $P < 0.05$ at 220–260 ms; TO1 > TO2, IN3 > IN4, IN5 > IN6, all $P < 0.01$ at 260–300 ms).

At anterior scalp electrodes, a broad SP developed over the same time range as the posterior SN (Figs. 1 and 2). The SP to high SF stimuli was significant throughout the range of 140–300 ms, with generally higher significance levels for targets and at longer latencies (Table 1). The SP did not exhibit significant lateral asymmetries.

The ERPs elicited by low SF stimuli (Fig. 1, bottom) differed markedly from those elicited by high SF stimuli. In contrast to the high SF waveforms, the low SF stimuli did not elicit an early negative C1 component. Instead, the low SF standards elicited a bilaterally distributed positive

deflection onsetting at around 60–70 ms (the early phase of the P1), with maximal amplitude over lateral occipital scalp sites. As in the case of the high SF stimuli, there was no effect of attention on either the standard or target ERPs to the low SF stimuli prior to 100 ms, nor were there significant lateral asymmetries (Tables 1 and 2). However, there was a tendency for the P1 component to be larger over the right hemisphere in the 60–100 ms interval ($F(1, 11) = 3.32$, $P < 0.10$, for hemisphere; $F(4, 44) = 1.86$, $P < 0.14$, for hemisphere by electrode).

The earliest attention effect to the low SF stimuli was a positive deflection observed in the difference wave at 100–140 ms (Fig. 2, bottom). This component (termed the PD130) had an onset latency of approximately 100 ms and peaked at about 130 ms with maximal positive voltage over medial occipital areas (Fig. 5, bottom row). The onset latency and midline occipito-parietal distribution of the PD130 were very different from those of the evoked P1 component (Fig. 5, top row), which began as early as 60–80 ms and had bilateral amplitude maxima over the occipital scalp. The posterior scalp topography of the PD130 (100–140 ms interval) differed significantly from that of the unattended P1 (60–100 ms interval); $F(4, 44) = 4.24$, $P < 0.01$ for interaction of component (standard PD130 vs. standard P1) and electrode site. The PD130 was not laterally asymmetrical.

The low SF difference wave was also analyzed in successive 40 ms intervals (Fig. 6). In the interval following the PD130 (140–180 ms), the difference wave was significantly

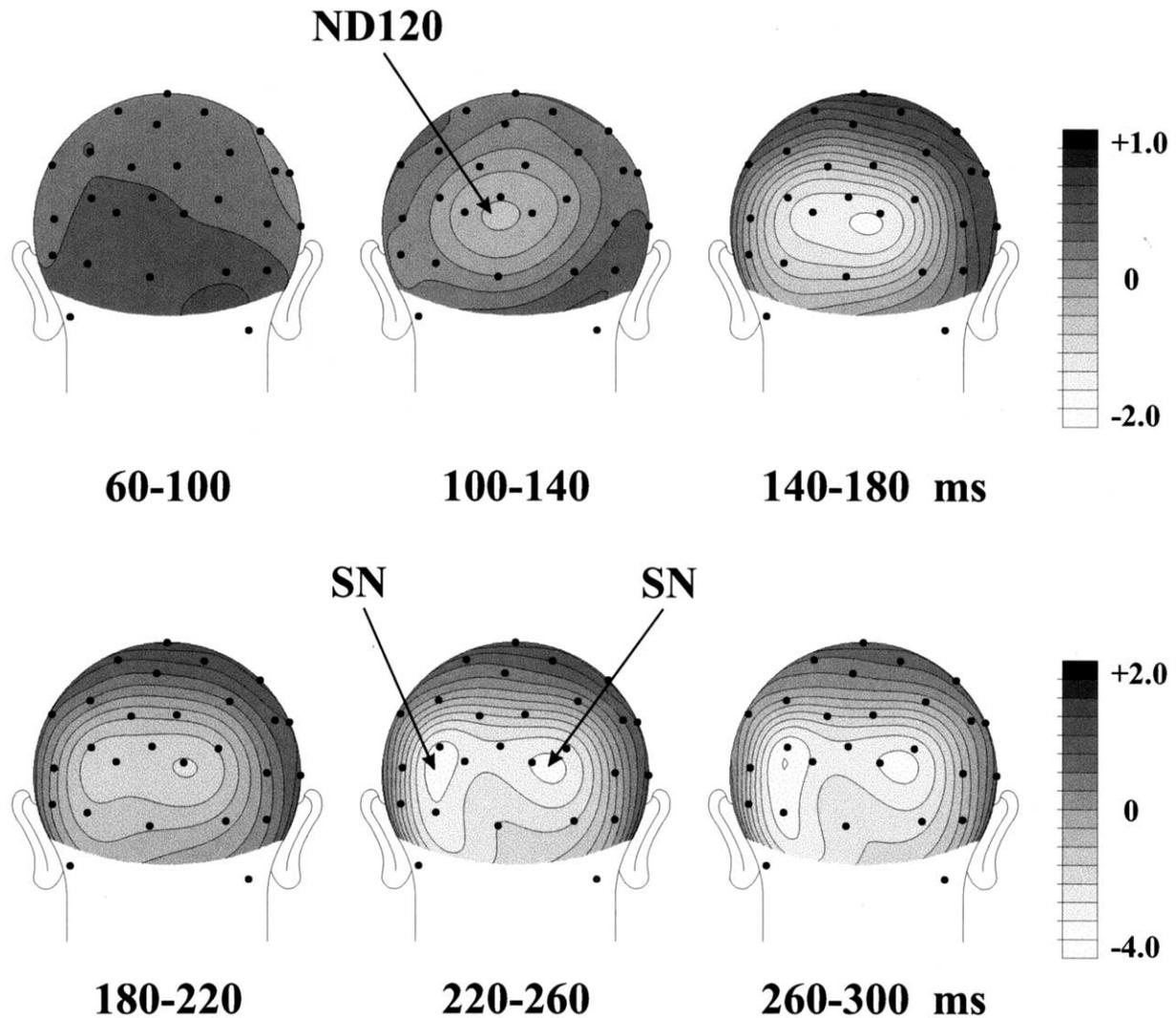


Fig. 4. Topography of high SF attention effects for standard stimuli. Voltage topographies of the high SF standard difference wave (attended minus unattended ERPs) in the intervals used for statistical analyses. The peak of the early phase of the attention effect (ND120) was included in the 100–140 ms interval, whereas the SN was maximal during the intervals 220–260 and 260–300 ms. The SN was larger over the left hemisphere at the longer latencies. Note different voltage scales for upper and lower rows.

different from baseline for targets but not for standard stimuli. Beginning at 180 ms a broad, bilaterally distributed SN appeared, which remained significant relative to baseline until 260–300 ms, with targets generally showing higher significance levels (Table 1). The peak of the SN (at 220–260 ms) in the low SF difference wave also showed significant asymmetry: $F(4, 44) = 3.82$, $P < 0.01$, for interaction of attention \times hemisphere \times electrode sites). Post hoc analyses showed this SN asymmetry to be localized to the most ventro-lateral pair of electrodes (IN5/IN6) with greater negative amplitude at the right hemisphere site (IN6 $>$ IN5, $P < 0.05$).

3.3. Dipole source modeling

From the grand-averaged topographical data described above, the dipolar sources of the evoked C1 and P1 compo-

nents as well as the attention effects (ND120, PD130, and SN/SP components) to standard stimuli were modeled using the BESA algorithm. Table 3 lists the Talairach coordinates of each modeled dipole, obtained by co-registering the dipole locations in the BESA sphere with the MRI scans of 7 individual subjects (see Section 2).

The sensory-evoked C1 and P1 components were modeled for the ERPs elicited by unattended high SF standards. A pair of dipoles, mirror-symmetrical in location but unconstrained in orientation, was fit to the unattended grand average C1 distribution over the interval of 64–80 ms. To account for the evoked P1 component, another pair of dipoles (also constrained to be mirror-symmetrical in location but allowed to vary orientation) was added to the model and fit over the time interval of 80–124 ms. The resulting dipole locations in the BESA sphere are shown in Fig. 7 (top) along with the time course of the modeled activity for

Unattended Low Frequency Standards

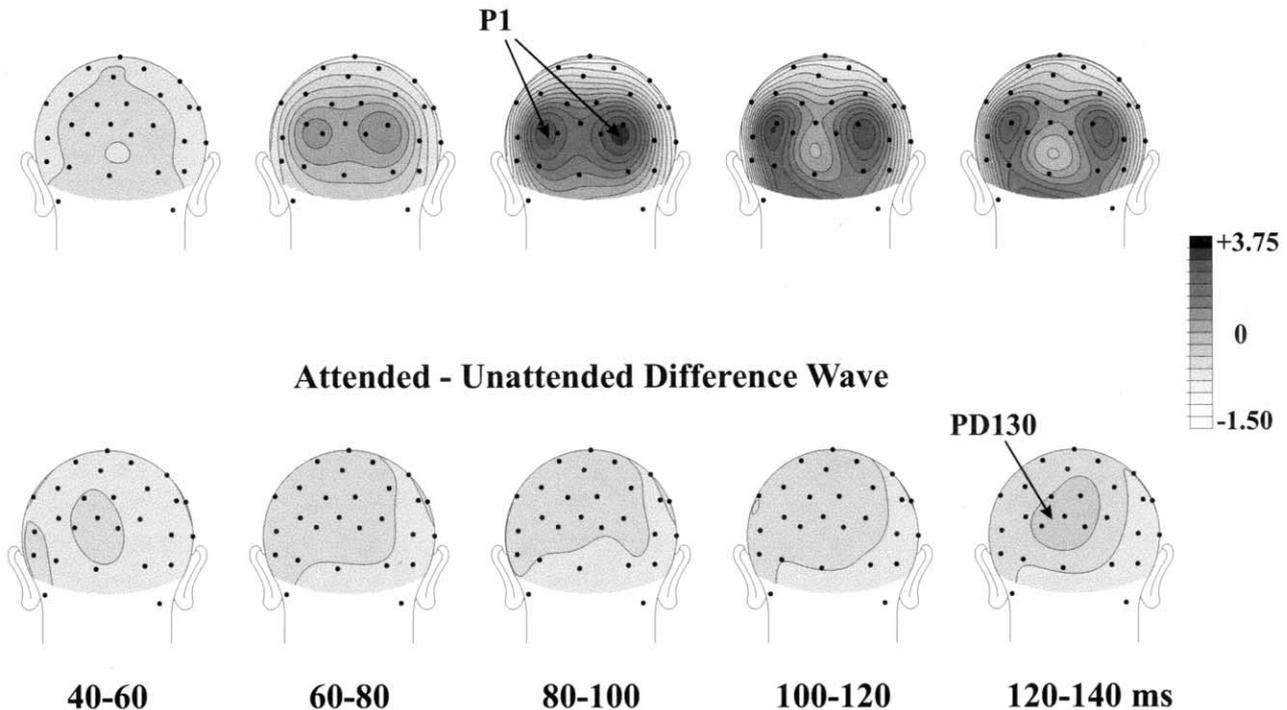


Fig. 5. Topographical distributions of ERPs to unattended low SF standards (top) compared with the early phase of the attentional difference wave for standards (bottom). Voltage topography maps at 20 ms intervals show the differences in onset latency and distribution of the unattended P1 component (top) and the PD130 attention effect (bottom).

each dipole. Fig. 7 (bottom) shows the locations of the modeled dipoles projected onto the corresponding brain sections of a single subject. This projection is intended to give only an approximation of the anatomical region of component origin. The dipoles corresponding to C1 (1 and 2) were situated in medial occipital cortex in or near the calcarine fissure, whereas the dipoles accounting for P1 (3 and 4) were localized to lateral extrastriate cortex in or near the middle occipital gyrus. Together, these paired C1 and P1 dipoles accounted for 96.3% of the variance in the scalp distribution of the unattended high frequency ERPs over the latency range of 64–124 ms.

The attentional difference wave for the high SF standard stimuli was fit sequentially with paired dipoles over the intervals of 102–120 ms (to account for the ND120) and 186–274 ms (to account for the SN). A pair of location-symmetrical dipoles situated in medial dorsal occipital cortex, lateral to the calcarine fissure, accounted for the ND120 attention effect, whereas the SN dipole pair was localized in ventral occipital cortex within the fusiform gyrus (Fig. 8). This BESA model accounted for 98.5% of the variance in the 102–274 ms latency range. Interestingly, the source waveform for the dipole accounting for the ND120 extended well beyond the 102–120 ms interval for which it was fit, suggesting that the early attention-related activity was sustained and overlapped with the SN.

The ERPs elicited by unattended low SF standards were also modeled sequentially with two pairs of dipoles symmetrically constrained in location. The first pair, fit in the latency range of 54–80 ms, accounted for the early phase of the evoked P1 component and was localized in dorso-medial occipital cortex. The late phase of the evoked P1 was modeled over the interval 72–128 ms and was localized to more lateral portions of dorsal extrastriate cortex (Fig. 9). Together, these two dipole pairs accounted for 97.4% of the total variance in the data across the interval 54–128 ms.

The low SF standard attentional difference wave was modeled in two successive latency ranges, 106–142 and 142–278 ms in order to account for the PD130 and the longer-latency SN, respectively. Both attention effects were fit with pairs of dipoles constrained to be mirror-symmetrical in location. The PD130 dipoles were situated in dorsal occipital cortex, whereas the SN dipole pair was localized to ventral occipital cortex within the fusiform gyrus (Fig. 10). This dipole model for the low SF attention effects accounted for 96.4% of the total variance in the latency interval of 106–278 ms.

4. Discussion

The present experiment investigated the spatio-temporal

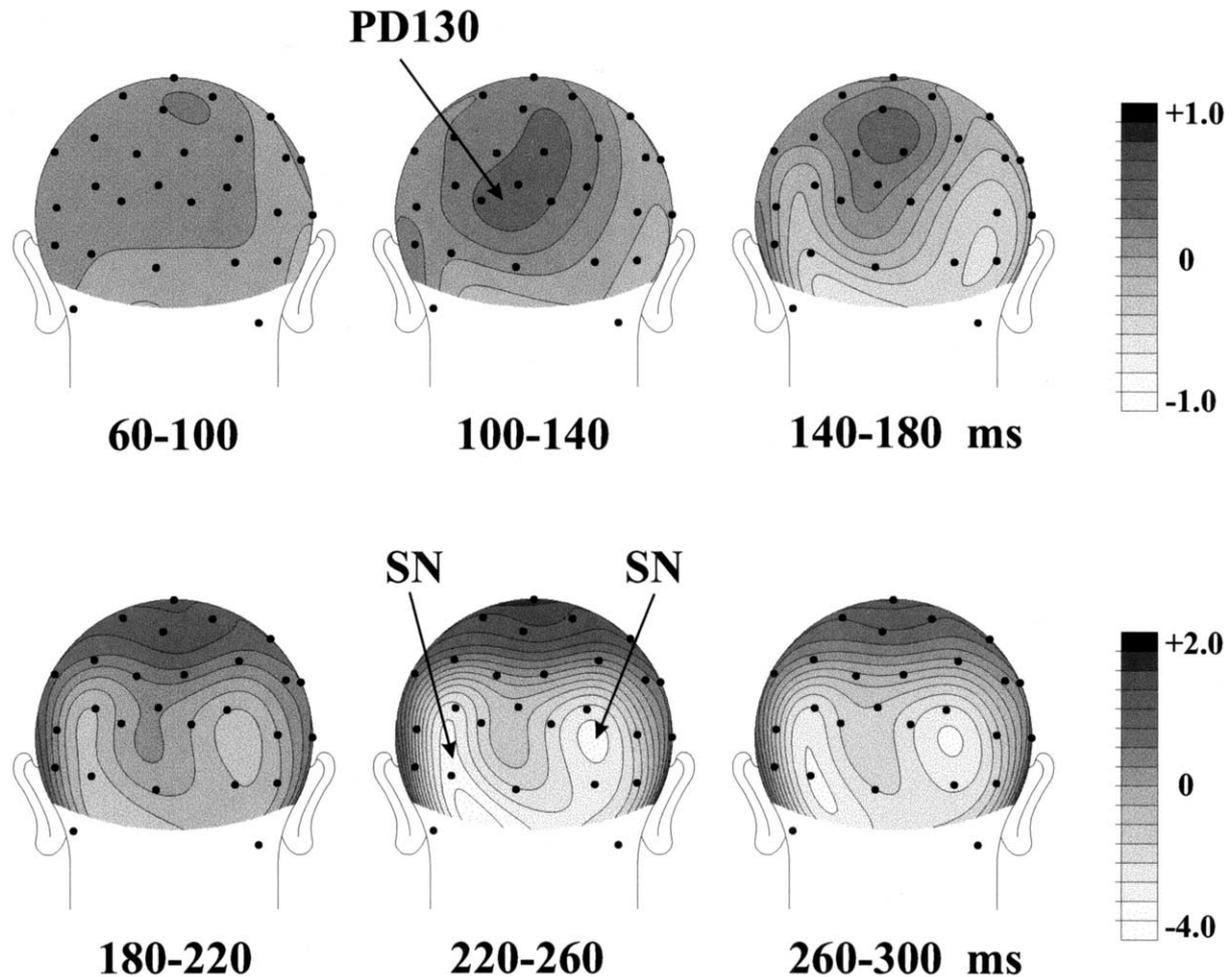


Fig. 6. Topography of low SF attention effect for standard stimuli. The voltage topography of the attentional difference wave formed by subtracting unattended low SF standards from attended low SF standards is shown for the same 40 ms intervals used for statistical analyses. The PD130 was maximal in the 100–140 ms latency range, whereas the SN peaked at 220–260 ms. The SN at longer latencies showed greater negative amplitude over the right hemisphere at ventral–lateral scalp sites.

characteristics of the brain processes underlying selective attention to SF. The major focus was on finding out whether attention to SF produces a modulation of sensory-evoked neural activity beginning at the earliest stages of visual processing, as has been reported previously for attention to location. This issue was investigated by recording ERPs in a paradigm that required highly focused attention on the SF content of attended stimuli in order to discriminate infrequent targets. The behavioral results obtained in this experiment indicate that subjects were able to effectively focus attention on a given SF and accurately detect targets. A detailed spatio-temporal analysis of the ERP attention effects, however, did not support the hypothesis that the earliest sensory-evoked components were modulated by attention. Rather, the ERP attention effects occurred at longer latencies and arose from different neural generators than the early sensory-evoked responses. In addition, lateral asymmetries were observed in the ERPs associated with attention to high and low SF stimuli that were indicative of hemispheric specialization for the processing of SF information.

4.1. Short-latency evoked components

The high and low SF stimuli evoked distinctly different early sensory components as seen both in the attended and unattended waveforms. The high SF standards evoked a short-latency (onset at 50–60 ms, peak at 90–100 ms) negative component, here termed the C1, which had a narrowly focused midline occipital scalp distribution. A similarly distributed early negativity peaking at around 115 ms (the N115) was observed by Zani and Proverbio (1995) in response to high SF checkerboards. Inverse dipole modeling of the neural generators of the C1 was in accord with recent evidence (Clark et al., 1995; Clark and Hillyard, 1996; Bruin et al., 1998; Lange et al., 1998; Martínez et al., 1999; Kenemans et al., 2000) that this early negativity (sometimes called the NP80) originates from sources in primary visual (striate) cortex and probably represents the initial volley of sensory information into the primary visual cortex. The ERP to the high SF stimuli also included an early positive (P1) component in the latency range 70–

Table 3
Talairach coordinates of modeled dipoles^a

Low spatial frequency				High spatial frequency			
	<i>x</i>	<i>y</i>	<i>z</i>		<i>x</i>	<i>y</i>	<i>z</i>
<i>Unattended wave</i>							
P1 (early, RH)	17	−83	24	C1 (RH)	5	−97	−3
P1 (early, LH)	−15	−83	23	C1 (LH)	−5	−97	−3
P1 (late, RH)	34	−71	19	P1 (RH)	48	−78	2
P1 (late, LH)	−39	−72	18	P1 (LH)	−39	−82	2
<i>Difference wave (attended–unattended)</i>							
PD130 (RH)	23	−82	25	ND120 (RH)	13	−85	16
PD130 (LH)	−23	−81	24	ND120 (LH)	−13	−85	16
SN (RH)	22	−63	−13	SN (RH)	23	−45	−16
SN (LH)	−23	−64	−14	SN (LH)	−24	−47	−14

^a Talairach coordinates of the calculated dipolar sources averaged across subjects for high and low spatial frequency attention effects (top), and sensory-evoked components in the unattended waveforms (bottom).

130 ms that was more laterally distributed over the occipital scalp and had dipolar sources estimated to lie in lateral extrastriate occipital cortex.

In contrast with the ERPs to the high SF stimuli, no midline C1 component was evoked by the low SF stimuli. Instead, low frequency stimuli evoked only a prominent P1 component during the interval 60–150 ms, which had bilateral amplitude maxima over the lateral occipital scalp. This P1 included early and late phases (peaking at roughly 80 and 120 ms, respectively) that could be modeled accurately by pairs of dipolar generators localized to medial and lateral occipital extrastriate visual cortex, respectively.

Many previous studies have demonstrated waveform differences between early ERP components evoked by high and low SF stimuli similar to those observed here (reviewed in Kenemans et al., 2000). The general finding has been that higher SF stimuli (both checkerboards and linear gratings) elicit a larger early negativity (C1) over midline occipital areas in the interval 50–110 ms. On the basis of a dipole modeling analysis, Kenemans et al. (2000) concluded that this early negativity to higher SF stimuli had a likely origin in striate cortex, while the bilaterally distributed positivity (P1) to low SF stimuli arose from more lateral extrastriate sources; this accords well with the present analysis. These ERP differences as a function of SF may be related to the mapping of SF in the visual cortex. In an fMRI study, Tootell et al. (1998) found that the foveal representations in the retinotopic visual areas were selectively activated by high SFs, whereas the cortical representations of the peripheral retina responded preferentially to low SFs. Since the foveal projection in striate cortex is at the occipital pole, it might be expected that midline-recording sites over the pole would pick up a large early response to high SF stimuli. Given the close spatial and temporal proximity of early striate and extrastriate activations, however, it is possible that the earliest ERP components represent an amalgam of these sources, which would vary in location according to the mapping of SF onto the different visual–cortical areas.

4.2. Short-latency attention effects

The earliest effect of attention on the ERP to high SF was an increased negativity over midline occipital sites in the latency range 100–140 ms (ND120). Zani and Proverbio (1995) observed a similar effect, which they interpreted as a modulation of early sensory-evoked neural activity, perhaps in primary visual cortex. The evidence reported here, however, shows a clear temporal dissociation between the ND120 attention effect and the earliest evoked component (C1) that has been ascribed to primary visual cortex generators. Whereas the C1 had an onset latency of 60 ms following stimulus presentation, the ND120 seen in the attentional difference wave did not begin until around 100 ms. This latency difference indicates that the earliest effect of attention to high SF (i.e., the ND120) does not represent a modulation of the initial sensory-evoked neural response in striate cortex. The lack of attentional modulation of the C1 component found here is consistent with previous studies showing no attention effects on C1 (NP80) in spatial attention tasks (Clark and Hillyard, 1996; Wijers et al., 1997; Bruin et al., 1998; Martínez et al., 1999).

The scalp topography of the ND120 attention effect was similar to that of the earlier C1 component but differed significantly from it in being distributed more broadly and superiorly over midline occipital areas. The resulting dipole model accounting for the ND120 placed the sources in dorsal extrastriate cortex superiorly and lateral to the calcarine fissure, whereas the dipoles fit to the C1 distribution were situated more medially, within or adjacent to the calcarine fissure. Considering the inherent uncertainties of inverse dipole modeling, however, the possibility cannot be ruled out that the C1 and ND120 arise in part from common neural generators, perhaps in both striate and extrastriate areas. If this were the case, the ND120 would evidently reflect delayed activity in those early visual areas, perhaps resulting from feedback from higher areas (see Martínez et

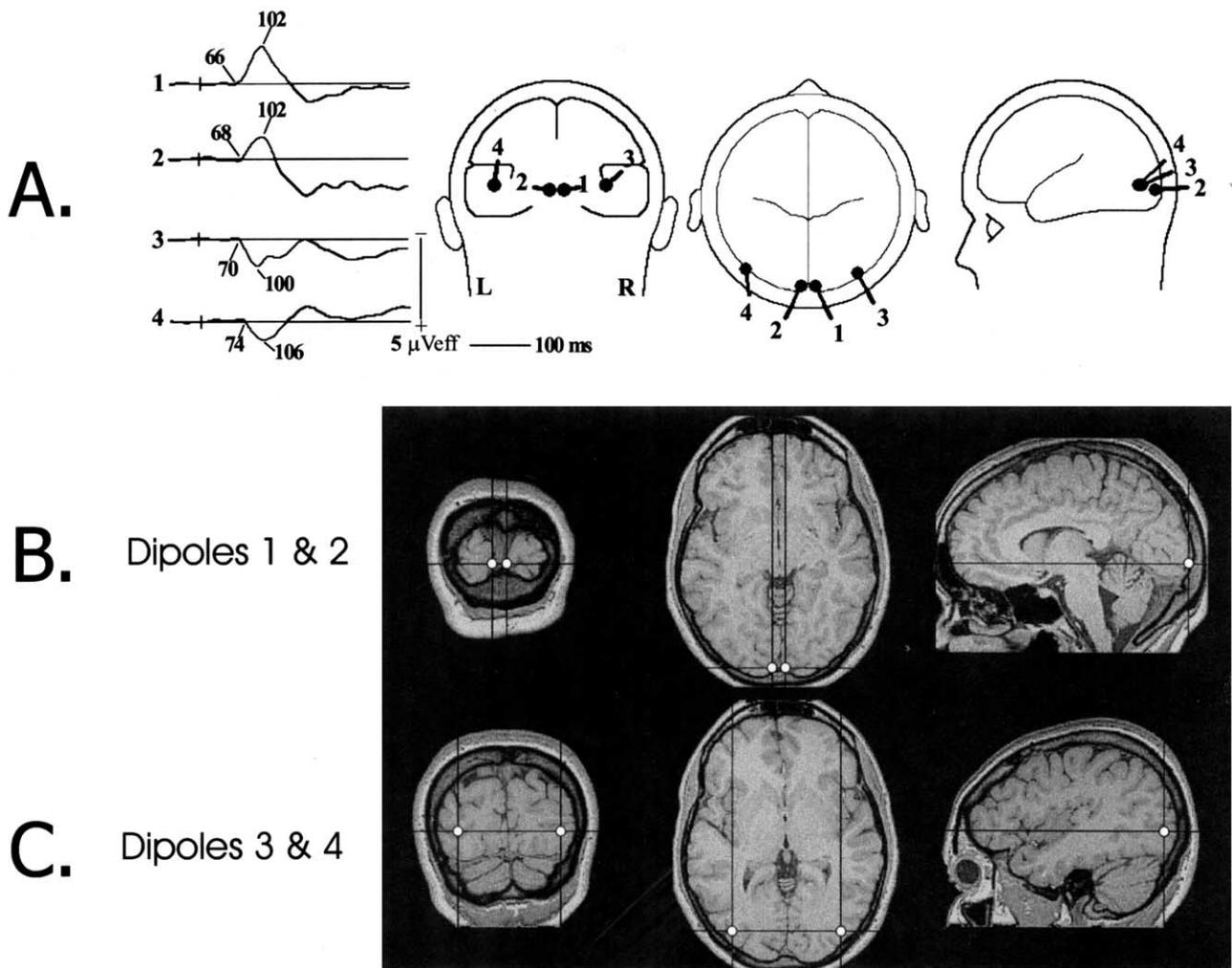


Fig. 7. Dipole model of ERPs to unattended high SF standard stimuli. (A) The positions of the estimated dipolar sources for the unattended C1 (64–80 ms, dipoles 1 and 2) and P1 components (80–124 ms, dipoles 3 and 4) elicited by high SF stimuli are shown in the BESA sphere. Source waveforms at the left show the time course of the modeled activity for each dipole. The estimated anatomical locations (in Talairach coordinates) of the C1 (B) and P1 (C) dipole pairs (indicated by white dots) are shown projected onto coronal, axial, and sagittal sections from an individual subject. The left hemisphere is shown on the left of the coronal and axial images. Sagittal images are of the right hemisphere.

al., 1999; Martínez et al., 2001). In any event, differences in timing and scalp distribution make it clear that the ND120 does not represent a modulation of the earliest evoked activity in the visual cortex.

The attention effect for high SF stimuli reported by Zani and Proverbio (1995) also included an early positivity (P1 at 70–110 ms) that was enlarged at lateral occipital sites to attended stimuli. In contrast, we found the early P1 in the same latency range to remain unaffected by attention and the longer-latency attention effect (ND120) to be uniformly negative over the posterior scalp. The reason for this discrepancy is unclear, but differences between the two studies in discrimination task, stimulus presentation rate, and number of alternative stimuli may be responsible. In particular, in the present study stimuli having only two distinctive SFs were presented at a rapid rate (inter-stimulus intervals, ISIs, of 0.3–0.55 ms), while in the study of Zani and Proverbio (1995) 6 alternative SFs were presented at ISIs of 1.0–1.5 s.

It is important to note, however, that virtually identical patterns of attention effects were observed here for the standard and slightly deviant target stimuli, which indicates that the subjects' attentional focus was broad enough to encompass both the standard and target SFs.

In contrast with high SF, attending to low SF stimuli was associated with an initial positive shift (PD130) in the latency range 100–140 ms in the attentional difference wave. Zani and Proverbio (1995) also observed an increased initial positivity in response to attended low SF checkerboards, but their effect occurred earlier (70–110 ms) and overlapped in time with the unattended P1 component. In the present study, however, the PD130 attention effect was clearly dissociable from the unattended P1, which onset earlier (60–70 ms) and had a very different topographical distribution. Whereas the unattended P1, (both early and late phases) had bilateral amplitude maxima over the lateral occipital scalp, the PD130 had a central occipital maximum.

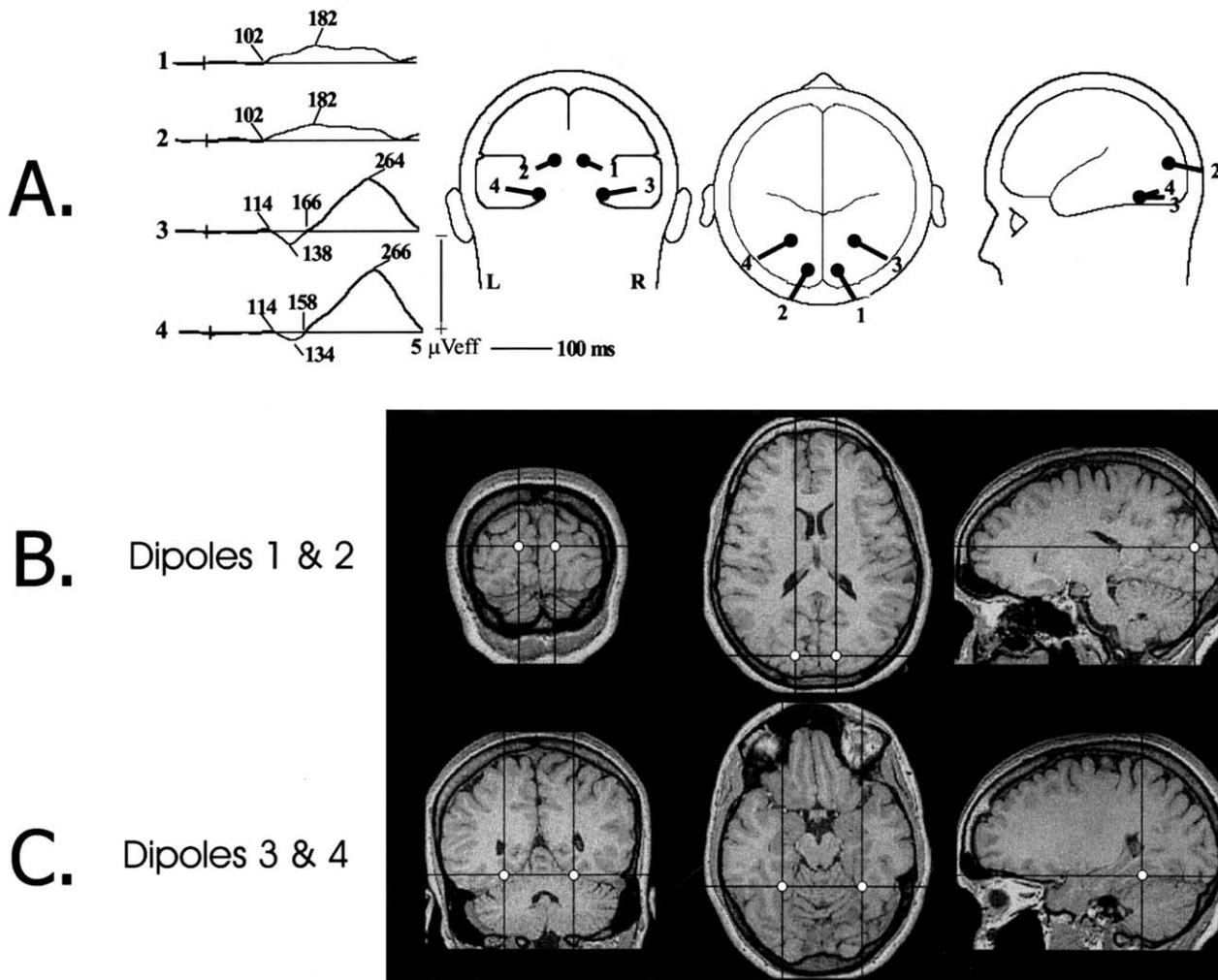


Fig. 8. Dipole model of standard high SF attention effects. (A) The early and late phases of the attentional difference wave for high SF *standard* stimuli were modeled in the latency ranges of 102–120 and 186–274 ms, respectively. The source waveforms of the ND120 (dipoles 1 and 2) and the SN (dipoles 3 and 4) are shown on the left. The estimated locations of these dipoles are projected onto anatomical images of an individual subject in (B, C), respectively, with registration procedures and image orientations as in Fig. 7.

These differences in timing and topography are not consistent with the hypothesis that attention to SF involves an amplitude enhancement of the early sensory-evoked P1 under the conditions of the present study.

The PD130 attention effect observed here was not only delayed in relation to the P1 attention effect reported by Zani and Proverbio (1995), but its midline scalp topography contrasted with the lateral occipital maxima of their P1 effect. Kenemans et al. (1993) also reported a small but significantly enlarged early positivity (70–110 ms) to attended SF stimuli in a design where subjects attended jointly to SF and orientation; this enlarged positivity, however, was recorded at medial occipital sites, at which Zani and Proverbio had found reduced early positivity. This picture is further complicated by reports of Heslenfeld et al. (1997) and Kenemans et al. (in press), who used designs very similar to that of Kenemans et al. (1993) and failed to replicate such an early positive modulation. Clearly, further work is needed to define the conditions under

which early positivity in the P1 range may be enhanced by attention to SF and to establish its reliability.

4.3. Mechanisms of early attention effect

The present ERP data strongly suggest that paying attention to high and low SFs is mediated by distinctive brain mechanisms indexed by the ND120 and PD130, respectively. It is not clear, however, whether these components reflect qualitatively different selection operations, or whether they differ in polarity because of the cortical geometry associated with the mapping of high and low SFs onto the visual areas. It is also difficult to determine whether these distinctive ERP patterns represent endogenous cortical activity related to attention or an amplitude modulation of longer-latency exogenous (evoked) components in the 100–150 ms range. Although exogenous components having a similar time course and scalp distribution to the ND120 and PD130 attention effects were not

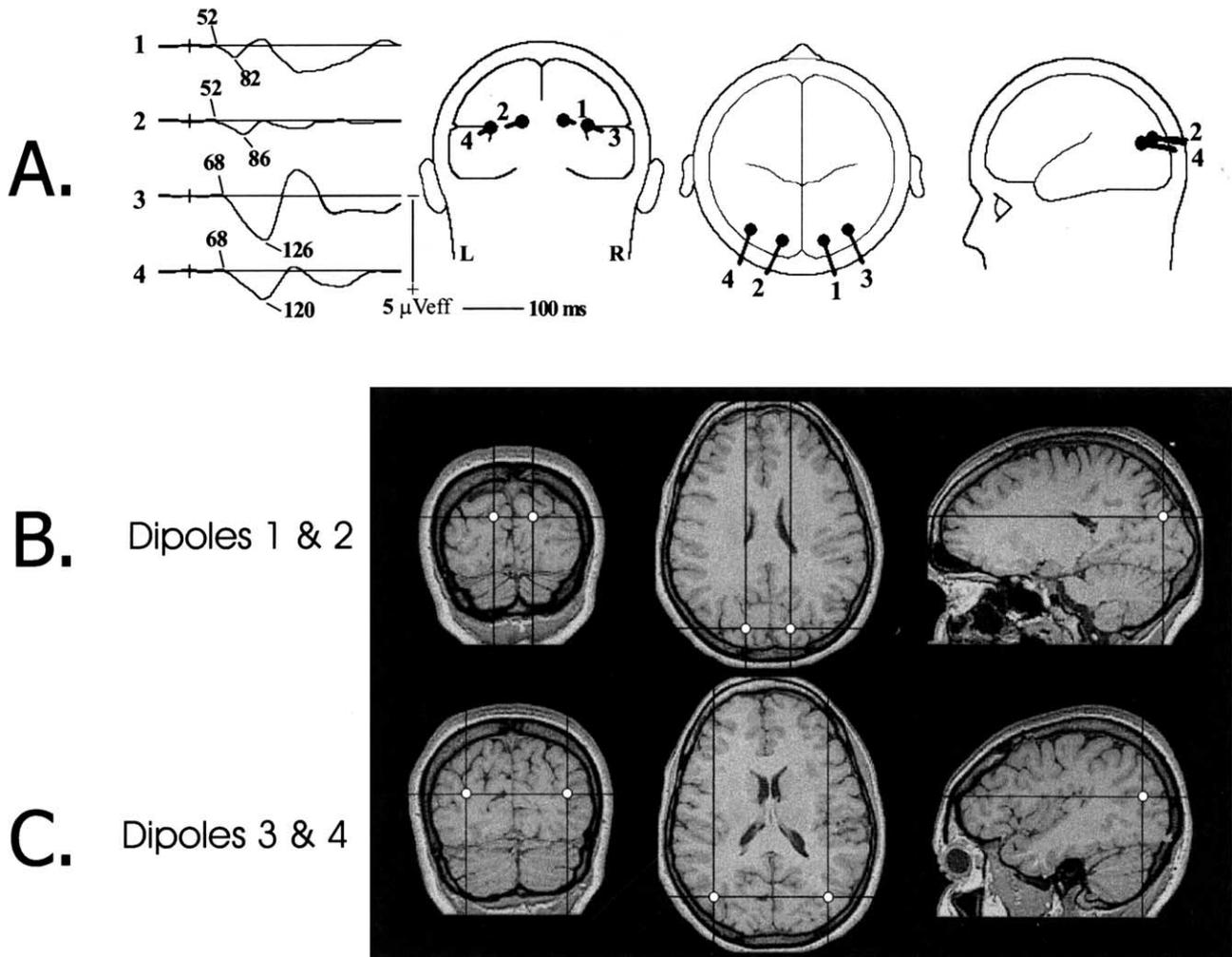


Fig. 9. BESA model of ERPs to unattended low SF standard stimuli. (A) The early and late phases of the P1 component elicited by unattended low SF standards were modeled in the latency intervals of 54–80 and 72–128 ms, respectively. The symmetrical dipole pairs (dipoles 1 and 2, early phase; dipoles 3 and 4, late phase) are projected onto anatomical images of an individual subject in (B, C), respectively. Co-registration procedures and image orientations are as in Fig. 7.

evident in the unattended waveforms, the presence of such components at low amplitude cannot be ruled out. If these attention effects do represent a modulation of SF-specific evoked neural activity, however, it should be emphasized that this was not evident for the earliest frequency-specific components in the 60–100 ms range. Rather, the initial selection for SF was manifested in neural activity beginning at about 100 ms after stimulus onset with estimated sources in dorsal extrastriate visual cortex.

An alternative mechanism to consider is that spatial attention makes a contribution to the ND120/PD130 effects observed here. This possibility derives from the close similarity of the scalp distributions of the ND120 and PD130 attention effects, which suggests that they could arise at least in part from a common source of neural activity. Indeed, the scalp topographies of the ND120 and PD130 did not differ significantly (after conversion to a common polarity), as evidenced by a non-significant component \times electrode site interaction in the 100–140 ms interval;

$F(4, 44) < 1$. According to one scenario, a component that is elicited in the 100–140 ms range by both high and low SF stimuli might be increased in positive amplitude during the attend-low SF condition and reduced in positive amplitude during attention to high SF. Such an effect could occur, as was recently proposed by Heinze et al. (1998), if attention to low SF stimuli entailed an expansion of the diameter of the ‘spotlight’ of spatial attention, thereby facilitating visual input over a broader area and increasing the relative amplitude of the positive-going component in that condition. Again, however, it should be cautioned that no such component with a midline distribution was evident at 100–140 ms in the unattended waveforms.

Another possible mechanism to consider is that subjects might attend to some small portion of the display that distinguished the high and low SF stimuli rather than to the overall SF cue. This is conceivable because each of the 4 types of stimuli (high and low SF, standards and targets) was identical on every presentation, such that some small region of

the display might have a light/dark pattern that differentiated among the attended and unattended stimuli. Such a possibility also exists in previous studies of attention to SF where the check phase was also kept constant from one presentation to the next of each stimulus. In the present study, however, the finding that the attention-related ERP modulations were nearly identical for the standards and targets at each SF greatly reduces the possibility that a small patch of the display was used as the basis for selecting high from low SF stimuli. Since the standards and targets differed slightly in SF, the phase difference between them shifted continuously across the display, and subjects would be hard-pressed to locate a small zone of the display that would easily differentiate both the standards and targets of one SF from both the standards and targets of the other SF. Thus, the ERP results indicate that the subjects did indeed use the SF cues to distinguish between relevant and irrelevant stimuli.

A variant on the above mechanism might come into play if subjects attempted to perform the task by directing attention to one side of the display rather than by maintaining attention centered on the stimulus. This also would seem to be an unlikely strategy, primarily because the reduction in visual acuity at increased eccentricities would impair performance. Moreover, if attention were directed laterally, this would be revealed in a particular ERP signature – an enlarged P1 component over the hemisphere contralateral to the attended visual field (Heinze et al. 1990, 1994). The expected result would be that this contralateral P1 would be elicited by stimuli of both SFs that were presented during runs when attention was so lateralized. If attention was differentially lateralized during the attend-high and attend-low SF conditions, then P1 asymmetries of opposite polarity would be seen in the attentional difference waves for the high and low SF stimuli. Since no such pattern was discernable in the data, we suggest that lateralized spatial attention

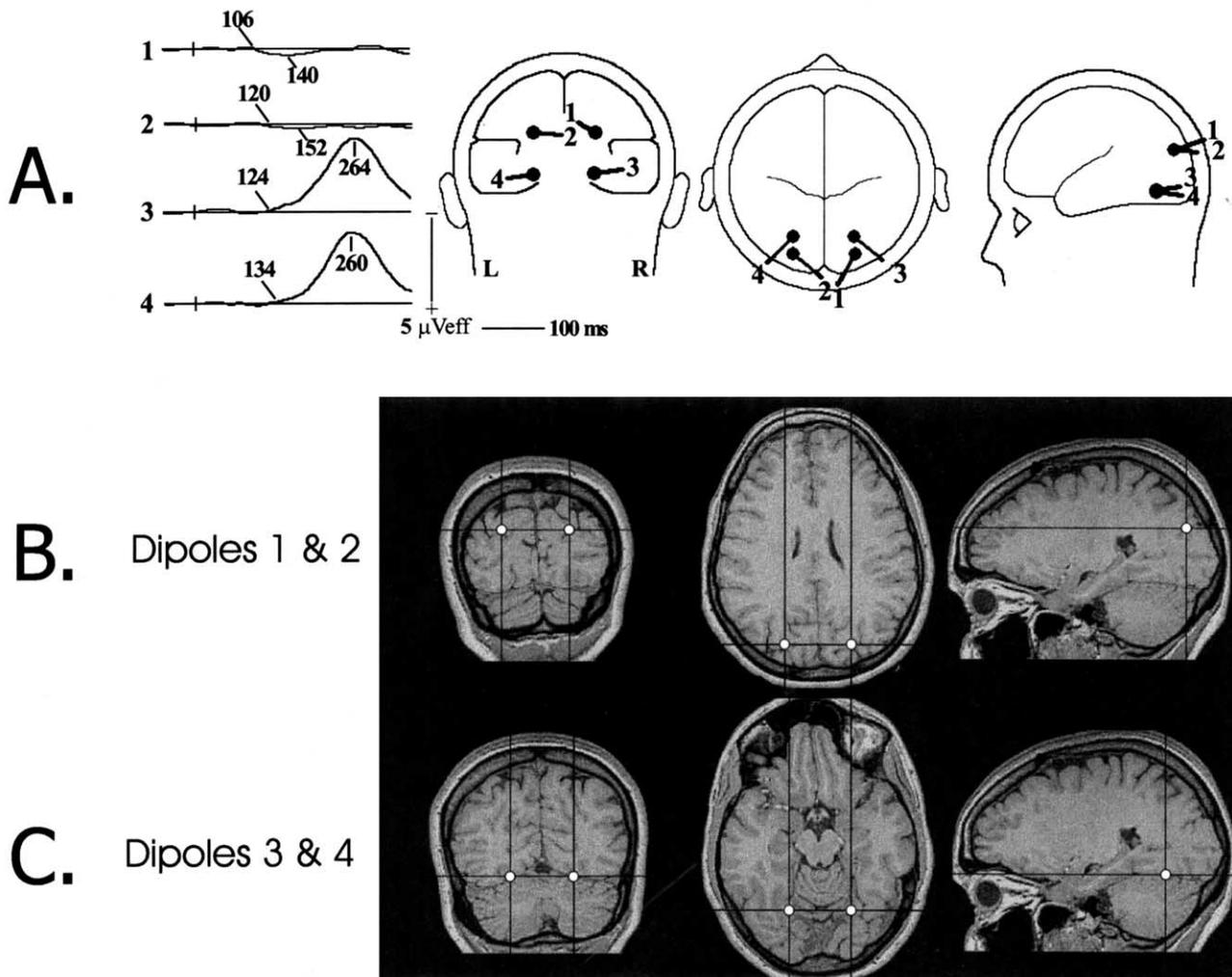


Fig. 10. BESA model of standard low SF attention effects. (A) The PD130 attention effect for low SF standard stimuli was modeled in the interval 106–142 ms (dipoles 1 and 2), and the longer-latency SN associated with attention to low SFs was fit in the interval 142–278 ms. These dipole positions are projected onto anatomical images of an individual subject in (B, C), respectively, with registration procedures and image orientations as in Fig. 7.

was not likely to have played a role in the ERP asymmetries that were found in this study.

4.4. Selection negativity

As in previous reports (Harter and Previc, 1978; Kenemans et al., 1993; Zani and Proverbio, 1995, 1997; Heslenfeld et al., 1997), the most prominent ERP manifestation of attention to SF was a broad SN extending over the latency range of 150–350 ms post-stimulus onset. For both high and low SFs, the SN was bilaterally distributed over the occipital scalp and dipole modeling identified bilateral generators located within ventral occipital cortex in or near the fusiform gyrus. Previous dipole modeling studies have also localized the SN associated with attention to color (Anllo-Vento et al., 1998) and SF (Heslenfeld et al., 1997) to ventral occipital cortex.

Variations in scalp topography have been reported for SNs elicited by the selection of different types of stimulus features (Anllo-Vento and Hillyard, 1996), suggesting that these SNs may reflect activity within different ventral visual areas specialized for processing the specific task-relevant feature dimension. In the present study, however, it is important to note that the earliest attention effects (ND120 and PD130) differed markedly in scalp topography (and in estimate source location) from the later SN, indicating that the initial selection for SF is carried out by different mechanisms from those manifest in SN.

4.5. Hemispheric asymmetries

The SNs associated with attending to high and low SFs were found to be asymmetrically distributed between the cerebral hemispheres in the 220–300 ms range. The SN elicited by attended high SF standards was enhanced at ventral-lateral electrode sites of the left hemisphere, whereas low SF standards elicited a SN with greater negative amplitude over ventral-lateral right hemispheric scalp sites. These hemispheric asymmetries are consistent with numerous behavioral and neuropsychological studies suggesting that the cerebral hemispheres are differentially biased for processing high and low SF. In particular, it has been hypothesized that the right hemisphere preferentially processes low SF information, whereas the left hemisphere is specialized for processing information contained in high SFs (see Ivry and Robertson, 1998).

A significantly asymmetrical distribution was also observed for the early phase of the high SF attention effect (ND120), with greater amplitude over ventro-lateral scalp sites of the left hemisphere. Zani and Proverbio (1995) similarly found their N115 to be more prominent over the left hemisphere for higher SFs, but this asymmetry was not related to attention. In general, these results are concordant with proposals that some degree of hemispheric specialization exists for processing high vs. low SF information. Moreover, the present ERP data suggest that this lateralized specialization affects the earliest phases of attentional selec-

tion as well as longer-latency processing in the ventral visual-cortical areas.

5. Conclusions

In contrast with the reports of Zani and Proverbio (1995, 1997) but in agreement with the studies of Heslenfeld et al. (1997), de Rooter (1998) and Kenemans et al. (in press), we found no evidence that attention to SF involves modulation of early-evoked activity in size-specific neural pathways in the 60–100 ms range. Instead, the earliest ERP signs of selection for SF began at around 100 ms in the form of increased negativity (ND120) to attended high SF stimuli and increased positivity (PD130) for attended low SF stimuli. This polarity difference plus the lateralization of the ND120 to the left hemisphere suggests that specialized cortical mechanisms participate in the selection of high and low SF information. Following this initial selective processing, which was estimated to take place in dorsal extrastriate occipital cortex, a broad SN was elicited by attended stimuli of both SFs in ventral visual areas in or near the fusiform gyrus. This SN resembles that elicited by stimuli that are selected on the basis of other non-spatial stimulus features and may index neuronal activity within ventral visual stream areas specialized for the processing of different visual features including SF information. The SNs elicited during attention to high and low SF were asymmetrically lateralized to the left and right hemispheres, respectively, consistent with current models of hemispheric specialization for SF processing.

The present results add to the body of evidence indicating that only spatial attention involves a mechanism of amplitude modulation of the early-evoked components prior to 100 ms. Studies employing scalp topography and source localization techniques have found that the increase in P1 amplitude for attended-location stimuli represents at least in part an amplitude modulation of the P1 elicited by unattended stimuli (reviewed in Mangun, 1995; Heslenfeld et al., 1997; Hillyard and Anllo-Vento, 1998). Indeed, the ERP pattern of enhanced occipital P1 (70–120 ms) together with occipital N1 (160–190 ms) and frontal N1 (140–160 ms) amplitudes has been proposed to be a unique index of spatial attention (Hillyard and Anllo-Vento, 1998). The increased P1 amplitude reported by Zani and Proverbio (1995, 1997) during attention to SF appears to represent an exception to this proposal, however, at least insofar as P1 is concerned. Another apparent exception is the finding by Valdes-Sosa et al., (1998) of increased P1 (115–180 ms) and N1 (215–290 ms) amplitudes to attended color-motion conjunctions, although the latencies here were longer than those generally observed in spatial attention experiments. These important findings need to be followed up to determine the conditions under which such early ERP effects may occur during attention to non-spatial features and to carry out the spatio-temporal

analyses required to verify a mechanism of amplitude modulation of early-evoked components.

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