Neural Sources of Focused Attention in Visual Search

Previous studies of visual search in humans using event-related potentials (ERPs) have revealed an ERP component called 'N2pc' (180–280 ms) that reflects the focusing of attention onto potential target items in the search array. The present study was designed to localize the neuroanatomical sources of this component by means of magnetoencephalographic (MEG) recordings, which provide greater spatial precision than ERP recordings. MEG recordings were obtained with an array of 148 magnetometers from six normal adult subjects, one of whom was tested in multiple sessions so that both single-subject and group analyses could be performed. Source localization procedures revealed that the N2pc is composed of two distinct neural responses, an early parietal source (180–200 ms) and a later occipito-temporal source (220–240 ms). These findings are consistent with the proposal that parietal areas are used to initiate a shift of attention within a visual search array and that the focusing of attention is implemented by extrastriate areas of the occipital and inferior temporal cortex.

Introduction

Searching a cluttered visual scene for objects of interest is a fundamental task for the primate visual system. To study this aspect of visual perception, many researchers have used visual search tasks in which subjects search for a predefined target in an array containing multiple items (Treisman and Gelade, 1980; Luck and Hillyard, 1995; Braun and Julesz, 1998; Luck and Ford, 1998). The present study examines the neural substrates of visual search by localizing the source of an event-related potential (ERP) component that reflects the focusing of attention onto a visual search target (Luck et al., 1990, 1997b; Luck and Hillyard, 1994a,b). This ERP component is called the 'N2pc' wave to indicate its latency range (180–280 ms) and its unique posterior contralateral scalp distribution. Specifically, the N2pc is observed as a negative-going voltage deflection at scalp sites contralateral to the position of a target object within a bilateral stimulus array. That is, the N2pc is more negative at left hemisphere electrode sites for right visual field (RVF) targets than for left visual field (LVF) targets, and it is more negative at right hemisphere electrode sites for LVF targets than for RVF targets (Luck and Hillyard, 1994a,b).

Several experiments have linked the N2pc wave with the focusing of attention. First, the N2pc component is present for targets and also for nontarget stimuli that require careful scrutiny to be distinguished from the distractors, but it is absent for nontargets that can be rejected on the basis of a salient feature (Luck and Hillyard, 1994b). Second, the N2pc is substantially reduced in amplitude when attentional demands are reduced by eliminating the distractors (Luck and Hillyard, 1994b) or by reducing the number of nearby distractors (Luck et al., 1997b).

Third, the N2pc component is larger for conjunction targets than for feature targets (Luck and Hillyard, 1995; Luck et al., 1997b), which corresponds with the greater attentional requirements of conjunction targets. Fourth, the N2pc switches rapidly from hemisphere to hemisphere during difficult visual search tasks, mirroring the shifts of attention predicted by serial models of visual search performance (Woodman and Luck, 1999). Moreover, the N2pc component appears to be related to attention-related modulations of single-unit activity that have been observed in monkeys in the infero-temporal cortex and area V4 (Chelazzi et al., 1993, 1998; Chelazzi and Desimone, 1994; Luck et al., 1997b). Specifically, both the N2pc and these single-unit attention effects are larger for difficult discrimination tasks than for simple detection tasks, are larger when distractors are near to the target and are larger for tasks that require target localization. Thus, localization of the N2pc component will be very useful for understanding the neural and cognitive mechanisms of attention in visual search.

Previous ERP experiments have shown that the N2pc component has a largely posterior scalp distribution, focused over the lateral occipital cortex (Luck and Hillyard, 1994a). However, ERP localization is greatly limited by the spatial blurring of the voltage distribution produced by the high resistance of the skull. Alternatively, recording the event-related magnetic response of the brain (for a comprehensive outline of this method see Williamson and Kaufman, 1987; Hari and Lounasmaa, 1989; Hämäläinen et al., 1993) is much less compromised by limitations due to skull and scalp conductivities (Hämäläinen et al., 1993) and allows a fairly high localization accuracy (Yamamoto et al., 1988). With the recent availability of whole-head recording systems, magnetoencephalography (MEG) has provided valuable knowledge about cortical regions involved in visual processing (Aine et al., 1995; Portin et al., 1998; Aihlors et al., 1999; Halgren et al., 2000; Vanni and Uutela, 2000). The present study aimed to provide a more detailed localization of the N2pc component by recording the magnetic analog of the N2pc component. We expected that the majority of N2pc activity would occur along the ventral pathway, potentially including a number of visual areas (e.g. the human homologues of area V4, TEO, TE). This prediction is based on the N2pc scalp distribution observed in previous electrical recordings (Luck and Hillyard, 1994a) and the similarity between the N2pc and single-unit effects in area V4 and in infero-temporal cortex (Luck et al., 1997b). In addition, because of the important role of the parietal lobes in controlling the direction of attention (Mesulam, 1981; Corbetta et al., 1995; Ralaf and Robertson, 1995), we anticipated that parietal activity might precede the predicted ventral-stream activity.
Materials and Methods

Subjects
Twelve subjects were initially screened in a conventional ERP experiment (data not presented here). From this group, six subjects with good fixation, low noise levels (<20% rejected trials due to eye movement artifacts) and a substantial N2pc effect (>1.5 µV) were selected for the main MEG experiment (three male and three female subjects, mean age 26.5 years, all right handed). Each subject had normal visual acuity and was paid for participation. One of the subjects, labeled AA01, was run in three additional sessions on separate days, resulting in almost 5000 trials per condition for that subject. All experiments were undertaken with the understanding and written consent of each subject.

Stimuli and Procedure
The stimuli used in this experiment are illustrated in Figure 1. Subjects were instructed to attend either to a red bar or to a green bar, and to discriminate whether the attended-color bar was horizontal or vertical in each stimulus array. The stimuli were presented via microcomputer-controlled back projection at a viewing distance of 120 cm. Each stimulus array contained 24 randomly distributed bars, including 22 blue distracter bars (11 on each side) plus one red bar and one green bar that served as potential targets. The red and green bars were always presented on opposite sides of the vertical meridian, either both above or both below the horizontal meridian. Each bar was 0.14 × 1.0° of visual angle and was either horizontally or vertically oriented, selected at random. The minimum distance between bars was 1.4°. Each array was presented for 750 ms, with a variable-duration blank interval of 600–900 ms between arrays. A fixation point was continuously present in the center of the screen, and subjects were instructed to fixate this point and to minimize blinking. Fixation was monitored by an infrared video camera with a zoom lens. Subjects were informed about the quality of fixation between runs. The obtained data were not used during subsequent data analysis.

At the beginning of each trial block, the to-be-attended color for that block (red or green) was designated. For each stimulus array, the subject was instructed to press a left-hand button if the bar of the attended color was vertical or a right-hand button if the bar was horizontal. Speed and accuracy were stressed equally. Subjects performed 12 trial blocks, six with each of the two attended colors. Each block consisted of 200 stimulus presentations, yielding 1200 trials with an LVF target and 1200 trials with an RVF target for each subject. It should be noted that, because both red and green items were present in each array and only the attentional instructions varied, the same physical stimuli were used for LVF and RVF targets, thus avoiding any physical stimulus confounds (Luck et al., 1997b).

Recording and Analysis
The MEG and electroencephalogram (EEG) signals were recorded simultaneously using a BTi Magnes 2500 whole-head MEG system with 148 magnetometers (Biomedical Technologies, Inc., San Diego, CA) for the MEG and an electrode cap (Electrocap International, Eaton, OH) in conjunction with a 32-channel Synamps amplifier (NeuroScan, Inc., Herndon, VA) for the EEG. The EEG was recorded with reference to the right mastoid. The MEG and EEG signals were filtered with a bandpass of DC–50 Hz and digitized with a sampling rate of 254 Hz. The MEG was also subjected to an online noise reduction process that removes a weighted sum of environmentally induced magnetic noise (first-order spatial gradients of the field) recorded by eight remote reference channels that do not pick up brain activity (Robinson, 1989). Artifact rejection was performed offline by removing epochs with peak-to-peak amplitudes exceeding a threshold of 3.0 × 10–12 T for the MEG and 100 µV for the EEG.

Individual head shapes and the sensor frame coordinate system were spatially co-registered by using a Polhemus 3Space Fastrak system to digitize individual skull/scalp landmarks (nasion and left and right preauricular points). The locations of these landmarks in relation to sensor positions were derived on the basis of precise localization signals provided by five spatially distributed coils attached to the head with a fixed spatial relation to the landmarks. These landmarks, in turn, were matched with the individual subjects’ anatomical magnetic resonance (MR) scans. The 32 EEG electrode locations were also digitized to permit co-registration with the coordinate system. To compute the grand average activity over all subjects, the coordinate system for each subject was readjusted to the coordinate system of one subject whose anatomical MR scan was used for the grand-average source analyses. This MR scan was, in turn, spatially normalized into the standardized reference frame of Talairach and Tournoux for the purpose of reporting MEG source localization coordinates (Talairach and Tournoux, 1988).

Separate averages for both MEG and EEG were computed for targets occurring in the LVF and the RVF, and the data were collapsed over the two target colors (red and green). The N2pc was then isolated by computing LVF-minus-RVF difference waves (i.e., difference waves constructed by subtracting the RVF-target waveforms from the LVF-target waveforms). These difference waves eliminated activity due to purely sensory responses, because all arrays contained a red pop-out item in one visual field and a green pop-out item in the other field, with red being attended in some trial blocks and green being attended in others. Any higher-level cognitive activity that was equal for ipsilateral and contralateral targets was also eliminated in these difference waves, leaving only lateralized cognitive responses (primarily the N2pc wave). Statistical analyses of the N2pc were conducted using within-subjects analyses of variance (ANO Vas) with the Greenhouse–Geisser epsilon adjustment for nonsphericity.

MEG source analysis was performed on the LVF-minus-RVF difference waves using the multimodal neuroimaging software Curry 3.0 (NeuroScan, Inc., Sterling, VA). First, a 3-D reconstruction of the head and cortical surface was created using the boundary element method (Hämäläinen and Sarvas, 1989). Second, this model of the head and brain was used in conjunction with the observed MEG fields to compute a model of the distribution of current over the cortical surface (henceforth called a distributed-source model) using the minimum norm least squares method (Fuchs et al., 1999).

The distributed-source model had the following characteristics. (i) The BEM surface grid served as a predefined source compartment. (ii) Due to the large number of parameters, the minimum norm least square model minimized the data misfit by taking into account an additional model term that used a diagonal location weighting matrix to remove the natural bias towards high gain source locations that would overemphasize superficial source locations. The regularization parameter necessary to link the model term to the data was determined by the chi-square criterion relying on the assumption that the data misfit is in the order of the amount of noise in the data (see Philips Electronics N.V., User Guide Curry, version 3.0, 1998, pp. 151–154).

Finally, to provide discrete estimates of the current sources, equivalent current dipoles were also fitted to the MEG data. These procedures were applied to the MR and MEG data from the single-session data from each subject, to the multi-session data from subject AA01 and to the grand-average data. This multipronged approach was used to gain the advantages of both grand-average analyses (e.g., improved signal-to-noise ratios) and single-subject analyses (e.g. direct linkage between anatomical and electromagnetic data).

Figure 1. Example stimulus array. While fixating the central cross, subjects were required to attend to red or to green and to press one of two buttons to indicate whether the bar of the attended color was horizontal or vertical.
Results

Electrical Waveforms and Distributions
The ERP waveforms and scalp distributions for the grand-average data are shown in Figure 2A, with the multisession data from one subject (AA01) shown in Figure 2B. These waveforms were recorded at lateral occipital scalp sites TO1 (halfway between O1 and T5) and TO2 (halfway between O2 and T6). The corresponding difference waves (LVF-minus-RVF) are superimposed as thick lines. In both the grand-average and single-subject data, the N2pc wave can be seen as a more negative response for the contralateral waveform relative to the ipsilateral waveform between 180 and 280 ms post-stimulus. To test the statistical significance of this effect in the group data, the N2pc was measured as the mean amplitude from 180 to 280 ms, relative to a 100 ms pre-stimulus baseline, and these data were entered into a two-way within-subjects ANOVA with factors of electrode site (O1, TO1, PO1, T5, P3 and their right hemisphere equivalents) and target lateralization (ipsilateral or contralateral relative to the electrode site). In this analysis, the more negative voltage for contralateral targets relative to ipsilateral targets led to a significant main effect of target lateralization \[ F(1, 5) = 14.14, \] \[ P < 0.02 \].

An analogous ANOVA was conducted for subject AA01. Separate measurements were obtained from the subject for each of the four sessions, and these data were entered into the ANOVA with session as the random factor. This analysis also yielded a significant main effect of target lateralization \( \left[ F(1, 3) = 12.24, \right. \] \[ P < 0.05 \]. Thus, a significant electrical N2pc component was present both in the group and in subject AA01.

The scalp distributions of the LVF-minus-RVF difference waves are shown in Figure 2 for two different time intervals, 180–200 ms and 220–240 ms. These distributions show peak voltages at lateral and superior occipital sites, with similar but subtly different distributions in the two time ranges.

Magnetic Waveforms and Distributions
The magnetic field distributions of the LVF-minus-RVF difference waves are shown for the group and for subject AA01 in Figure 3. Two different time intervals, 180–200 ms and 220–240 ms, are shown. These field distributions are quite complex, so we will first discuss in detail the data for 220–240 ms in subject AA01 (Fig. 3C). Peaks of magnetic flux leaving the cortex (shown in red lines) can be observed over both the left and right occipital lobes, with a transition to magnetic flux entering the cortex (shown in blue lines) near the occipito-temporal border. The polarity-reversal regions, which are typically associated with the location of the underlying current dipole, are marked with large black circles. The polarity of the magnetic field for this LVF-minus-RVF difference wave appears to be the same over the left and right hemispheres, whereas opposite polarities were observed over the left and right hemispheres in the ERP distributions (see Fig. 2), but this superficial difference between the potential distribution and the magnetic fields was expected. Specifically, the magnetic field flowing out of the left occipital lobe and into the left occipito-temporal region is consistent with a downward-pointing current dipole (due to the right-hand rule), whereas the magnetic field flowing out of the right occipital lobe and into the right occipito-temporal region is consistent with an upward-pointing current dipole. Thus, the magnetic field distribution shown in Figure 3C indicates the presence of opposite-polarity current sources in the left and right hemispheres, consistent with the corresponding potential distribution shown in Figure 2B.

The grand-average magnetic field distribution of the LVF-minus-RVF difference wave for the 220–240 ms interval is shown in Figure 3D. This field is qualitatively similar to the single-subject field but is somewhat more complex, presumably due to differences in the distributions across the subjects who were...
averaged together to create the grand average. In particular, there is evidence of a midline parietal source in the grand-average data that is weak or absent in the data from subject AA01.

Magnetic field distributions (LVF-minus-RVF difference) from subject AA01 and from the grand average are shown for the 180–200 ms interval in Figure 3A and B, respectively. The polarity reversals — again indicated with black circles — were more medial and dorsal than the distributions observed at 220–240 ms, and the response appeared to be much stronger over the left hemisphere than over the right hemisphere. The different field distributions in the 180–200 and 220–240 ms time ranges suggest that the N2pc component is composed of at least two separate sources, an early source that is relatively dorsal, medial and left-lateralized, and a later source that is relatively ventral, lateral and bilaterally symmetrical.

Grand-average MEG waveforms, as well as difference waves (LVF-minus-RVF) from selected sites, are shown in Figure 4. As discussed above, the opposite voltage polarities observed in the left and right hemispheres are not accompanied by opposite magnetic field polarities, and it is therefore not useful to create the sort of ipsilateral and contralateral waveforms that were used to display the ERPs in Figure 2. The waveforms in Figure 4 instead show the responses for LVF and RVF targets at pairs of sensors located on opposite sides of magnetic field polarity inversions. For example, the sites labeled A1 and A2 are located on opposite sides of the magnetic field inversion shown in the circled area in Figure 3B, and these sites show opposite-polarity effects in the 180–200 ms time range. Similarly, the sites labeled B1 and B2 are located on opposite sides of the magnetic field inversion shown in the circled area in Figure 3D, and these sites show opposite-polarity effects in the 220–240 ms time range. These effects are the magnetic analog of the electrical N2pc component.

**Distributed Source Estimates**

To estimate the internal distribution of electrical current responsible for the observed magnetic field distributions, the data were subjected to distributed source analyses of the MEG LVF-minus-RVF difference waves. A separate analysis was conducted for each subject using a 3-D reconstruction of his or her cortical surface. An additional source analysis was performed for the grand-average data using a 3-D reconstruction of the cortical surface of a single subject; this leads to less anatomical precision, but this is partially compensated for by the increased signal-to-noise ratio and greater generality of the grand-average data.

The MEG field distributions shown in Figure 3 indicated that the N2pc component is accompanied by different patterns of activity at different latencies, and separate source analyses were therefore conducted using two different latency ranges. For the grand-average data, these ranges were 180–200 and 220–240 ms; for the individual subjects, these ranges were widened to
180–220 ms and 220–280 ms to offset the smaller signal-to-noise ratios of the single-subject data.

Figure 5A shows the estimated pattern of activity in a posterior view of the cortex for each of the six subjects. To maintain comparability across subjects, the activity for subject AA01 (subject 1) in this figure was derived from his first session, not averaged across all four of his sessions. For all six subjects, the estimated activity was relatively dorsal and medial in the early interval and relatively ventral and lateral in the late interval. For both intervals, the relative strength of the activity in the left and right hemispheres varied across subjects, and there was no obvious and consistent dominance of one hemisphere in either interval. This is also evident in a within-subject comparison. Figure 5D illustrates the time course of source activity for the second session of subject AA01. While the pattern unfolding over time consistently shows an early parietal source followed by later ventral sources, the early right parietal source was more prominent in this session.

It is important to note that the single-subject data were relatively noisy, and the differences in the estimated patterns of activity may reflect noise in the recordings rather than variability in the actual generator sites of the neural activity. However, despite the noise, there was quite a bit of consistency across subjects in the general pattern of an early parietal focus and a later occipito-temporal focus.

Figure 5B shows the estimated patterns of activity in the multi-session single-subject data and Figure 5C the grand-average data. In the 180–200 ms interval, the estimated activity was primarily present in the left parietal lobe, although some activity was also present in the right parietal lobe (mostly below the plotting threshold). In the 220–240 ms interval, the estimated activity was focused in the region of the occipital-temporal border, with approximately equal levels of activity in the two hemispheres. These patterns were quite similar for the grand-average and single-subject data, although the parietal effect was more dorsal in the single-subject data. These estimates are also similar to the estimates that were obtained for the single-session data from the six individual subjects (see Fig. 5A), indicating that the estimates from the grand-average data are not significantly distorted by averaging over subjects and that the estimates from the multi-session single-subject data are reasonably representative of the larger sample.

Dipole Source Estimates

To provide discrete estimates of these areas of activity, dipoles were fitted to the MEG distributions from 180 to 280 ms for the group and also for subject AA01. Because there were three obvious sources in the minimum norm estimates, one in the left parietal lobe and one in each inferior temporal lobe, three dipoles were used in this analysis. Each dipole was initially located near the center of the region of activity as determined by the minimum norm analyses, but the locations and orientations were then allowed to vary to maximize the fit between the dipole model and the observed magnetic field distributions.

The best-fit dipole solutions for the group data are illustrated in Figure 6A. A single dipole was first fit from 180 to 200 ms. This best-fit dipole accounted for 70% of the variance, and was located at the magnetic polarity reversal circled in Figure 3B, near the center of the activity in the minimum norm solution. Due to temporal overlap of the parietal source with the subsequent temporal sources, estimates using three dipoles were computed for the early time window (180–200 ms) and a later time window (200–220 ms). The explained variance (70%) was not significantly altered between 180 and 200 ms, but was increased to 81% between 200 and 220 ms, indicating an initial contribution of the ventral sources in this later time window. According to reference coordinates in the Talairach and Tournoux system (x, y, z: -5, -77, 55), this dipole is located in the posterior part of the parietal lobe (Brodmann’s area 7).

Two dipoles, one in each hemisphere, were used to fit the group data from 220 to 240 ms. The best-fit dipoles in this time range explained >90% of the variance in the field distributions, and they were located in the posterior half of the left and right inferior temporal lobes, with a somewhat more posterior location in the left hemisphere than in the right. The Talairach and Tournoux coordinates of the dipole in the left hemisphere indicated a region in the posterior part of the fusiform gyrus (x, y, z: -33, -65, -7), whereas the coordinates of the dipole in the right hemisphere dipole indicated a region in the posterior middle temporal gyrus close to the border to the inferior temporal gyrus (x, y, z: 53, -45, 1).

A similar pattern was obtained in the analysis of subject AA01, as shown in Figure 6B. In this analysis, a dipole in the parietal lobe — somewhat more superior and medial to that estimated from the group data — explained 70% of the variance from 180 to 200 ms. In the 220–240 ms time range, one of the two dipoles was located in the left inferior temporal lobe, quite close to the dipole estimated from the group dipole. The second dipole, however, was substantially more dorsal than the corresponding dipole from the group analysis. Together, these two dipoles explained 92% of the variance from 220 to 240 ms.

It should be noted that the purpose of estimating these dipole locations was simply to provide a discrete location in the standard Talairach reference frame, and these estimates are not intended as strong claims about the center of mass of the activity. The distributed source estimates shown in Figure 5 provide a more reasonable estimate of the actual pattern of activity, but are not easily reduced to a simple set of coordinates.

Forward Solution

In contrast to the magnetic field distribution, there was no clear indication of separate parietal and temporal sources for the early and late N2pc intervals in the ERP scalp distribution. To gain clarification about this discrepancy, a more direct estimation of the relation between the magnetic source configuration and the ERP scalp distribution is of interest. To this end the grand-average potential distribution was simulated by forward computation using the set of dipole parameters (location, orientation) as revealed by the magnetic source analysis. As illustrated by traces in Figure 7, the time course of relative contribution (dipole strength) of the early parietal and the later two temporal dipoles was modeled by separate but overlapping sine waves (2sin2πt). The first map (A) shows the potential distribution that would result from a predominant contribution of the parietal dipole. This distribution is not visible in the original grand average (Fig. 2A). Map C shows the resulting potential distribution when the two temporal dipoles alone contribute to the forward solution. Here the forward solution resembles the original ERP distribution, particularly in the 220–240 ms time range. Interestingly, during the time range of overlap (map B) the potential distribution resembles the distribution in map C but shows a slight deformation over the left hemisphere that can also be seen in the original average ERP distribution between 180 and 200 ms. Taken together, the forward solution gives some indication that the early parietal source may not have been causing significant ERP effects due to the particular orientation, relatively low...
dipole strength and temporal overlap with the much stronger temporal sources that follow. Alternatively, the larger inter-individual variability of the parietal source localizations — as revealed by the distributed source analysis — could have obscured the occurrence of an ERP effect in the grand average. It should be noted that these forward solutions cannot perfectly match original potential distributions because the estimation of current dipoles solely from the magnetic field emphasizes tangential source orientation whereas the ERP scalp distribution usually reflects both radial and tangential sources.

**Discussion**

Two main conclusions can be drawn from this experiment. First, the N2pc component that has been observed in previous ERP experiments has a magnetic analog. Second, the greater spatial resolution of the MEG technique has made it possible to distinguish two temporally and spatially distinct subcomponents of the N2pc wave. The initial portion of the N2pc appears to reflect neural activity in the parietal lobe, whereas the later portion of the N2pc appears to reflect neural activity in lateral posterior regions of the cortex that probably correspond with the anterior occipital and posterior infero-temporal visual areas.

Previous ERP experiments as well as the present ERP data were lacking of any clear evidence for separate cortical processes contributing to the N2pc effect. Results of a forward reconstruction of the ERP data using a MEG dipole configuration seem to indicate that this is because the N2pc of the ERP is dominated by activity in lateral posterior temporal regions. The parietal subcomponent, on the other hand, seems not to contribute to the electric field, most probably due to its particular orientation, strength and partial overlap with the temporal components.

The present results provide the first clear indication that the

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**Figure 5.** Distributed source model of the N2pc in each of the six subjects (A), the single-subject multisession data (B), and the grand-average data (C) for early (upper rows) and late time periods (lower rows). (D) shows the source distribution of subject AA01 (second session) evolving over time. The model was computed based on the LVF-minus-RVF target MEG difference waves.

**Figure 6.** Dipole localizations from the grand-average data (A) and from the single-subject multisession data (B). The model was computed based on LVF-minus-RVF target MEG difference waves. The top rows show the single dipole used to model the early time period, and the middle and bottom rows show the two dipoles used to model the late time period.

**Figure 7.** Forward solution. Simulated grand average electric field distributions that were computed using parameters of the magnetic dipoles. Traces illustrate the time course of relative contributions (dipole strength) of the parietal (broken line) and the two temporal dipoles (solid line).
N2pc reflects activity in a circuit that includes both parietal and occipito-temporal areas. The activation of these areas makes sense for visual search tasks, given that the parietal lobes appear to be involved in the control of attention (Mountcastle et al., 1981; Posner et al., 1984; Corbetta et al., 1993) and occipito-temporal areas appear to be involved in the implementation of attentional selection (Moran and Desimone, 1985; Corbetta et al., 1991; Chelazzi et al., 1993; Heinze et al., 1994). That is, the parietal lobes may initiate a shift of attention to the location of the task-relevant item (Corbetta et al., 1995) and the occipito-temporal region may then filter out the information from the distracter items surrounding the attended item (Heinze et al., 1994).

Previous research has shown that the human N2pc component is closely related to modulations of single-unit activity that have been observed in area V4 and infero-temporal cortex in monkeys (Luck et al., 1997b). The estimated distribution of MEG activity during the later portion of the N2pc is roughly consistent with a set of generators that include the human homologues of monkey area V4 and infero-temporal cortex, although these data cannot specify the precise subregions of the ventral stream that contribute to the N2pc.

It is notable that the estimated N2pc activity during the 220–240 ms interval was primarily present at anterior occipital and posterior temporal sites, and was not clearly present at more posterior occipital sites (some posterior occipital activity was present, but it was too weak to reach the plotting threshold in Figure 5). This pattern of minimal posterior effects and strong anterior effects is consistent with a previous fMRI study in which attention effects were stronger at more anterior sites than at more posterior sites along the ventral pathway (Kastner et al., 1998, Tootell et al., 1998) and with previous single-unit studies showing that the proportion of neurons showing attention effects increases between striate cortex and infero-temporal cortex (Moran and Desimone, 1985; Luck et al., 1997a). This pattern probably reflects the increase in receptive field sizes along the ventral pathway — as receptive field sizes increase, there is an increase in the probability that multiple competing stimuli will fall inside a given neuron’s receptive field, leading to the need to use attention to eliminate interference from the non-target stimuli (Desimone and Duncan, 1995; Duncan et al., 1997; Luck et al., 1997b).

Electromagnetic source localization is an underdetermined problem, and it is therefore important to consider what degree of confidence is appropriate for these estimated patterns of neural activity. In this study, several steps were taken to maximize the level of confidence. First, each subject received 1200 trials per condition, yielding a very high signal-to-noise ratio and making it possible to perform source analyses for the individual subjects. As shown in Figure 5A, the general pattern of an early parietal source and a later occipito-temporal source was found in each of the six subjects. Secondly, source analyses were also performed on the multisection data from subject A01 and on the grand average, which had even better signal-to-noise ratios. As illustrated in Figure 5B,C, these analyses provided converging evidence by exhibiting the same pattern of early parietal and late occipito-temporal activity. Thirdly, the source analyses were performed on difference waves that isolated the N2pc component, minimizing the complexity of the magnetic field distributions. Fourthly, 3-D reconstructions of the cortical surface were created for each subject and used to constrain the source analyses. Finally, distributed source analyses were conducted to provide estimates of the distribution of cortical activity rather than assuming point dipoles (although we also performed dipole localization procedures to provide discrete localizations). For these reasons, it is very likely that the parietal and occipito-temporal regions identified by this study closely match the actual distribution of activity that underlies the N2pc component.

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