

Neural Substrates of Perceptual Enhancement by Cross-Modal Spatial Attention

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Abstract

■ Orienting attention involuntarily to the location of a sudden sound improves perception of subsequent visual stimuli that appear nearby. The neural substrates of this cross-modal attention effect were investigated by recording event-related potentials to the visual stimuli using a dense electrode array and localizing their brain sources through inverse dipole modeling. A spatially nonpredictive auditory precue modulated visual-evoked neural activity first in the superior temporal

cortex at 120–140 msec and then in the ventral occipital cortex of the fusiform gyrus 15–25 msec later. This spatio-temporal sequence of brain activity suggests that enhanced visual perception produced by the cross-modal orienting of spatial attention results from neural feedback from the multimodal superior temporal cortex to the visual cortex of the ventral processing stream. ■

INTRODUCTION

Our perceptions of objects and events in the environment are generally improved by focusing attention on the locations of the stimuli (Wright, 1998). Most investigations of attention have involved presentation of stimuli from isolated sensory modalities, but there is increasing evidence that the neural mechanisms mediating spatial attention are not specific to individual modalities. Studies have shown that directing attention to a stimulus in one modality facilitates the speed of responding to a spatially coincident stimulus in another modality (Schmitt, Postma, & de Haan, 2000, 2001; Ward, 1994; Ward, McDonald, & Golestani, 1998; Ward, McDonald, & Lin, 2000; Mondor & Amirault, 1998; Spence & Driver, 1996, 1997; Spence, Nicholls, Gillespie, & Driver, 1998). Such cross-modal facilitation has been observed when attention was directed either voluntarily or involuntarily and for all combinations of auditory, visual, and tactile stimuli (McDonald, Teder-Sälejärvi, Heraldez, & Hillyard, 2001; Driver & Spence, 1998).

The neural bases of cross-modal spatial attention have been investigated using electrophysiological techniques (Kennett, Eimer, Spence, & Driver, 2001; McDonald & Ward, 2000; McDonald, Teder-Sälejärvi, Heraldez, et al., 2001; Eimer & Schröger, 1998; Eimer & Driver, 2000; Teder-Sälejärvi, Münte, Sperlich, & Hillyard, 1999; Hillyard, Simpson, Woods, Van Voorhis, & Münte, 1984). The general finding is that attending to a stimulus in one

modality enhances the neural activity elicited by a spatially coincident stimulus appearing in a second modality. Such neural enhancements have been consistently found in event-related potential (ERP) studies of voluntary attention (e.g., Teder-Sälejärvi et al., 1999; Eimer & Schröger, 1998; Hillyard et al., 1984) and, more recently, in ERP studies of involuntary attention (Kennett et al., 2001; McDonald & Ward, 2000; McDonald, Teder-Sälejärvi, Heraldez, et al., 2001). The latter studies followed the methodology of recent spatially nonpredictive visual cueing experiments (e.g., McDonald, Ward, & Kiehl, 1999; Hopfinger & Mangun, 1998), except that the cue and subsequent target occurred in different modalities.

In one ERP study of involuntary cross-modal attention (McDonald & Ward, 2000), a spatially nonpredictive auditory cue was followed after a short (100–300 msec) or long (900–1100 msec) delay by a visual target on the same side of fixation (valid trials) or on the opposite side of fixation (invalid trials). The ERPs to visual targets on invalid trials were subtracted from those on valid trials to determine whether an involuntary shift of attention to the preceding sound modulated subsequent visual processes. At the short stimulus onset asynchrony (SOA), the ERPs were more negative on valid trials than on invalid trials between 200 and 400 msec after the appearance of the visual target. This ERP difference was called a negative difference (Nd) because it resembled Nd waveforms that have been reported in previous auditory and visual symbolic spatial cueing studies (e.g., Eimer, 1994; Schröger, 1993, 1994).¹ Unlike previously reported Nd waves, the Nd

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observed by McDonald and Ward (2000) extended to the occipital scalp in the hemisphere contralateral to the target location. Similar negative ERP differences have been found in studies using tactile cues and visual targets (Kennett et al., 2001) and visual cues and auditory targets (McDonald, Teder-Sälejärvi, Heraldez, et al., 2001). In each case, enhanced neural responses appeared to occur in cortical areas normally considered to be specific to the target modality. However, no attempts have been made to localize the cortical generators of these ERP attention effects. It has been proposed that the cross-modal modulation of unimodal cortical activity depends on feedback from the multimodal cortex (McDonald & Ward, 2000; Driver & Spence, 1998; Ward et al., 1998; for a related neuroimaging study, see Macaluso, Frith, & Driver, 2000), but little is known about the spatio-temporal dynamics of these attention effects.

Although the cross-modal facilitation of motor responses has been well documented, these studies do not answer the key question of whether a nonpredictive stimulus in one modality actually improves the perceptual processing of a spatially coincident stimulus in a different modality. Reaction time studies do not provide unambiguous evidence in this regard, because response speed can also be influenced by postperceptual factors. Evidence that the involuntary orienting of auditory attention does in fact improve visual perception comes from recent studies in which the appearance of a sound improved the discriminability or detectability of a subsequent visual target appearing at the same location (McDonald, Teder-Sälejärvi, & Hillyard, 2000; Dufour, 1999). These findings suggested that the involuntary orienting of spatial attention enhances the perceptual salience of stimuli in the natural environment.

The present study investigated the cortical mechanisms underlying cross-modal spatial attention in a task where a preceding noise burst was found to improve visual target detectability (McDonald et al., 2000). The ERPs to the visual stimuli were recorded from 60 scalp locations, and the cerebral sources of precisely timed patterns of evoked neural activity were localized using dipole-modeling techniques. The aim was to determine whether the improvement in visual perception by involuntary attention to sound was associated with an enhancement of sensory-evoked activity in the modality-specific visual cortex and whether such enhancement was preceded by activation of multimodal areas of cortex. Thus, the present study provided the first look at the neural processes that mediate perceptual enhancement by involuntary cross-modal attention, and through the spatio-temporal analysis of ERP data, it provided a critical test of the hypothesis that such perceptual enhancement involves immediate neural feedback from multimodal to unimodal brain areas.

RESULTS

As shown in Figure 1, on each trial, a nonpredictive auditory cue appeared to the right or left side of fixation and was followed after a brief interval by a visual mask at the same location (valid trials) or opposite location (invalid trials). A visual target was presented at the masked location on half the trials and was absent on the other half. The task was to press a button each time the target was detected, with an emphasis on accuracy rather than speed. Participants were informed that the sound provided no information about the location of the visual stimuli or whether the target would be present or absent. As previously reported (McDonald et al., 2000), perceptual sensitivity (d') was higher for visual targets on valid trials (1.72) than on invalid trials (1.58) [$F(1,17) = 6.5, p = .02$]. In addition, participants responded to targets more quickly [$F(1,17) = 21.0, p = .0002$], and more accurately [$F(1,17) = 11.3, p = .0004$], on valid trials (539 msec, 79.4% correct) than invalid trials (566 msec, 74.1% correct).

To investigate the effects of the auditory cue on visual-evoked activity, we first compared ERPs elicited by the masks on valid trials and invalid trials for the target-absent trials. Masks in each visual field elicited ERPs with enhanced negativity on valid trials relative to invalid trials (Figure 2). This enhanced negativity appeared as a multiphasic Nd in the difference waveforms (Figure 3).

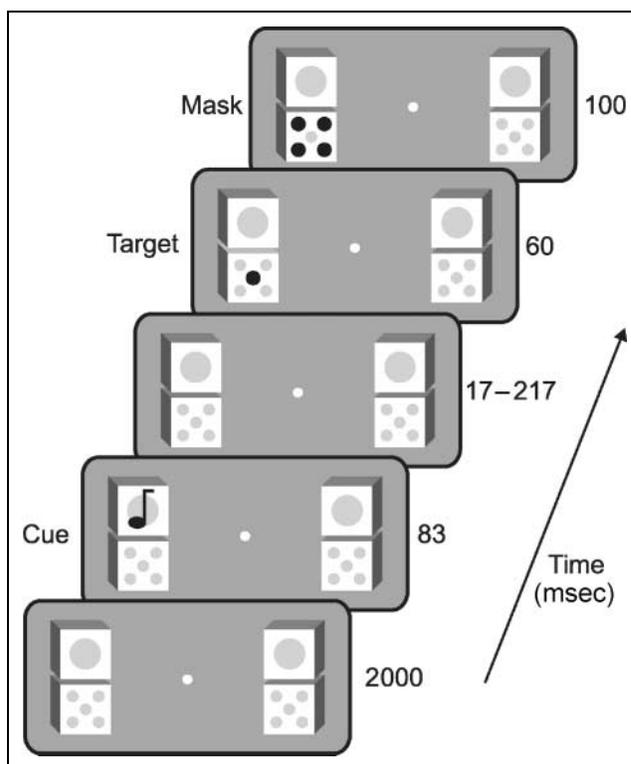


Figure 1. Illustration of events occurring on a valid, target-present trial.

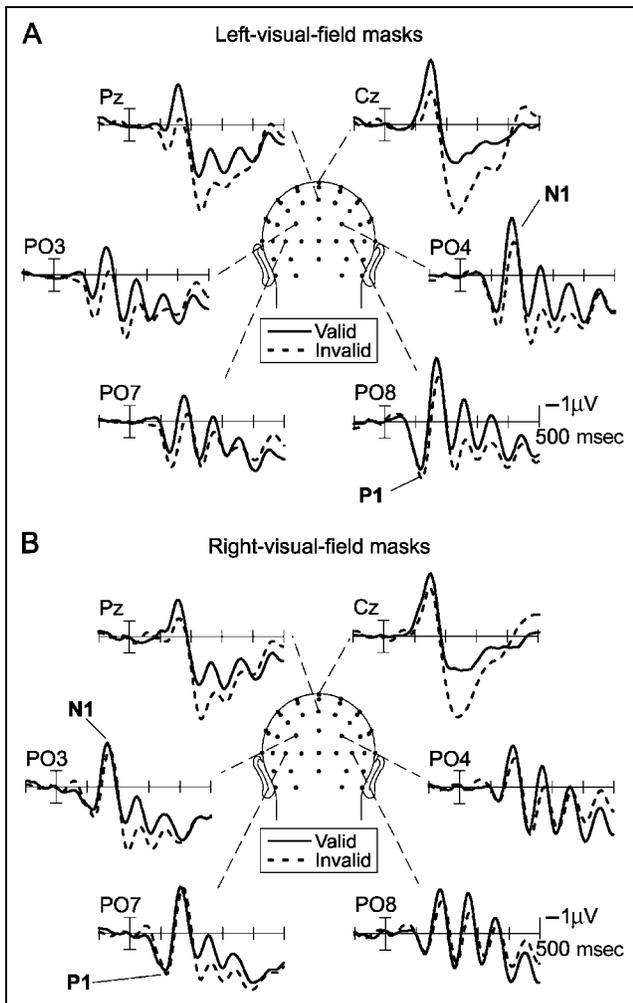


Figure 2. Grand average ERPs to visual masks following valid (same location) and invalid (opposite location) auditory cues. The waveforms shown were obtained on target-absent trials. (A) Left visual-field masks. (B) Right visual-field masks.

The first phase of the Nd (Nd1) began 100 msec after mask onset and peaked in the 120–170-msec interval. The second phase of the Nd (Nd2) began 200 msec after mask onset and peaked in the 240–260-msec interval. The scalp distribution of the Nd waves changed over time (Figure 4), indicating that the auditory cue modulated visual-evoked brain activity in multiple brain areas. The early portion of the Nd1 (120–140 msec) was distributed primarily over the midline parietal scalp (Figure 4, top), whereas the late portion of the Nd1 (150–170 msec) was distributed primarily over the more posterior parietal and occipital regions (Figure 4, middle). Additional foci were observed over the right fronto-central regions for right visual-field masks. The Nd2 distribution was centered over the fronto-central scalp with an extension to the contralateral occipital scalp (Figure 4, bottom).

The significance of each Nd wave was tested by comparing their amplitudes on valid and invalid trials

at different scalp areas. The early Nd1 was significant at central [$F(1,17) = 22.2, p = .0002$], parietal [$F(1,17) = 18.7, p = .0005$], and occipital sites [$F(1,17) = 6.3, p = .02$], as was the late Nd1 (all F 's $> 19, p < .001$), and the Nd2 (all F 's $> 45, p < .0001$). Similar effects of cue validity were observed on target-present trials (ERPs not shown), but in this case, Nd latencies were time-locked to the onset of the target rather than the mask. Thus, the Nd1 peaked at 132–172 msec after target onset and was significant at the central, parietal, and occipital sites (all F 's $> 9, p < .01$); the Nd2 peaked at 228–260 msec after target onset and was significant at each site as well (all F 's $> 28, p < .0001$). For both target-absent and target-present trials, the Nd2 was larger at electrodes contralateral to the stimulated visual field than at ipsilateral electrodes (occipital: F 's $> 15, p < .001$; parietal: F 's $> 9, p < .01$).

To localize the neural sources of these enhanced negativities, best-fitting dipolar sources were calculated for the Nd waves on the target-absent trials. Three location-symmetrical pairs of dipoles were found to account for 97.6% of the variance in scalp voltage topography over the 120–260-msec time range (Figure 5).² A pair of dipoles that was fit over 120–140 msec (Dipoles 1 and 2) was located in the posterior temporal lobe and accounted for the early parietal and fronto-central negativities in the Nd1 latency range. These dipoles were constrained to have symmetrical locations in the two hemispheres but were allowed to rotate independently because of the obvious hemispheric asymmetry of the Nd1 to right field stimuli. A second pair of mirror-symmetric dipoles that was fit over 150–170 msec (Dipoles 3 and 4) was situated in the ventral occipito-temporal cortex and accounted for the occipital negativities in both Nd1 and Nd2 latency ranges. A third pair of mirror-symmetric dipoles that was fit over 240–260 msec (Dipoles 5 and 6) was located in the anterior, inferior parietal lobe and

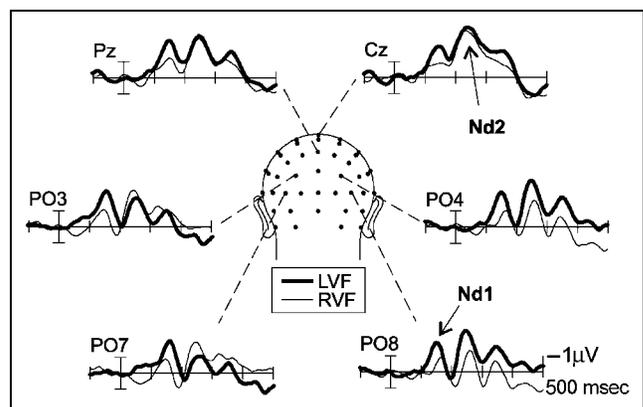


Figure 3. Difference waveforms obtained by subtracting ERPs to masks on invalid trials from ERPs to masks on valid trials. The difference waveforms shown were obtained on target-absent trials.

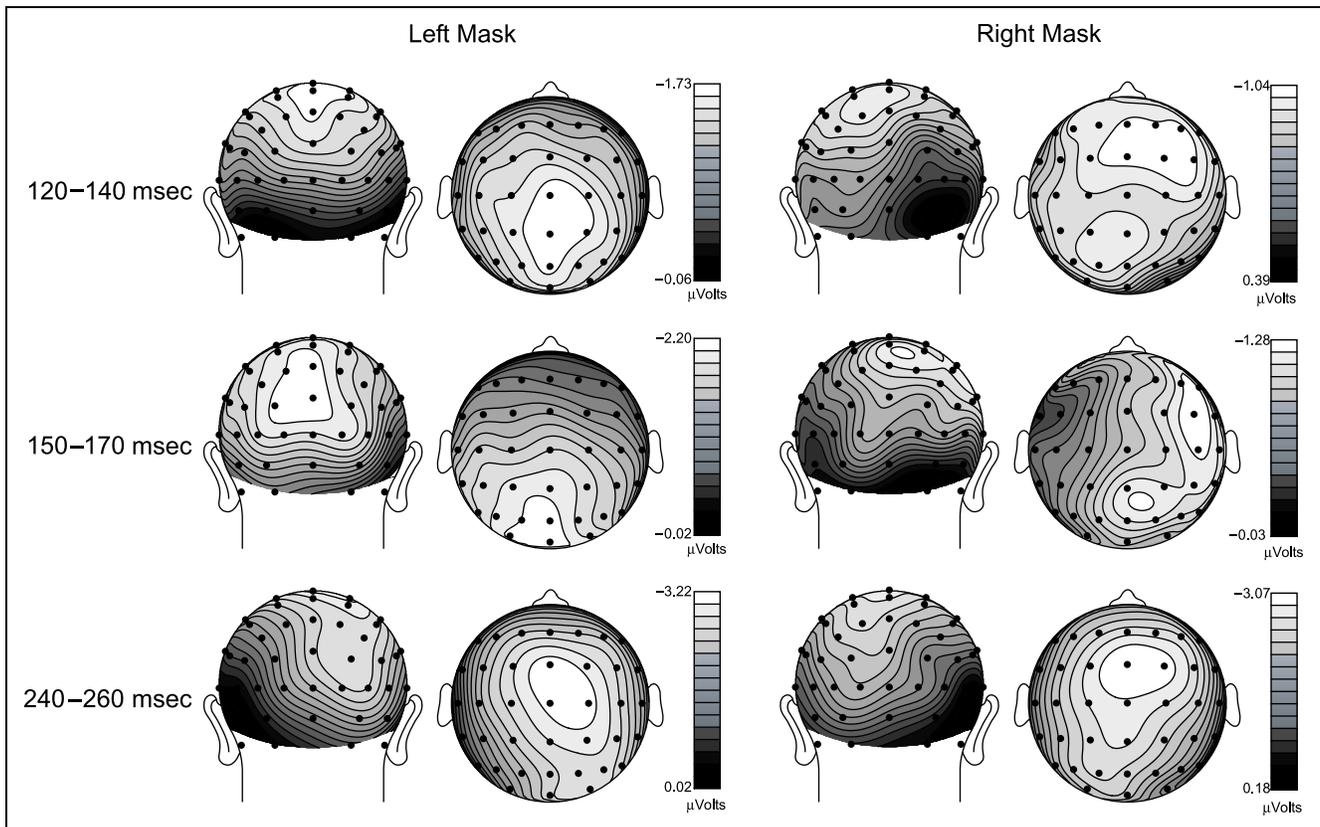


Figure 4. Scalp topography of the early phase of Nd1 (120–140 msec), the late phase of Nd1 (150–170 msec), and the Nd2 (240–260 msec) on target-absent trials.

accounted for the fronto-central negativity in the Nd2 latency range (200–300 msec).

The source waveforms of the dipole pairs show an earlier onset for the posterior temporal dipoles fit to the early phase of the Nd1 (112–114 msec) than for the ventral occipito-temporal dipoles fit to the late Nd1 (125–128 msec). To estimate the positions of these ERP sources with respect to cortical anatomy, the best-fitting dipoles were projected onto MRIs of individual participants' brains and the dipoles' coordinates were transformed into standard atlas coordinates (Figure 6). Dipoles 1 and 2 were located in the region of the superior temporal sulcus/gyrus (STS/STG, with Talairach coordinates of $x = \pm 43, y = -32, z = 9$). Dipoles 3 and 4 were situated in the fusiform gyrus of the ventral extrastriate visual cortex ($x = \pm 33, y = -58, z = -5$). Dipoles 5 and 6 were located in the peri-sylvian parietal cortex near the postcentral gyrus ($x = \pm 35, y = -25, z = 35$).

The modulation of ventral occipital activity was analyzed further by plotting topographical maps of scalp current density (SCD) in the late-phase Nd1 interval (Figure 7) and by performing an analysis of variance (ANOVA) on the Nd1 latencies at occipital electrode sites. The SCD maps showed tightly focused current sinks over lateral occipital electrode sites, thus confirming that the late portion of the Nd1 negativity was

generated in the ventral occipital cortex. The latency analysis revealed that the Nd1 occurred earlier over the hemisphere contralateral to the visual stimulus than in the hemisphere ipsilateral to the visual stimulus (146 vs. 161 msec, mask location by recording hemisphere interaction, $F(1,17) = 18.2, p = .0005$). Similar interhemispheric latency differences can be seen in the source waveforms of Dipole Pair 3–4. This indicates that the fusiform activity contributing to the Nd1 began earlier in the hemisphere contralateral to the stimulus than in the hemisphere ipsilateral to the stimulus.

DISCUSSION

The present study showed that a precisely timed sequence of neural events in widely distributed cortical areas accompanies the perceptual enhancement of a visual stimulus that results from an involuntary shift of attention to an irrelevant sound (McDonald et al., 2000). A visual stimulus preceded by a spatially coincident sound elicited enhanced negativity first in the region of the STS/STG (at 120–140 msec poststimulus), then in the fusiform gyrus of the ventral occipito-temporal cortex (at 150–170 msec poststimulus), and finally, in the peri-sylvian cortex of the inferior parietal lobe (at 200–300 msec poststimulus). This spatio-temporal sequence is in accord with the hypothesis that an

involuntary shift of attention to sound first modulates visual-evoked brain activity in a multimodal brain region and subsequently in the extrastriate visual cortex.

The STS has been identified as a site of multisensory convergence and integration on the basis of anatomical and neurophysiological data from nonhuman primates and neuroimaging data from humans. In nonhuman primates, neurons in the STS respond to auditory and visual stimulation (Stein, Meredith, & Wallace, 1993; Hikosaka, Iwai, Saito, & Tanaka, 1988; Bruce, Desimone, & Gross, 1981; Desimone & Gross, 1979) and show superadditive response enhancement to multimodal stimulation that is spatially and temporally coincident (Meredith & Stein, 1986; for a review, see Stein & Meredith, 1993). Cross-modal interactions have also been observed with fMRI and MEG in a region of human STS located posterior to the temporal–parietal junction in response to concurrent audiovisual speech stimulation (Calvert et al., 1997; Calvert, Campbell, & Brammer, 2000; Sams et al., 1991).

The modulation in the STS/STG region was followed by enhanced negativity localized to the ventral occipito-temporal cortex in the fusiform gyrus, which is generally considered as belonging to the ventral stream of extrastriate visual processing. Neurons in this area respond to a variety of visual stimuli (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher, Woods, Jacoboni, & Mazziotta, 1997; Allison, McCarthy, Nobre, Puce, & Belger, 1994; Corbetta, Miezin, Dobmeyer, Shulman, & Peterson, 1991; Lueck et al., 1989), and their activity can be modulated by visual attention (Martinez et al., 2001; Corbetta et al., 1991; Corbetta, Kincade, Ollinger, McAvoy, & Schulman, 2000; Hopfinger, Buonocore, & Mangun, 2000; Kastner, De Weerd, Desimone, & Ungerleider, 1998). The present ERP data thus provide evidence that cross-modal cueing can enhance processing of visual information in ventral stream areas starting at 150–170 msec, first in the contralateral hemisphere and then in the ipsilateral hemisphere. We propose that this enhancement is a neural correlate of the perceptual analysis that leads to the improved detectability of the validly cued visual targets.

Several ERP studies have shown that visual patterns can be discriminated within 150 msec after presentation (Van Rullen & Thorpe, 2001; Schendan, Ganis, & Kutas, 1998; Thorpe, Fize, & Marlot, 1996), but it is likely that the neural activity underlying perceptual analysis would be sustained for considerably longer in difficult discrimination tasks (Supèr, Spekreijse, & Lamme, 2001). Thus, the initial fusiform activity at 150–170 msec and its resurgence at 250–270 msec are strong candidates for the neural correlates of visual–perceptual processing in the present study. The neural processes that gave rise to the Nd1 may be particularly important for the cross-modal enhancement of perceptual processing because the Nd1 was absent in a speeded manual response task

in which perceptual enhancement was less likely to have occurred (McDonald & Ward, 2000; cf. Santee & Egeth, 1982).

The Nd2 that was observed at 200–300 msec replicated the occipital Nd reported previously (McDonald & Ward, 2000). Our source analyses indicated that the Nd2 arose from neural generators localized to the peri-sylvian cortex of the inferior parietal lobe as well as a second wave of activity in the fusiform gyrus. A recent fMRI study (Macaluso et al., 2000) found that activity in the inferior parietal lobe was coupled with enhanced activity in the occipital lobe when spatially congruent tactile and visual stimuli were displayed. The authors proposed that congruent tactile information might be conveyed to the visual cortex via back projections from the inferior parietal area. In the present study, however, no parietal activity was observed prior to the initial enhancement in

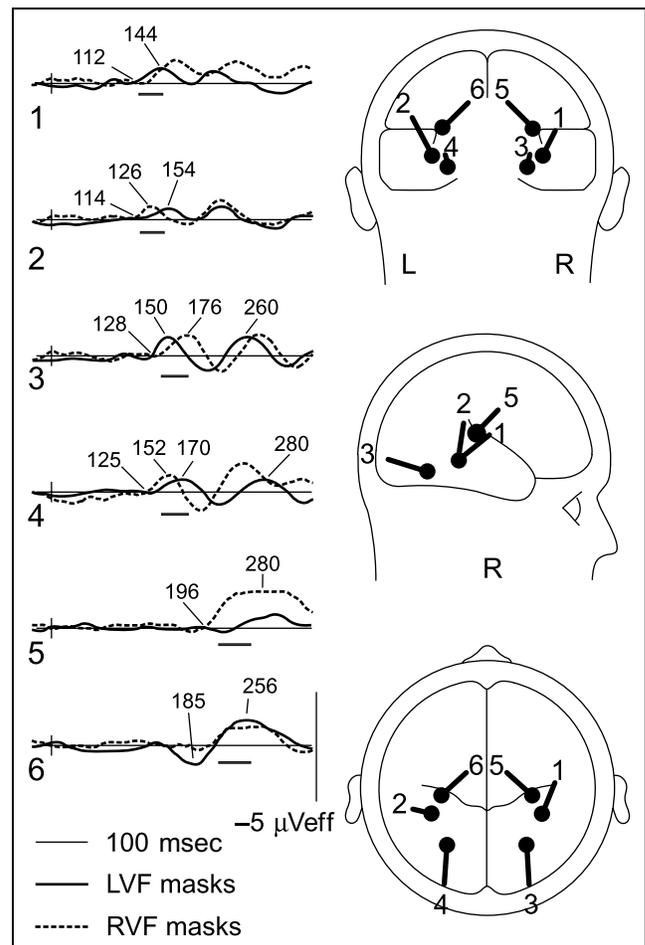
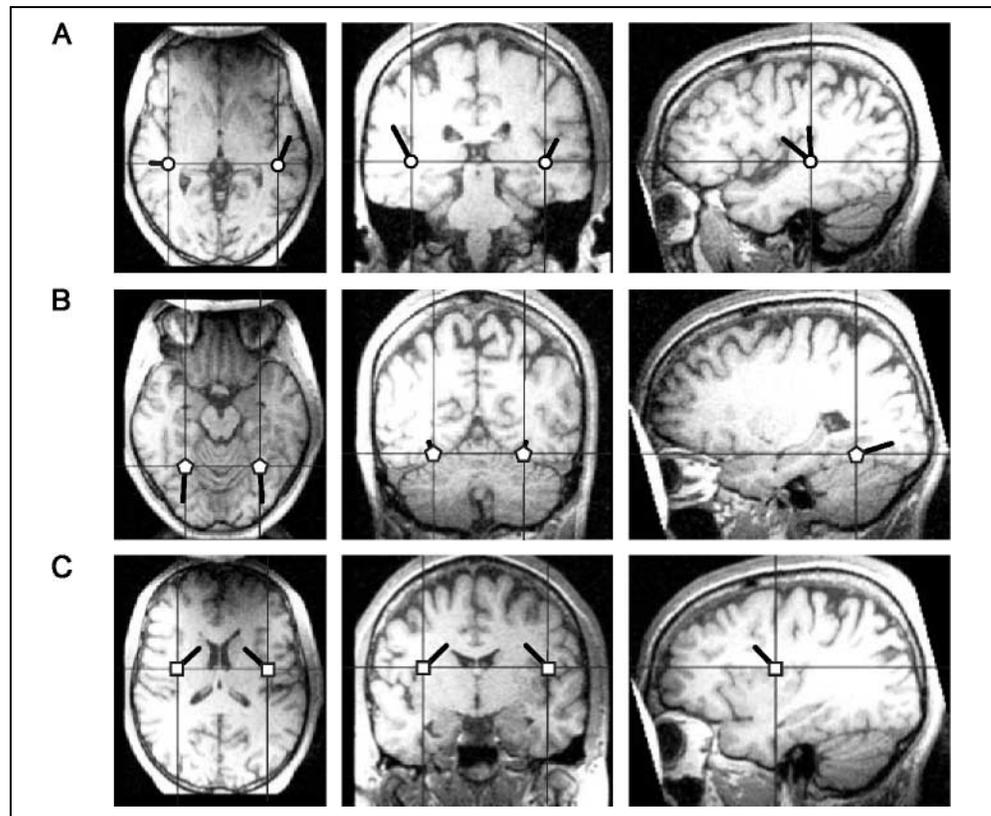


Figure 5. Dipole models of neural sources of grand average valid-minus-invalid difference waveforms on target-absent trials. Three location-symmetrical pairs of dipoles accounted for 97.6% of the variance in voltage topography over the 120–260-msec interval following mask onset. Source waveforms show time course of modeled activity for left-field (solid line) and right-field (dashed line) masks. The horizontal lines beneath each source waveform indicate the time interval that was used for fitting the dipole.

Figure 6. Projections of calculated dipolar sources onto the corresponding brain sections of an individual participant. Dipoles were based on grand-averaged ERP data. (A) Dipoles 1 and 2 are shown as circles. (B) Dipoles 3 and 4 are shown as pentagons. (C) Dipoles 5 and 6 are shown as squares.



the visual cortex. It is possible that the coupling of fMRI activations reflected attentional control operations in the parietal lobe that served to bias activity in the visual cortex, whereas the spatio-temporal sequence of ERP modulations reported here reflected enhanced perceptual processes following such attentional control operations. It is also possible that the coupling of fMRI activations reflected the neural mechanisms underlying the perceptual integration of tactile and visual stimuli rather than those underlying cross-modal attention (McDonald, Teder-Sälejärvi, & Ward, 2001).

The present spatio-temporal analysis strongly suggests that feedback from multimodal to unimodal brain areas underlies the cross-modal attention effect on visual perception. The orienting of attention to the location of a sudden sound first facilitates processing of spatially coincident visual stimuli in the STS/STG region, perhaps because this multimodal area receives rapid input from visual area MT as well as from auditory areas (Schroeder, Mehta, & Givre, 1998; Hietanen & Perrett, 1996). The subsequent enhancement of fusiform activity may then be a consequence of re-entrant feedback from the STS/STG to the ventral processing stream. Such feedback may underlie a wide range of cross-modal influences on perception and sensory-guided behavior (Macaluso et al., 2000; McDonald & Ward, 2000; Driver & Spence, 1998; Ward et al., 1998). An alternative possibility, however, is that the auditory cue facilitated visual input into the multimodal STS/STG and the fusi-

form area independently, via separate pathways. In any case, the present data show that the cross-modal facilitation of evoked activity in the ventral visual pathway goes hand in hand with improved perceptual processing of spatially coincident visual input.

METHODS

Participants

Eighteen healthy adults (9 women; ages 19–37 years) participated after giving written informed consent. Each participant had normal or corrected-to-normal vision and reported having normal hearing.

Stimuli and Procedures

Participants sat in a sound-attenuating booth and faced a fixation light positioned 100 cm in front of them. Speakers were placed 46 cm to the left and right of the fixation light. A visual display consisting of one central green light-emitting diode (LED) and four outer red LEDs was situated immediately below each speaker. On each trial, an auditory cue (76 dB SPL noise burst, 83 msec duration, 2.5 msec rise/fall) was presented randomly from either the left or the right speaker. This was followed after a random delay of 100–300 msec by a 60-msec target interval and then a 100-msec mask (illumination of all four red LEDs). A faint green target was presented at the masked location during the target

interval on half of the trials and was absent during the target interval on the other half of the trials. The mask was presented randomly from the left or right with no spatial relation to the noise burst. Participants pressed a button to indicate that a target was present and refrained from pressing the same button to indicate that a target was absent. Emphasis was placed on accuracy rather than speed, and participants were informed that the sound provided no information about the location of the visual stimuli or whether the target would be present or absent. Trials on which the auditory and visual stimuli appeared on the same side of fixation or on different sides of fixation are referred to as valid trials and invalid trials, respectively (Figure 1).

Each participant completed a short practice session and 15 experimental blocks. The intensity of the target was adjusted during the practice session so that the hit rate was between 70% and 80%, and further adjustments were made between blocks when a participant's hit rate fell above or below the 70–80% interval. Each block consisted of 28 valid trials, 28 invalid trials, and 14 catch trials in which no visual stimulus occurred (to reduce anticipatory responses). Thus, participants completed 840 noncatch trials and 210 catch trials following the practice session. There were 105 noncatch trials in each combination of cue validity (valid and invalid), mask location (left and right), and target presence (present and absent).

ERP Procedures and Data Analysis

Electrophysiological recordings were obtained from tin electrodes located at 60 scalp sites, including 56 sites from the 10-10 system (FPz, FP1, FP2, Fz, F1, F2, F3, F4, F5, F6, F7, F8, FCz, FC1, FC2, FC3, FC4, FC5, FC6, Cz, C1, C2, C3, C4, C5, C6, T7, T8, CPz, CP1, CP2, CP3, CP4, CP5, CP6, Pz, P1, P2, P3, P4, P5, P6, P7, P8, P9, P10, POz, PO3, PO4, PO7, PO8, Oz, O1, O2, Iz, and the left mastoid) and four nonstandard sites located inferior to the occipital row of electrodes. The horizontal electrooculogram (EOG) was recorded bipolarly using electrodes at the left and right external canthi, and the vertical EOG was recorded using an electrode below the left eye. All scalp electrodes, as well as the electrode below the left eye, were referenced to an electrode on the right mastoid. Electrode impedances were kept below 5 k Ω . All signals were amplified with a gain of 20,000 and a bandpass of 0.1–100 Hz (–12 dB/octave; 3 dB attenuation), digitized at a rate of 250 Hz, and stored on disk for off-line averaging. Automated artifact rejection was performed to discard stimuli when an eye movement, blink, or amplifier blocking occurred within an epoch that started 200 msec before each stimulus and lasted for 800 msec. Between 5% and 25% of the trials in each combination of cue validity, mask location, and target presence were rejected due to the presence of an artifact. ERPs from the remaining trials were averaged for each subject in

3000-msec epochs that started 1500 msec before the target stimulus. The averages were digitally low-pass filtered with a gaussian finite impulse function (3 dB attenuation at 46 Hz) to remove high-frequency noise produced by muscle movements and external electrical sources. The filtered averages were digitally re-referenced to the average of the left and right mastoids.

ERPs elicited by visual masks were averaged separately for all combinations of cue validity (valid and invalid), mask location (left and right), and target presence (present and absent). Difference waveforms were obtained by subtracting ERPs on invalid trials from ERPs on valid trials. Mean voltages of the ERPs were measured with respect to a 100-msec prestimulus period in time intervals that corresponded to Nd waves in the difference waveforms. The principal analyses were carried out on Nd waves elicited by the masks on target-absent trials; mean amplitudes were measured in the 120–140, 150–170, and 240–260 msec postmask intervals, which are referred to as the early Nd1, late Nd1, and Nd2 intervals, respectively. These Nd amplitudes were averaged over multiple electrode sites in central (left: C1,

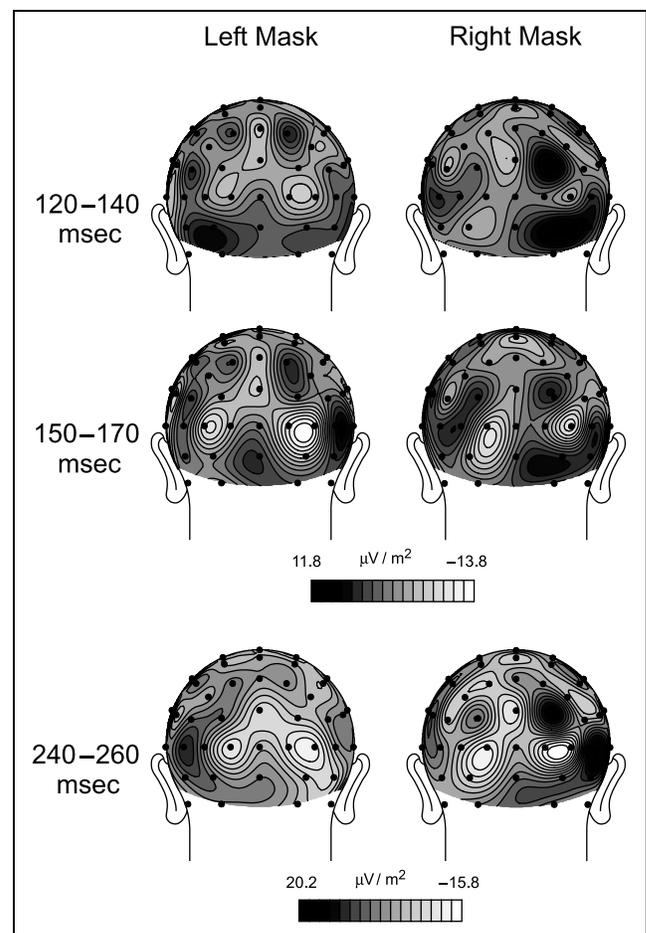


Figure 7. SCD maps of grand average valid-minus-invalid difference waves in the time intervals of the early Nd1 (120–140 msec), late Nd1 (150–170 msec), and Nd2 (240–260 msec). Derived from target-absent trial data.

C3, FC1, and FC3; right: C2, C4, FC2, and FC4), parietal (P1, P3, CP1, and CP3; right: P2, P4, CP2, and CP4), and occipital (left: O1, PO3, and PO7; right: O2, PO4, and PO8) scalp regions. Voltages for each time interval (early Nd1, late Nd1, Nd2) and each scalp region (central, parietal, occipital) were subjected to a separate ANOVA with cue validity, mask location, and recording hemisphere treated as within-subjects factors. Data from target-present and target-absent trials were analyzed separately because their Nd waves differed in latency. Latencies of the Nd1 were determined at lateral occipital sites (PO7/PO8) on target-absent trials and were subjected to an ANOVA with mask location and recording hemisphere as within-subject factors.

The cue–target SOA was varied over a 200-msec range (rectangular distribution) so that the ERPs elicited by the cue would be partially cancelled out in the averaged ERPs to the subsequent visual stimuli. The adjacent-response (Adjar) filter procedure (Woldorff, 1993) was used to estimate and remove the residual overlap originating from the cue ERPs.

Source Localization

Topographical voltage maps were constructed for the early Nd1, late Nd1, and Nd2, and then transformed into SCD maps by spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989). To determine the locations and orientations of intracranial sources of the early Nd1, late Nd1, and Nd2, inverse source analyses of the scalp voltage distributions were performed using the brain electricity source analysis (BESA) algorithm (version 2.1). This algorithm estimates the location and orientation of multiple equivalent dipolar sources by calculating the scalp distribution that would be obtained for a given dipole model and comparing it to the original ERP distribution (Scherg, 1990). Interactive changes in the location and orientation of dipole sources lead to minimization of the residual variance between the model and the observed spatio-temporal ERP distribution. This modeling approach assumes that the underlying neural activity patterns are localized in discrete regions rather than being diffusely distributed, and it is subject to the same limitations as other approaches for solving the “inverse problem” (Kutas & Dale, 1997).

Dipole pairs were fit sequentially over the latency ranges of the early Nd1, late Nd1, and Nd2, and the waveforms elicited by the left- and right-field masks were fit concurrently. The energy criterion was set at 15% to reduce the interaction among dipoles, and the separation criterion was set at 10% to optimize the separation of the source waveforms that differed over time. In these calculations, BESA assumed an idealized three-shell spherical head model with an 85-mm radius and scalp and skull thicknesses of 6 and 7 mm, respectively. To estimate the positions of the dipoles with respect to brain anatomy, the calculated dipoles were projected

onto magnetic resonance images of individual participants (e.g., Anllo-Vento, Luck, & Hillyard, 1998; Pantev et al., 1995; Giard et al., 1994), and the corresponding brain regions were identified using a brain atlas (Talairach & Tournoux, 1988; for details, see Martinez et al., 2001; Clark & Hillyard, 1996).

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Notes

1. In the present paper, we shall also use Nd to refer to negative deflections in the valid minus invalid difference waveforms, while recognizing that this term has been applied to a variety of attention-related negativities in different modalities that most likely arise from different neural generators.
2. The residual variance was 2.19%, 3.11%, and 1.64% in each of the three fitting windows (120–140, 150–170, and 240–260 msec), respectively.

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