

Cross-modal cueing of attention alters appearance and early cortical processing of visual stimuli

Viola S. Störmer^{a,1}, John J. McDonald^{b,1}, and Steven A. Hillyard^{c,1}

^aMax Planck Institute for Human Development, Center for Lifespan Psychology, Lentzeallee 94, 14195 Berlin, Germany; ^bDepartment of Psychology, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, Canada V5A 1S6; and ^cDepartment of Neurosciences, University of California at San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0608

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The question of whether attention makes sensory impressions appear more intense has been a matter of debate for over a century. Recent psychophysical studies have reported that attention increases apparent contrast of visual stimuli, but the issue continues to be debated. We obtained converging neurophysiological evidence from human observers as they judged the relative contrast of visual stimuli presented to the left and right visual fields following a lateralized auditory cue. Cross-modal cueing of attention boosted the apparent contrast of the visual target in association with an enlarged neural response in the contralateral visual cortex that began within 100 ms after target onset. The magnitude of the enhanced neural response was positively correlated with perceptual reports of the cued target being higher in contrast. The results suggest that attention increases the perceived contrast of visual stimuli by boosting early sensory processing in the visual cortex.

contrast | cross-modal attention | event-related potentials

It is well-established that directing attention to a visual stimulus can increase the speed and accuracy of its processing (1, 2). More controversial, however, is the question of whether attention can alter the subjective appearance of objects that we see. Some influential early psychologists as well as modern researchers have proposed that attention boosts sensory impressions so that attended objects appear more intense than unattended objects (3–5), whereas others have proposed that attention makes our perceptions of objects more veridical without altering their appearance (6, 7). While the evidence to date is mixed, a series of recent psychophysical studies by Carrasco and colleagues have demonstrated a consistent effect of both involuntary (i.e., automatic, exogenous) and voluntary (endogenous) attention on the apparent contrast of visual stimuli (3, 8–11). In their basic exogenous cueing paradigm, a small black dot (the cue) was used to summon attention to either a left or right peripheral location before the appearance of two Gabor patches at both left and right locations (the targets) that varied in contrast. Observers were required to judge the orientation of the target that appeared higher in contrast without moving their eyes away from a centrally presented fixation point. When the target contrasts were similar or identical, observers tended to report the orientation of the target on the cued side. It was found that orienting attention to the location of the cue enhanced the perceived contrast of the same-location target by an estimated 6% for above-threshold stimuli.

The psychophysical paradigm outlined above has yielded consistent results, but some researchers have questioned whether it has provided convincing evidence for an attentional modulation of subjective appearance (12–14). The main concerns are that the cue effect on target contrast appearance judgments may have been caused by sensory interactions between the cue and target (13, 14) or by a bias in making psychophysical decisions or executing responses (12, 14). According to the alternative sensory-interaction account, the presentation of a peripheral cue would alter the appearance of the cued-location target independently of attention by means of luminance assimilation or another low-level sensory process. Consistent with this account, one study in which observers

were asked to judge the brightness of visual stimuli found that light and dark cues had opposite effects on perceived brightness: light cues increased target brightness, whereas dark cues reduced target brightness or had no effect (13; see also ref. 15). In a different experiment, however, both light cues and dark cues were found to increase apparent luminance contrast of a Gabor patch (9). While this finding provides strong evidence against simple sensory interactions between cue and target (such as brightness assimilation) as being responsible for the increase in apparent contrast, it does not entirely rule out the possibility of more complex sensory effects. For example, considering that light and dark cues are equally high in contrast when set against a gray background, it is possible that the contrast of the cue might influence the perceived contrast of the target in a similar direction for both dark and light cues. The possibility of such effects is difficult to rule out completely when the cue and target appear in the same sensory modality.*

Several control procedures have been used in recent studies by Carrasco and colleagues that have effectively rebutted simple response bias accounts of the contrast-appearance effect, according to which observers would tend to respond simply on the basis of the cue's location. For example, it was shown that presenting the cue before the paired targets was effective at enhancing perceived contrast, but cueing after the target was not (8). Moreover, the time course of the cue-induced enhancement of target contrast appearance was found to be in line with the temporal profile of involuntary attention effects, and not response bias (3). However, Schneider and Komlos (13) reported that cueing effects on perceived contrast disappeared when a different methodology (same-different judgments) was used; the authors concluded that attention biases decisions without altering early perceptual representations and subjective appearance of the targets.

In the present study, we extended the study of attention-related effects on visual appearance in two ways using a modified version of Carrasco and colleagues' contrast-appearance judgment task (3). First, to eliminate any possibility of intra-modal sensory interactions between cue and target we replaced the visual cue with a spatially nonpredictive auditory cue. This modification also served to extend Carrasco et al.'s psychophysical paradigm to the study of involuntary *cross-modal* attention. Previous studies have shown that involuntarily orienting attention to the location of a sudden sound enhances visual perceptual sensitivity (16) and facilitates the per-

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¹to whom correspondence may be addressed. E-mail: stoermer@mpib-berlin.mpg.de, jmc@sfu.ca, or shillyard@ucsd.edu.

*Liu et al. (2009) ruled out sensory interactions in a study of voluntary attention, in which participants directed attention to peripheral locations in response to centrally presented symbolic cues. That study provided evidence that voluntary attention enhances apparent contrast but does not rule out the possibility of sensory interactions between peripheral cues and targets in exogenous cueing tasks.

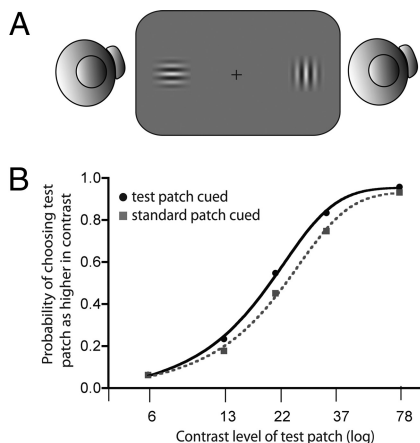


Fig. 1. Experimental procedure and behavioral results. (A) Illustration of a target display on an equal-contrast trial. The auditory cue was presented with equal probability from the left or right loudspeaker. The left-right positions of the standard and test patches also varied at random from trial to trial. (B) Probability of reporting the contrast of the test patch to be higher than that of the standard patch, averaged over all participants and plotted as a function of test-patch contrast. The probabilities are depicted for cued-test and cued-standard trials separately. The standard-patch contrast was fixed at 22%.

ceived timing of visual events (17), but it is unclear whether attention to sound location affects visual appearance.

Second, to provide converging physiological evidence that the cue-induced enhancement of luminance contrast results from an early perceptual enhancement rather than a late response or decision bias effect, we recorded evoked neural activity from the visual cortex in response to the cued targets. To reveal the effect of attention on the electrophysiological brain response elicited by physically identical visual stimuli, targets of equal contrast were presented on a large proportion of the trials. Target stimuli were presented at contrast levels well above threshold. On each trial, the contrast of one Gabor patch (standard patch) was fixed at 22% while the contrast of the other Gabor (test patch) varied at random in five steps between 6% and 78%. On each trial, the target display was preceded by a sound localized to the left or right target location (Fig. 1A).

If the cross-modal capture of attention by the auditory cue enhances apparent contrast, observers should tend to judge the visual target on the cued side as higher in contrast than a target of equal physical contrast on the uncued side. Moreover, if such a cross-modal attention effect on contrast-appearance judgments reflects changes in the perceptual representation of the visual target, the auditory cue should influence early components of the event-related brain potential (ERP) generated by the target in visual cortex. In contrast, if the cross-modal attention effect on contrast-appearance judgments reflects decision bias rather than changes at the perceptual level, the auditory cue would influence the target-elicited ERPs at relatively late stages and have no influence on the early ERP components over visual cortex (18).

Based on our previous study of attention effects on visual time-order perception (17), we expected to find an enhanced positive ERP over the occipital scalp contralateral to the cued target beginning ~100 ms after target presentation. A critical question of interest here was whether the amplitude of this positive ERP would correlate with observers' reports of perceived contrast. Such a correlation would provide converging evidence that changes in contrast appearance arise from changes in early cortical processing of visual stimuli. Indeed, we found that attention cueing increased apparent contrast in association with an enhanced early neurophysiological response in visual cortex. These results support

the hypothesis of Carrasco and colleagues that attention alters the apparent contrast of visual stimuli at an early perceptual level.

Results

Attention to Sound Location Alters Contrast Appearance Judgments. To investigate the effect of the nonpredictive (exogenous) auditory cue on contrast appearance judgments, we calculated the percentages of trials on which observers reported the contrast of the test patch to be higher than that of the standard patch, separately for cued-test trials and cued-standard trials (Fig. 1B). The cued-test and cued-standard data points were fit separately using a four-parameter Boltzmann sigmoidal function, $\psi = L + (U - L) / \{1 + \exp[(C_{50} - X)/S]\}$, where ψ is the proportion of the response, X is the contrast, L and U are the lower and upper asymptotes, respectively, C_{50} is the contrast at which the proportion of response is halfway between the upper and lower asymptotes, and S is the slope. The goodness of fit was high for each function ($R^2 > 0.998$), and there were no systematic deviations from the fitted curves (runs tests: $P = 1.00$, n.s.; Kolmogorov–Smirnov test, n.s.).

When the test and standard targets had the same physical contrast, observers reported the orientation of the test patch more frequently when it was cued than when it was uncued (54.8% vs. 45.2%, $t[15] = 4.07$, $P < 0.001$). The point of subjective equality (PSE)—the test contrast at which observers judged the test patch to be higher in contrast on half of the trials—was estimated from the curves of Fig. 1B to be 20% when the test patch was cued and 25% when the standard patch was cued. These results indicate that the cue boosted the apparent contrast of the test target.

Attention to Sound Location Modulates Neural Activity in the Visual Cortex.

The effect of the nonpredictive auditory cue on early visual processing was evident in the ERPs elicited over the occipital scalp by the equal-contrast pair of targets in the latency range 90–240 ms after target onset. With physically identical bilateral stimuli, the early ERP components recorded over the left and right occipital scalp are typically equal in amplitude, but directing attention to one side can result in a lateralized asymmetry of the early ERP components measured over occipito-temporal scalp, with larger amplitudes over the hemisphere contralateral to the attended side (19–21). It is well established that such short-latency evoked responses arising from modality-specific cortex reflect early sensory processes that can be modulated by selective attention (22). In contrast, postperceptual processing including decision making, working memory encoding, and response selection are associated with longer latency components in the 250–500 ms range that arise from multiple cortical generators (23).

In the present study, we observed a cue-related asymmetry in the early occipital ERPs elicited by physically identical Gabor patches. Fig. 2 shows target ERPs recorded contralaterally and ipsilaterally to the cued side, separately for trials on which observers reported the cued target (Fig. 2A) or the uncued target to be higher in contrast (Fig. 2B). Over the posterior scalp, the ERP waveforms were comprised of prominent positive and negative peaks, including the P1 at 140 ms (relative to target onset) and the N1 at 190 ms. Starting at approximately 90 ms after presentation of the targets, the waveform recorded contralaterally to the cued side became more positive than the waveform recorded ipsilaterally to the cued side only for those trials in which observers judged the cued target to be higher in contrast (Fig. 2A). This enlarged contralateral positive ERP was observed during the early phase of the P1 (90–150 ms) and again during the time range of the N1 (180–240 ms). Statistical analysis of the mean ERP amplitudes revealed significant differences between the contralateral and ipsilateral waveforms in the time range 100 to 140 ms and 180 to 240 ms post target-onset at occipital electrode sites PO3/PO4, PO7/PO8, P7/P8, and I5/6. Post-hoc statistical tests of the individual electrode pairs revealed that this asymmetry was significant at all four electrode pairs in both intervals (all $P < 0.05$). Conversely, there was no significant

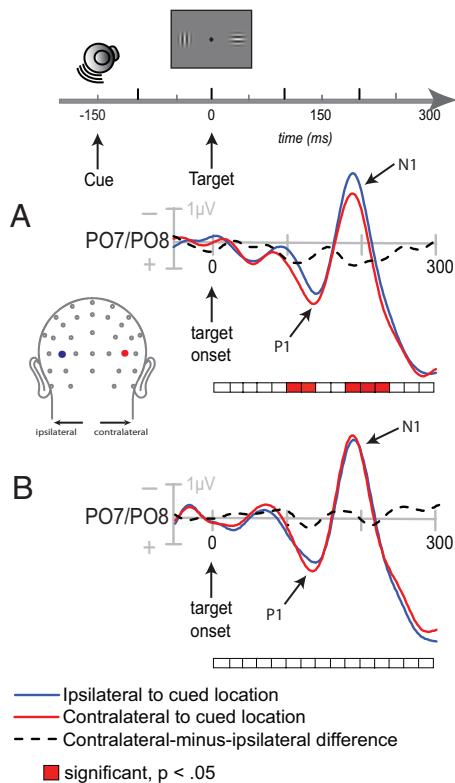


Fig. 2. Grand-average ERP waveforms to equal-contrast targets. ERPs at occipital sites (PO7/PO8) were collapsed over left- and right-cue conditions and left and right hemispheres to obtain waveforms recorded ipsilaterally and contralaterally to the side of the cue. Statistically significant ($P < 0.05$) differences between contralateral and ipsilateral waveforms are denoted in red on the time axis. (A) Enlarged ERP positivity contralateral to the cued target was found when observers reported the cued target as being higher in contrast than the uncued target. (B) No significant differences between ipsilateral and contralateral ERP waveforms were found when observers reported the uncued target as being higher in contrast than the cued target.

difference between ipsilateral and contralateral ERP waveforms when observers judged the uncued target to be higher in contrast than the cued target (all $P > 0.05$).

If the cue effects on contrast appearance judgments were due to changes in perceptual processing, we would expect individuals with greater cue-induced modulations of early ERP activity to have stronger tendencies to report the cued target as being higher in contrast. Such a relationship was indeed evident in the between-subject correlations between the amplitude of the contralateral positivity at occipital sites and the observer's reports of perceived contrast. The index of each observer's tendency to report the cued target as having higher contrast was calculated as the difference between the probabilities of choosing the cued minus the uncued test patches on equal-contrast trials. The cue-induced modulation of early target processing was calculated for each observer as the amplitude difference between the contralateral and ipsilateral ERPs elicited by equal-contrast targets. The behavioral tendency to report the cued target as having higher contrast was correlated with the cue-induced modulations of early ERP activity over several distinct time intervals (all $r_s > 0.53$, all $P < 0.032$; see Fig. 3)—including those of the P1 (120–140 ms) and N1 (180–200 ms) components (Fig. 3). The behavioral reports correlated with the ERP measure most strongly in the time interval of the P1, emphasizing the importance of cue-induced amplitude changes in early stages of visual cortical processing.

The topographical voltage maps of the ERPs to the equal-contrast targets in the time intervals of the P1 and N1 components

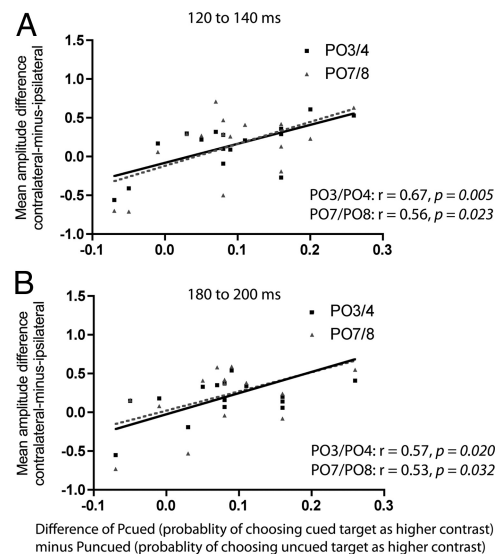


Fig. 3. Correlations between individual participants' tendencies to report the cued-side target to be higher in contrast and the magnitude of the enlarged contralateral ERP positivities recorded at occipital electrode sites (PO7/PO8, PO3/PO4) at different time intervals (120–140 ms and 180–200 ms). The tendency to report the cued-side target as being higher in contrast (x axis) is indexed by the difference between the probability of choosing the cued patch minus the probability of choosing the uncued patch on equal-contrast trials. The magnitude of the enhanced positivity (y axis) was calculated as the mean contralateral minus ipsilateral amplitude difference in the indicated time windows averaged over all equal-contrast trials for each subject.

are plotted in Fig. 4A. For each map, the right side shows the voltage topography over the scalp contralateral to the cued target and the left side shows the topography observed ipsilateral to the cued target. These maps were obtained by collapsing the target ERPs elicited on left-cue and right-cue trials and rearranging the maps according to cue location. The P1 and N1 voltage maxima were observed at circumscribed regions of the lateral occipital scalp, and in both time intervals the ERPs elicited by the equal-contrast targets showed greater positivity over the hemisphere contralateral to the cued target. To isolate these cue-induced ERP asymmetries from other, overlapping components, the ERP recorded ipsilaterally to the cued location was subtracted from the ERP recorded contralaterally to the cued location for each pair of lateralized electrodes (e.g., PO7 and PO8 over left and right occipital scalp), and the resulting difference waves were plotted over one-half of the head (Fig. 4B). Similar contralateral voltage distributions were observed over the posterior scalp in the P1 and N1 time intervals, suggesting that the contralateral positivity arose from a common neural generator that was continuously active throughout both intervals.

The anatomical locations of the neural sources of the enlarged contralateral ERP positivities shown in Fig. 4B were estimated using a distributed linear inverse solution based on a local autoregressive average (LAURA) model of the current density in the brain (24). The LAURA estimations (Fig. 4C) revealed source activity in the region of the fusiform gyrus, extending from the ventral surface of the occipital lobe anteriorly to the temporal lobe (Talairach coordinates of the maximum current density: $x = +32$, $y = -42$, $z = -11$). This source localization indicates that auditory cueing modulates early sensory-evoked activity in the ventral stream of visual processing.

Finally, we examined the ERPs to the paired Gabor patches of unequal contrast to determine whether physical changes in contrast produced changes in neural activity within the same region of visual cortex, as did the cross-modal cueing of attention. Fig. 5A compares

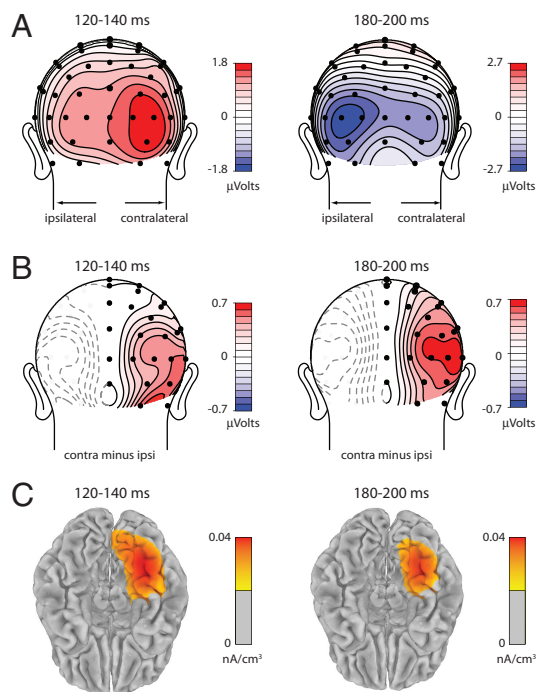


Fig. 4. Topographical distributions and estimated neural sources of the enlarged contralateral ERP positivities in the time interval of the P1 (120–140 ms) and N1 (180–200 ms) components. (A) Scalp topographies of the equal-contrast target ERP waveforms recorded contralaterally and ipsilaterally to the cued side. The ERP data were collapsed over cued side (left, right) and recording hemisphere (left, right) to show ipsilateral and contralateral ERP distributions on the left and right sides of the maps, respectively. (B) Topographical maps of the contralateral-ipsilateral difference waveforms, projected on the right side of the scalp (see *Methods* for details). (C) Localization of distributed cortical current sources underlying the contralateral minus ipsilateral ERP positivity, estimated by the LAURA algorithm. View is of the ventral cortical surface.

the ERPs elicited by the target pairs containing high-contrast (78%) and low-contrast (6%) test patches, recorded over the posterior scalp. Because each of the visual displays contained a standard patch, any differences in these ERP waveforms can be attributed to the contrasts of the test patches. As expected, the P1 component recorded contralaterally to the test patch was significantly larger and peaked 12 ms earlier for high-contrast test patches than for low-contrast test patches (amplitude: $F_{1,15} = 11.45$, $P = 0.004$; latency: $F_{1,15} = 6.71$, $P = 0.021$). These results are in accord with previously reported contrast effects on the early visual ERP components (25). The focal occipital scalp topography of the high minus low contrast difference in the time interval of the high-contrast P1 was similar to that of the cue-related contralateral ERP positivity (Fig. 5B). The distributed current sources underlying this enlarged P1 were localized using LAURA to the ventral, posterior cortical surface (Fig. 5C). This source activity was centered on the fusiform gyrus (Talairach coordinates $x = +25$, $y = -51$, $z = -10$), in the same occipito-temporal region as the source activity underlying the attention-induced contralateral ERP positivity (compare Figs. 4C and 5C).

Discussion

Does attention alter appearance? After 100 years of controversy, the issue of whether attention makes sensory impressions appear more intense is still vigorously debated (3, 8–12, 14, 26, 27). The lack of definitive answer to this question stems mainly from the fact that subjective reports of stimulus appearance are subject to alternative interpretations. In the contrast-appearance judgment task,

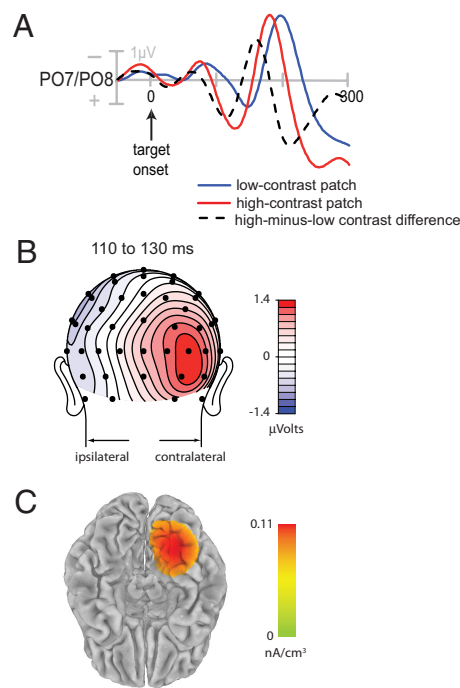


Fig. 5. Enlarged P1 positivity to high-contrast test patch. (A) Grand-averaged ERP waveforms to visual displays containing a high-contrast (78%) or low-contrast (6%) test patch, recorded occipitally, contralateral to the side of the test patch (PO7/PO8). The waveforms were collapsed over cue location and recording hemisphere. Gray box denotes time interval for analysis (110–130 ms). (B) Scalp topography of the high minus low voltage difference, calculated by subtracting the ERPs elicited by displays containing a low-contrast test patch from the ERPs elicited by displays containing a high-contrast test patch. The ERP data were collapsed over test-patch side and recording hemisphere to show the voltage distributions ipsilateral and contralateral to the test flash on the left and right sides of the maps, respectively. (C) LAURA estimations of the current sources underlying the high minus low difference waveforms, illustrated on the ventral cortical surface.

the cue could in principle influence processing at sensory, perceptual, decisional, or response stages, and changes in behavioral performance could potentially arise from changes at any stage (12, 14). Subjective reports are based on the accumulation of these processing stages and the distinction between sensory/perceptual and decision stages is difficult to pin down from perceptual reports alone (22). Recordings of neural activity from the visual cortex provide critical evidence about the level of processing at which attention exerts its effect on judgments of contrast-appearance. In particular, correlations between perceptual judgments and neural measures can provide converging evidence that changes in subjective appearance reflect changes at specific stages of processing.

In the present study, recordings of electrical brain activity revealed that cueing attention to one of two identical targets boosted early processing (at 100–140 ms) of the attended target in the ventral, occipito-temporal visual cortex of the hemisphere contralateral to the cued target. The magnitude of this enhanced cortical processing was correlated with the observers' subjective reports of contrast appearance. The larger the enhancement of early cortical processing, the more likely it was for an observer to report the cued target as having higher contrast. These results provide evidence that the cross-modal orienting of attention to the sound altered the contrast appearance judgments of the subsequent visual targets by enhancing early perceptual processing in the visual cortex. Notably, the cueing of attention enhanced neural activity within the very same ventral regions of the visual cortex that were found to be sensitive to physical differences in contrast. The present findings thus converge with the behavioral evidence that attention

affects stimulus appearance through modulations at an early sensory level rather than by affecting a late decision process (3, 8–10).

An alternative hypothesis to consider is that the attention-related modulation of activity in visual cortex may represent an enhancement of stimulus salience that gets translated into a boost in apparent contrast at some later, decision stage of processing. Indeed it was recently proposed (14) that attention acts to increase stimulus salience or priority without making the attended stimulus appear higher in contrast than the unattended stimulus. However, it seems hard to reconcile this salience hypothesis with previous findings that stimuli at the cued location are judged to have higher contrast even when the subject's task is to report which stimulus is lower in contrast (3). It is not clear why a stimulus of greater salience or priority would be chosen as higher in contrast under the "report-lower" task condition unless an actual change in appearance occurred. In any case, the present ERP data provide strong evidence that the perceptual judgments of higher contrast at the cued location are attributable to an effect of attention on early visual processing.

Because the cue was auditory rather than visual in the present study, the observed cueing effects on subjective reports and early target-evoked cortical activity cannot be attributed to low-level visual-visual interactions between cue and target (e.g., luminance assimilation) (13, 14). This finding is in line with previous studies that were able to rule out intra-modality sensory interactions between cue and target in influencing perceptual judgments (9, 11). The results of the present study support the view that cross-modal spatial cueing can influence visual contrast appearance, either by way of a supramodal attention system (28), or via direct inter-modal connectivity (29, 30).

Overall, the presentation of the spatially nonpredictive auditory cue affected subjective reports of visual contrast in a manner similar to increasing the contrast of the cued target by ~5%. This observed boost in subjective stimulus contrast was smaller than that reported by Carrasco and colleagues (3), who used a visual cue to summon attention in advance to one of the target locations. The difference in magnitude of the observed boosts in apparent contrast may have been due to the numerous differences in experimental paradigm, including cue modality (auditory vs. visual), stimulus eccentricity (25° vs. 4°), target size (8° × 8° vs. 2° × 2°), spatial frequency (1 cpd vs. 2 or 4 cpd), and number of test-contrast levels (5 vs. 9, 13, or 23).

The debate over whether attention alters the subjective appearance of visual objects parallels another long-standing debate over whether attention affects the perceived temporal order of rapidly presented sensory events (31). In both cases, researchers have debated whether the effects of cueing attention on observers' perceptual reports can be ascribed to changes in perceptual-level processes rather than decision- or response-level processes. A previous study of the effect of auditory cueing on visual time-order judgments revealed a contralateral ERP positivity with timing and topography very similar to the positivity observed here (17). In that study, the contralateral ERP positivity was associated with the subjective report that a visual stimulus on the cued side appeared earlier than a simultaneously presented visual stimulus on the opposite side of fixation. The earliest phase of this enlarged contralateral ERP positivity, which began within the first 100 ms of stimulus processing, was localized to the ventral fusiform gyrus. Together, these ERP studies provide evidence that the effects of auditory spatial cueing on the perceived timing and contrast of visual stimuli are mediated by enhanced neural activity in the ventral stream of processing within the visual cortex.

The shifts in the psychometric function for contrast appearance observed here and in prior studies that used visual cues (3, 8–10) are strikingly similar in form to the changes in neuronal firing rates produced in ventral stream area V4 of the monkey by changes in stimulus contrast or by attention (32–34). Based on such similarities, it was proposed that attention increases the effective contrast of a stimulus. Our electrophysiological findings in humans are consis-

tent with this view, namely that the attention-related enhancement of target-evoked activity in ventral visual cortex represents a boost in effective contrast that leads to the subjective appearance of a higher-contrast target. Indeed the timing of the enhanced positive ERP produced by the auditory cueing of attention in the present study (100–140 ms) corresponds closely with the latency of the contrast gain enhancement produced by attention in studies of single neurons in monkey area V4 (32, 33, 35), suggesting that homologous neural mechanisms of contrast gain control are at play in both human and nonhuman primates.

Methods

Participants. Eighteen observers participated in the study after giving informed consent. Data from two participants was excluded from the analysis because >30% of the trials were rejected due to eye movements, blinking, or amplifier blocking. Of the remaining 16 subjects (nine female, mean age 21.7 years), all reported normal or corrected-to-normal vision and normal hearing. The Human Research Protections Program of the University of California at San Diego approved all experimental procedures.

Stimuli and Apparatus. The experiment was conducted in a dark sound-attenuated chamber that housed a 24-in computer monitor and a pair of external loudspeakers. The background luminance of the monitor was set to 10 cd/m². A small black cross (0.5° × 0.5°) was presented at the center of an otherwise uniformly gray background throughout the entire experiment to serve as a fixation point. The target display consisted of two Gabor patches (sinusoidal gratings enveloped by a Gaussian; 8° × 8°) presented 25° to the left and right of fixation. The spatial frequency of each Gabor patch was fixed at 1 cpd. This spatial frequency was lower than those used in prior studies (e.g., ref 3), because the visual stimuli were presented here at a much greater eccentricity from fixation to produce clear auditory localization. On any given trial, the contrast of one Gabor patch was fixed at 22% (standard), whereas the contrast of the other Gabor patch (test) was randomly set at one of five log-increment levels, ranging from 6% to 78% contrast. The left-right positions of the standard and test patches were randomized. On each target display, one of the Gabor patches was oriented horizontally and the other was oriented vertically. To decrease any adaptation effects, the phase of the Gabor patches varied randomly from trial to trial.

The auditory cue was an 83-ms burst of pink noise (500 to 15,000 Hz, 78 dB SPL) delivered from loudspeakers positioned on the left and right sides of the computer monitor. The sounds were delivered in stereo with the amplitudes of the left and right channels adjusted so that each sound appeared to emanate from one of the two on-screen visual target positions.

Procedure. Participants were instructed to maintain eye fixation throughout each experimental block. After a variable inter-trial interval (ITI; 1,890–2,390 ms), an auditory cue was presented at either the left or the right target position. Then, after a 150-ms stimulus-onset asynchrony (SOA), the left and right Gabor patches appeared simultaneously for 53 ms. Participants were instructed to indicate the orientation (vertical vs. horizontal) of the Gabor patch that appeared to be higher in contrast by pressing one of two buttons on a game pad device. Approximately half of the participants pressed an upper button with their index finger to register a vertical-orientation response and a lower button with their middle finger to register a horizontal-orientation response; for the other half of participants the response buttons were reversed. Response hands were counterbalanced between participants. The two Gabor patches were equal in contrast on one third of the trials (test patch = 22%). On another third of the trials, the contrast of the test patch was lower (6% or 13%) or higher (i.e., 37% or 78%) than that of the standard. The location of the test patch varied randomly across trials such that the left Gabor or right Gabor was higher in contrast on an equal proportion of trials. The location of the auditory cue was chosen randomly and did not predict which of the two of targets was higher in contrast. The target display was omitted or presented after a longer (630-ms) cue-target SOA on one-third of the trials to allow separation of the overlapping ERPs elicited by cues and targets (see next section). All trial types were randomly intermixed. The entire experiment consisted of 15 blocks of 96 trials.

Electrophysiological Recordings and Analysis. Continuous recordings of the electroencephalogram (EEG) were obtained from 62 tin electrodes using our conventional recording and analysis procedures (16, 36). EEG and EOG were amplified with a gain of 10,000 within a pass band of 0.1–80 Hz and were digitized at a rate of 500 Hz. A semiautomatic procedure (37) was performed to remove epochs of EEG that were contaminated by eye movements, blinks, and amplifier blocking. Artifact-free data were then used to create averaged ERP waveforms,

which were digitally low-pass filtered (-3 dB cutoff at 25 Hz) to remove high-frequency noise.

ERPs to equal-contrast target pairs were averaged separately for left-cue and right-cue trials. The ERPs were collapsed across the two target orientation configurations (left-horizontal/right-vertical and the reverse). Because a short cue-target SOA was used in the present experiment, the resulting ERPs time-locked to the target contained event-related activity elicited by the target as well as by the immediately preceding auditory cue (cue+target ERPs). To separate the ERPs elicited by cues and targets, ERPs to cues for trials on which the target display was isolated or omitted (cue-only ERPs) were subtracted from the cue+target ERPs to isolate the target-related ERPs (38).

The ERP waveforms were collapsed across cued location (left, right) and hemisphere of recording (left, right) to obtain waveforms recorded contralaterally and ipsilaterally with respect to the cued location. The ERP waveforms were examined separately for trials on which observers judged the cued target to be higher in contrast and trials on which observers judged the uncued target to be higher in contrast. Mean amplitudes of the bilateral target ERP waveforms were measured for each participant with respect to a 100-ms prestimulus period in successive 20-ms intervals starting at target onset (0 ms) at four pairs of posterior electrodes at which the cueing effects were maximal (PO3/PO4, PO7/PO8, P7/P8, and I5/I6). The resulting mean amplitudes were analyzed in a repeated-measure analysis of variance (ANOVA) with the factor of electrode lateralization (contralateral vs. ipsilateral; relative to the cued location). When necessary, pairwise comparisons (ipsilateral vs. contralateral) were performed for individual left-right electrode pairs to identify the sites at which ERP activity was significantly lateralized.

The analysis of the ERPs to the high- and low-contrast test patches focused on the trials containing the target displays with the highest-contrast patch (78%) and the lowest-contrast patch (6%). The measurement of the mean amplitudes centered around the time window where the difference between the high- and low-contrast activity peaked (110–130 ms) and followed the same procedure as for the equal-contrast targets. The mean amplitudes of the ERP waveforms to the test patch were analyzed in an ANOVA with the factor of contrast (high vs. low) at posterior electrode sites (PO7/PO8). In addition, the peak latencies of the P1 component of the ERP waveforms were measured and compared by an ANOVA.

Topographical Mapping and Source Analysis. Topographical maps of the ERP voltages were constructed by spherical spline interpolation (39). To visualize the scalp distribution of the enlarged contralateral ERP positivity produced by auditory cuing, the contralateral minus ipsilateral voltage differences in the target ERPs were calculated for homologous left and right electrodes (e.g., PO7 and PO8), with the values at midline electrode sites (e.g., Oz) set to zero. This contralateral minus ipsilateral voltage topography could be projected to either side of the head, and we arbitrarily chose the right side in Fig. 4B.

The neural generators of the enlarged contralateral ERP positivities and the enlarged P1 to high-contrast test patches were estimated using the LAURA distributed linear inverse solution (24) implemented in BESA 5.2. The LAURA inverse solution is a weighted minimum norm algorithm that estimates the distributed source solution that most closely adheres to constraints based on biophysical laws (e.g., source activity falls off with distance). In the present study, LAURA was used to estimate the distributed source activity associated with the grand-averaged contralateral minus ipsilateral difference waveforms in the time intervals of the P1 (120–140 ms) and N1 (180–200 ms) components (for equal-contrast targets) and for the high minus low contrast difference waveforms in the time interval of the P1 (110–130 ms) component (for unequal-contrast targets). All LAURA computations were based on a default grid spacing of 7 mm. The data were regularized using a singular value decomposition (SVD) cutoff of .05%. The resulting LAURA images were projected onto the surface of a standard brain (Colin N27) using AFNI and SUMA (<http://afni.nimh.nih.gov/>). Because the contralateral minus ipsilateral difference wave distributions could be projected to either side of the head, only activity on the right side is illustrated. The coordinates of the LAURA maxima were converted to Talairach space in BESA 5.2. Anatomical regions within which the LAURA maxima were situated were determined in AFNI.

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