

Neural basis of auditory-induced shifts in visual time-order perception

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Attended objects are perceived to occur before unattended objects even when the two objects are presented simultaneously. This finding has led to the widespread view that attention modulates the speed of neural transmission in the various perceptual pathways. We recorded event-related potentials during a time-order judgment task to determine whether a reflexive shift of attention to a sudden sound modulates the speed of sensory processing in the human visual system. Attentional cueing influenced the perceived order of lateralized visual events but not the timing of event-related potentials in visual cortex. Attentional cueing did, however, enhance the amplitude of neural activity in visual cortex, which shows that attention-induced shifts in visual time-order perception can arise from modulations of signal strength rather than processing speed in the early visual-cortical pathways.

The effect of attention on the perceived timing of simultaneous and nearly simultaneous events has been of interest to psychologists for over a century. According to Titchener's 'law of prior entry'¹, objects to which we attend enter our consciousness before objects to which we do not attend. In more recent years, prior entry has been conceived not only in terms of the order in which attended and unattended stimuli enter consciousness, but also in terms of the speed with which information arising from attended and unattended stimuli is transmitted through sensory pathways²⁻⁷. According to this view, sensory signals arising from an attended stimulus arrive at some critical brain center earlier than sensory signals arising from unattended stimuli. Thus, directing attention to a stimulus was proposed to accelerate the rate of information processing in the cortical sensory pathways.

Critical evidence that attention affects the perceived timing of visual stimuli has come from the temporal order judgment (TOJ) task. In typical TOJ experiments, two target stimuli are presented simultaneously or in rapid succession, and observers are required to judge their temporal sequence, for example, by indicating which of the two stimuli came first³⁻⁸. Attention is directed to the location of one of the impending targets in advance, either by means of a symbolic cue or an attention-capturing peripheral stimulus. Two related findings have provided support for the attention-induced prior entry hypothesis. First, participants are maximally uncertain as to which stimulus arrived first when the unattended stimulus is presented before the attended stimulus. The unattended-stimulus lead time that results in maximal uncertainty about temporal order has been labeled the point of subjective simultaneity (PSS). Second, when the attended and unattended stimuli are presented simultaneously, participants often report that the attended stimulus appeared first. We will refer to these effects jointly as 'TOJ effects'.

Despite the evidence obtained from TOJ experiments, some investigators have questioned whether paying attention really results in prior entry to perceptual stages of processing^{3,4,9-12}. The main concern is that attention-induced TOJ effects could arise from changes at post-perceptual stages of processing rather than perceptual stages of processing. In particular, participants might report that they perceived the attended stimulus first simply because they are biased to respond in the direction of the cue. To reduce response bias, participants have been given additional response options (such as 'simultaneous'^{3,7}), different tasks (such as 'which came first' versus 'which came last'⁵) or instructions to respond to target features that are independent of the direction of the attentional manipulation^{5,6}. Unfortunately, the response-bias problem may not be eliminated by these strategies alone, as demonstrated by the observation of larger TOJ effects in 'which came first' tasks than in 'which came last' tasks, even when the response dimension is orthogonal to the attentional cueing dimension⁵.

In the present study, we used recordings of event-related brain potentials (ERPs) to investigate the neural basis of attention-induced TOJ effects. We used a cross-modal procedure in which an attention-capturing sound was presented to the left or right of fixation before the presentation of a pair of simultaneous or nearly simultaneous visual targets (**Fig. 1**). To minimize response bias, we used an orthogonal response procedure wherein observers indicated whether the target perceived to occur first was green or red. Our neurophysiological investigation was premised on the lateralized organization of the visual pathways from retina to cortex and the known lateralized attention effects on the ERPs to bilateral stimulus arrays. Specifically, the early components of the visual ERP arise predominantly from the hemisphere contralateral to the side of stimulation owing to the organization of

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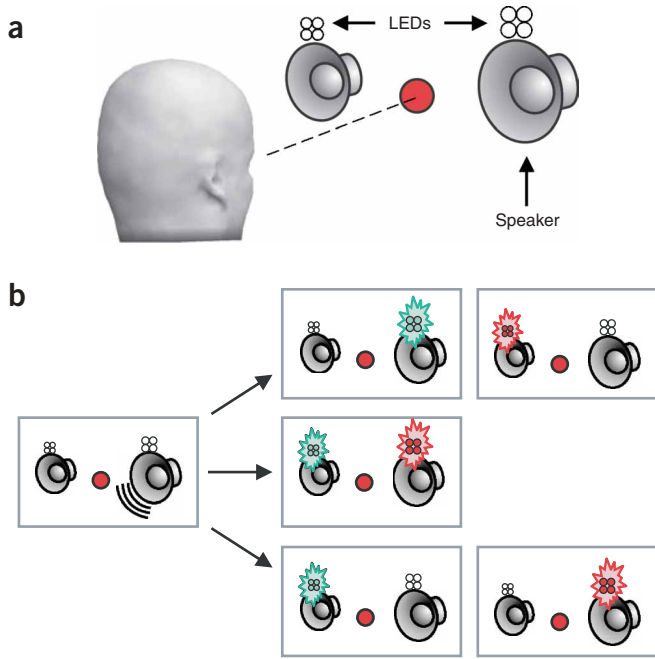


Figure 1 Experimental setup. **(a)** Schematic illustration of audiovisual apparatus. **(b)** Example of stimulus sequences on simultaneous-target and nonsimultaneous-target trials. The top and bottom rows illustrate nonsimultaneous-target trials (50% of all trials; target on cued side presented first in top row; target on uncued side presented first in bottom row), and the middle row illustrates a simultaneous-target trial (50% of all trials). The stimulus onset asynchrony (SOA) between the auditory cue and the first visual target event was 100–300 ms, and on nonsimultaneous-target trials, the SOA between targets was either 35 or 70 ms. Targets appeared simultaneously on 50% of the trials.

the visual pathways^{13,14}. Consequently, directing attention to one side of a bilaterally symmetrical visual display results in an enlarged early positive ERP (at 80–140 ms) over the contralateral relative to the ipsilateral occipital cortex^{15–18}.

From these findings, we hypothesized that if a reflexive shift of attention to a sudden sound affected the speed of information processing through the visual system, then early ERP activity in the 80–140 ms range elicited by simultaneous visual targets would occur at a shorter latency over the contralateral occipital scalp than over the ipsilateral occipital scalp. Such a latency shift would provide compelling evidence for the accelerated-processing view of prior entry (see ref. 6, p. 823). If, however, a reflexive shift of attention to a sudden sound influenced the processing of subsequent visual targets only at post-perceptual stages, then the timing and morphology of early ERPs would be highly similar over the contralateral and ipsilateral occipital cortices. A third possible outcome consistent with the aforementioned ERP studies would be that early ERP components would be larger, but not earlier, over the occipital cortex contralateral to the preceding sound cue. Indeed, the general finding has been that spatial attention modulates the amplitude of early ERP components without substantially affecting their latencies^{13,19}. Such a result would indicate that the attention-induced TOJ effects are caused by signal enhancements at early levels of sensory processing that are interpreted as timing differences at a subsequent stage of processing. In the present study we analyzed the amplitudes and latencies of early ERP components in order to distinguish between these alternative mechanisms that may underlie attention-induced TOJ effects.

RESULTS

The nonpredictive auditory cue had a substantial effect on TOJ performance (**Fig. 2**). When the two targets were presented simultaneously, participants reported seeing the target on the cued side first significantly more often than chance (78.9% versus 50%; $t_{27} = 12.7$, $P < 0.000001$). The PSS was estimated to be -68.5 ms, which indicates that the target on the uncued side needed to occur 68.5 ms before the target on the cued side in order for participants to have no lateralized preference in their temporal order judgments.

Amplitude of neural activity is related to perceived order

To investigate the effects of the auditory cue on visual processing, we first examined the ERPs elicited by the simultaneously presented visual targets that followed left and right auditory cues. **Figure 3** shows the simultaneous-target ERPs averaged over the 79% of trials in which participants judged that the target on the cued side appeared first. The ERP waveforms recorded over the posterior lateral scalp consisted of a series of positive and negative peaks, including prominent C1 (mean latency of 72 ms), P1 (110 ms), N1 (160 ms), P2 (210 ms) and N2 (260 ms) components (**Fig. 3a**). Starting at approximately 80 ms post-stimulus, the visual ERPs recorded over the left posterior scalp became more positive after the right auditory cue than after the left auditory cue. The converse was true for the right posterior scalp. This enhanced contralateral positivity lasted for approximately 140 ms and overlapped the P1, N1 and P2 components. Statistical tests confirmed that the enhanced contralateral positivity was significant between 80 ms and 220 ms post-stimulus (**Fig. 3b**).

To estimate the neural sources of these cue-induced, lateralized modulations of the target ERP, we first created spline-interpolated voltage maps of the ERPs to the simultaneous visual targets after left and right cues and the difference waveforms formed by subtracting the right-cued from the left-cued ERPs (**Fig. 4**). An enlarged positivity overlapped the time ranges of the P1 (90–120 ms post-stimulus) and subsequent N1 (135–175 ms post-stimulus) components: the P1 was larger over the hemisphere contralateral to the cued side, whereas the

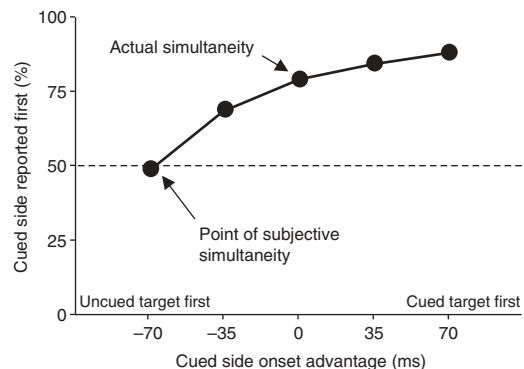


Figure 2 Mean percentage of trials in which participants reported seeing the target on the cued side before the target on the uncued side as a function of the cued side onset advantage (CSOA). The 0-ms CSOA indicates that the two targets appeared simultaneously. Negative CSOAs indicate that the target on the uncued side was presented before the target on the cued side, whereas positive CSOAs indicate that the target on the cued side was presented before the target on the uncued side. The PSS was estimated by fitting the data points with a third-order polynomial and interpolating the CSOA at which participants would have reported seeing the target on the cued side first 50% of the time. Data were collapsed across cued side (left, right) and target color (red, green).

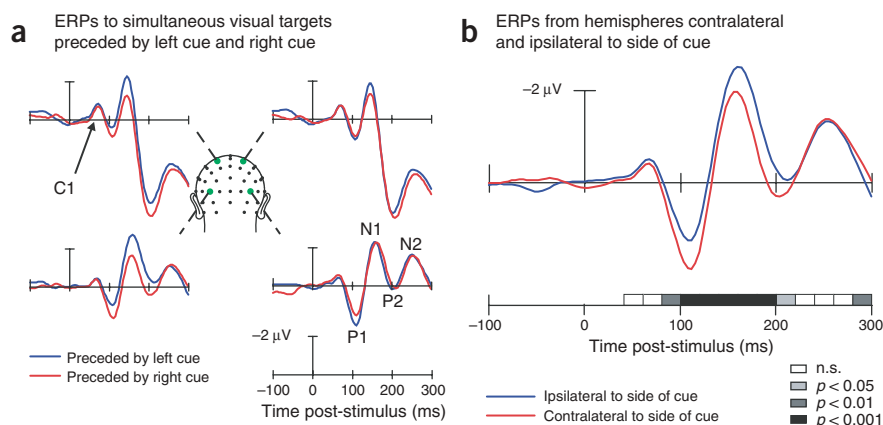


Figure 3 Grand-averaged ERPs to simultaneous visual targets, averaged over the 79% of trials in which participants indicated that the target on the cued side appeared first. **(a)** Target ERPs recorded over parietal (P1, P2) and occipital (P07, P08) brain areas, shown separately for left-cue and right-cue trials. **(b)** Target ERPs at the occipital sites collapsed over left- and right-cue conditions and left and right hemispheres so as to yield waveforms recorded contralateral and ipsilateral to the side of the cue. Statistical tests on the differences between the mean ERP amplitudes at contralateral versus ipsilateral recording sites were performed in successive 20-ms intervals from 40 ms to 300 ms post-stimulus. The *P* values from these tests are illustrated by shading above the time axis.

N1 was smaller (that is, more positive, owing to the overlapping positivity) over the hemisphere contralateral to the cued side. Each difference map in **Figure 4** shows a focal positivity over the right occipito-temporal scalp and a focal negativity over the left occipito-temporal scalp; the negativity appears because the subtraction inverted the sign of the contralateral positivity that was elicited when the cue was on the right.

The neural generators of the enlarged contralateral ERP positivity were modeled as dipolar current sources fit to the difference topographies shown in **Figure 4**. A pair of dipoles in ventral occipito-temporal cortex accounted for the contralateral positivity over a 100-ms latency range that spanned the P1 and N1 components (90–190 ms, **Fig. 5**). These dipoles were projected onto a standardized brain and were found to be situated in the fusiform gyrus of the occipito-temporal cortex (Talairach coordinates: $x = \pm 35$, $y = -46$, $z = -20$). A second pair of dipoles fit over 220–250 ms accounted for a brief phase of greater negativity over both hemispheres after the left cue. These dipoles were situated in the superior temporal region. The residual variance of this dipole model over the 96–240 ms latency range was 3.5%.

Timing of neural activity is unrelated to perceived order

In contrast to the significant effects of auditory cueing on the early positive amplitude of the simultaneous-target ERPs, auditory cueing had little or no effect on the peak latencies of the principal ERP components. The C1, P1, N1 and N2 components elicited by the simultaneous targets did not differ in latency between the hemispheres contralateral and ipsilateral to the preceding cue (all *P* values > 0.05), whereas the P2 peak latency was 5 ms earlier over the contralateral hemisphere ($P = 0.022$). To further examine the possibility of any cue-induced effects on the timing of target-elicited neural activity, we calculated best-fitting dipoles for each of the early ERP components elicited by the simultaneous targets in the following latency ranges: 80–120 ms (P1), 150–175 ms (N1) and 180–230 ms (P2). The resulting three dipole pairs (P1: $x = \pm 28$, $y = -62$, $z = -5$; N1: $x = \pm 21$, $y = -77$, $z = 12$; P2: $x = \pm 26$, $y = -41$, $z = 17$) provided a good fit to these early

components (residual variance = 1.9% within the 80- to 230-ms range). Notably, the source waveforms of dipoles located contralateral and ipsilateral to the auditory cue showed nearly identical time courses, with peaks in the relevant latency ranges occurring at approximately the same times (P1: 113 and 112 ms, N1: 158 and 161 ms, and P2: 204 and 204 ms, at contralateral and ipsilateral sites, respectively).

Finally, we examined the ERPs to nonsimultaneous visual targets to determine whether our procedure was sufficiently sensitive to latency shifts in the early ERP components. Of particular interest were the ERPs elicited when the target on the uncued side preceded the target on the cued side by 70 ms, because this particular target asynchrony was very close to the PSS (68.5 ms). If the timing of the activity in the visual system is related to the actual temporal asynchrony between events, the early ERP components elicited by the successive targets should be offset by approximately 70 ms (that is, the physical asynchrony). If, however, the timing of the activity in the visual system is related to the perceived temporal asynchrony between events, then the corresponding early ERP components elicited by the successive targets should occur at approximately the same time. The waveform contralateral to T1 consisted of T1-elicited P1 (at 116 ms), N1 (at 165 ms), P2 (at

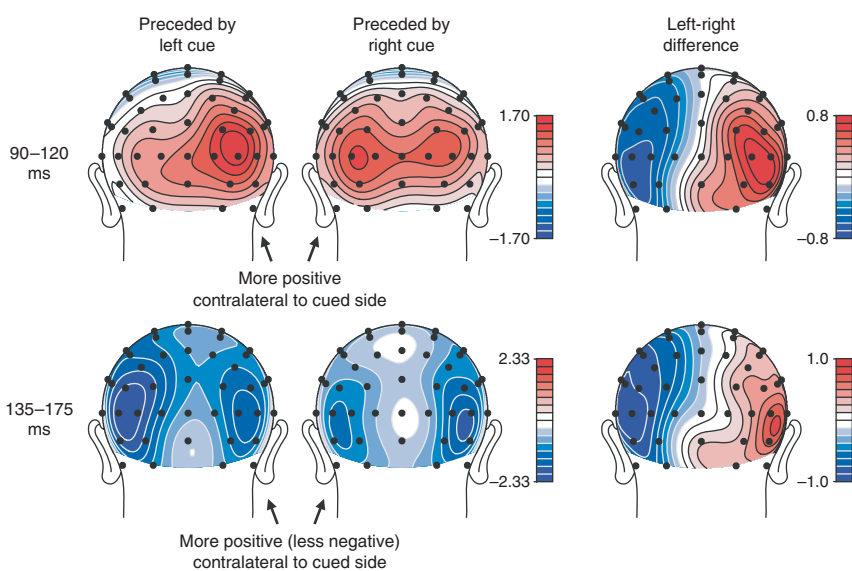


Figure 4 Scalp topographies of the simultaneous-target ERP waveforms after a left or right cue (left and center columns) and the difference wave created by subtracting the right-cued target ERP from the left-cued target ERP (right column).

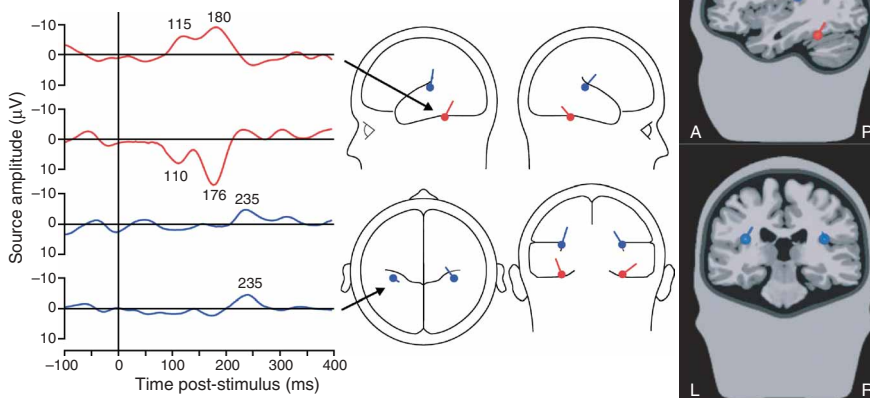


Figure 5 Dipole model of the neural sources of the left-cued minus right-cued difference wave. Dipoles 1 and 2 (red; $x = \pm 35$, $y = -46$, $z = -20$) were fit over the 90–190 ms interval, and dipoles 3 and 4 (blue; $x = \pm 35$, $y = -26$, $z = 18$) were fit over the 220–250 ms interval. The source waveforms on the left show the time courses of activity for the computed dipoles, and the images on the right show the locations of the dipoles with respect to brain anatomy.

200 ms) and N2 (at 240 ms) components (**Fig. 6a**), whereas the waveform contralateral to T2 consisted of T2-elicited P1 (at 185 ms), N1 (at 234 ms) and N2 (at 280 ms) components. The positive peak at 120 ms in the contralateral-to-T2 waveform was the delayed P1 elicited by T1 that is transferred from the contralateral to the ipsilateral hemisphere across the corpus callosum^{13,14}. Notably, the P1 and N1 components that were elicited by the successive targets were each offset by 69 ms, which closely approximates the actual time asynchrony between targets. A further analysis showed that the latencies of the P1, N1, P2 and N2 components did not differ appreciably between trials when the cued target was reported to be first and when the uncued target was reported to be first (**Supplementary Fig. 1**). The T1- and T2-elicited P1 peaks were maximal over the same ventral occipital areas (**Fig. 6b**).

DISCUSSION

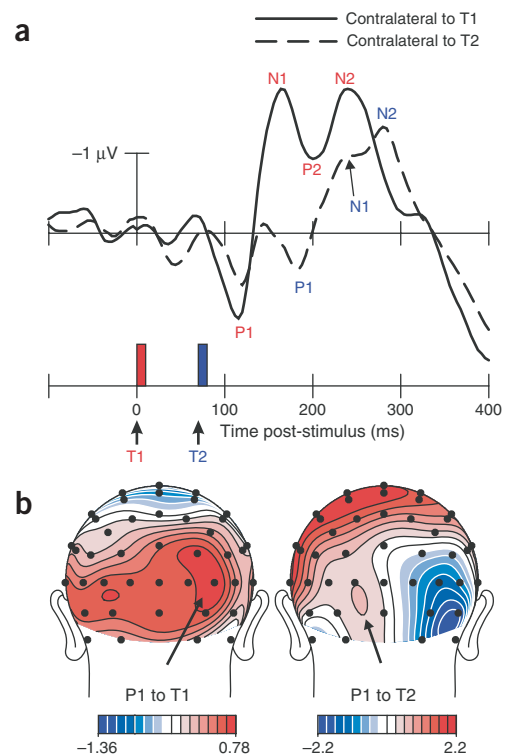
The behavioral results presented here fit well with recent reports that involuntary shifts of attention to sound can influence the perception of subsequent visual stimuli^{20–24}. As in the present study, a previous study²⁴ reported that a sound appearing to the left or right of fixation can affect the temporal perception of subsequent visual events when the cue-target stimulus-onset asynchrony (SOA) was between 0 and 300 ms. Similar results were obtained in that study when nonpredictive visual, auditory and tactile cues were used to orient attention and when participants were asked to judge the perceived motion of a

Figure 6 Target ERPs obtained at the point of subjective simultaneity. **(a)** Grand-averaged ERPs obtained when the uncued target was presented 70 ms before the cued target. The ERPs shown were recorded from occipital electrodes (PO7 and PO8) and were collapsed over cue side (left, right) and perceived temporal order (target on cued side first, target on uncued side first). The onsets of the uncued target (T1) and the cued target (T2) are denoted on the time axis, and the major contralateral ERP components elicited by T1 and T2 are labeled in red and blue, respectively. **(b)** Scalp topographies of the P1 components elicited by T1 (left) and T2 (right), plotted at 124 ms and 185 ms, respectively. The maps were constructed as if T1 were presented on the left and T2 were presented on the right. The arrows point to the contralateral P1 foci.

stationary line rather than the perceived temporal order of two visual stimuli. Taken together, these behavioral results indicate that modulations of visual perception by cross-modal attention are robust over a variety of psychophysical techniques.

Recent behavioral work on prior entry has shown that attention-induced shifts in the PSS may arise in part from post-perceptual effects such as response bias^{3–6}. In light of this, we used an orthogonal-response procedure, in which reflexive shifts of attention are known to produce substantial perceptual effects above and beyond any response-bias effects⁵. Thus, although response bias might not have been completely eliminated, the TOJ effects observed here were largely due to actual changes in the perceived timing of the stimuli. The exact contributions of perceptual and post-perceptual effects, however, remain to be determined.

The electrophysiological results presented here argue against the hypothesis that directing attention to one side accelerates the sensory processing of contralateral visual stimuli. A difference in visual component latencies between the hemispheres would be expected if their underlying neural generators were activated more rapidly in the hemisphere contralateral to the nonpredictive auditory cue. No inter-hemispheric differences in the latencies of the early ERP components or of their occipital dipole source waveforms were observed, however, when the targets were presented simultaneously, even though participants judged the target on the cued side to appear first on the majority of trials. The small difference in P2 latency (5 ms) that was measured



between the hemispheres may be attributed to the overlap of P2 with the terminal phase of the enhanced positivity, which was larger at contralateral hemisphere sites. In contrast, substantial interhemispheric differences in the latencies of the P1 and N1 were observed when the targets were presented successively with a time separation corresponding to that of the PSS, even though participants showed no lateral preference in their timing judgments because the reflexive attentional cueing counteracted the actual timing difference. In this case the interhemispheric latency difference corresponded to the actual time delay (70 ms) between the successive targets. This pattern of results indicates that the timing of early, stimulus-evoked neural activity in the visual cortex is more closely related to the actual timing of stimuli than to the perceived timing of stimuli. It should be cautioned, however, that the perceptual contribution to the shifted PSS (≤ 68.5 ms) may have been appreciably smaller than the actual target asynchrony.

Although auditory cueing did not affect the latencies of the early visual ERP activity, it did affect the amplitude of the ERP waveform. The earliest such effect was an enlarged positivity over the hemisphere contralateral to the cued side of the simultaneous-target display, which started 80 ms after target onset and lasted for about 140 ms. Topographical mapping and source analysis indicated that this enlarged contralateral positivity originated in the ventral occipito-temporal cortex. Very similar enhancements of early contralateral positivity have been reported in studies where attention was directed by endogenous cues to one side of a bilaterally symmetrical visual display^{15–17}.

The present study advances our understanding of how the timing of brain activity relates to the timing of our visual perceptions. In recent years, investigators have argued that sensory signals arising from attended objects are transmitted through the visual system more rapidly than sensory signals arising from unattended objects^{2,5–7}. We found no evidence for this widely accepted view. Instead, our study provides clear evidence that the timing of visual perception is not inevitably based on the timing of neural events in the visual-cortical pathways. On the basis of our ERP findings, we propose the alternative hypothesis that attention-induced effects on time-order perception may arise from changes in the strength of neural signals in ventral occipital areas that underlie visual object perception. It follows from this hypothesis that attention-induced enhancements in signal strength that occur at early stages of visual processing are interpreted as a timing difference by a later comparator mechanism. The challenge for future work is to define the subsequent neural events that convert the initial signal enhancement into a perceived time-order difference.

METHODS

Participants. Twenty-eight healthy adults (mean age 26.0 ± 6.3 s.d.; 16 female; 3 right-handed) participated after giving informed written consent. Each participant had normal or corrected-to-normal visual acuity and reported having normal color vision and hearing.

Apparatus. The experiment was conducted in a dimly lit sound-attenuated chamber with an ambient sound level of 32 dB (A). Auditory and visual stimuli were delivered from a custom apparatus consisting of two audiovisual displays and a fixation light arranged on a semicircular arc (Fig. 1). Participants sat 1 m from the arc and faced the fixation light. The audiovisual displays were positioned 20° to the left and right of fixation, and each consisted of a loudspeaker, four red light-emitting diodes (LEDs) and four green LEDs. The red and green LEDs were arranged in interleaved squares and were mounted directly above the speaker cone (Fig. 1).

Stimuli and procedure. At the beginning of each trial, a spatially nonpredictive auditory cue (500- to 15,000-Hz 'pink' noise burst, 76 dB SPL, 83 ms duration) was delivered randomly from either the left or right speaker. After a

randomized delay of 17–217 ms (100- to 300-ms SOA, rectangular distribution), a pair of visual targets was presented, one to each visual field. The target on one side was a green flash produced by turning on all green LEDs on that side for 10 ms; the target on the other side was a red flash produced by turning on all red LEDs on that side for 10 ms. The locations of the red and green targets were determined randomly, with equal numbers of left-red/right-green and left-green/right-red trials. The two targets were presented simultaneously on 50% of the trials; on the remaining trials, the left target appeared 35- or 70-ms before the right target, or the right target appeared 35- or 70-ms before the left target. These trials were delivered in random order. Participants were told to ignore the auditory stimulus and to indicate the color of the target that was perceived to occur earlier by pressing one of two buttons held in separate hands. Participants were instructed to respond as accurately as possible and were given 2 s to respond before the onset of the next trial. The color-button mapping was counterbalanced across participants. The experiment comprised 20 blocks of 32 trials.

Electrophysiological recording and analysis. Continuous EEG was acquired from tin electrodes mounted in an elastic cap (Electro-cap International). Fifty-six electrodes were positioned according to the 10-10 system, and four additional electrodes were positioned inferior to the occipital sites to ensure adequate spatial sampling of the posterior scalp²³. The horizontal electro-oculogram (EOG) was acquired using a bipolar pair of electrodes positioned at the external ocular canthi. All EEG electrodes were referenced to an electrode on the right mastoid (A2). The EEG and EOG channels were amplified with a gain of 20,000, filtered (2-pole Butterworth) with a bandpass of 0.1–100 Hz (-3 dB point; -12 dB per octave) and digitized at 250 Hz.

After the recording session, the EEG and EOG were averaged over 3-s epochs that started 1.5 s before the onset of each cue and target. Automated artifact rejection was performed before averaging to discard trials during which an eye movement, blink or amplifier blocking occurred. The averaged waveforms were digitally low-pass filtered (-3 dB point at 25 Hz; zero-phase) and re-referenced to the average of the left and right mastoids. Deflections in the averaged EOG waveforms were small (<1.5 μ V), which indicated good maintenance of fixation.

Cue and target ERPs were averaged separately for all combinations of cue side (left, right), target asynchrony (-70 ms, -35 ms, 0 ms, 35 ms, 70 ms, where negative values denote trials with the first target on the uncued side) and perceived target order (green first, red first). As the cue-target SOA was varied over a 200-ms range, the cue ERPs did not consistently overlap the target ERPs. The adjacent-response (Adjar) filter procedure²⁵ was used to remove any residual overlap originating from the cue ERPs. The target ERPs were collapsed across the two color combinations (left-red/right-green and left-green/right-red) to eliminate possible ERP lateralizations related to target color. The analysis of ERP amplitudes focused on the simultaneously occurring targets. Mean amplitudes of the bilateral-target ERP waveforms were measured with respect to a 100-ms prestimulus period in successive 20-ms intervals starting at 60 ms post-stimulus. These measurements were taken from a pair of lateral-occipital electrodes (PO7 and PO8) at which cueing effects were maximal. The mean amplitudes in each interval were analyzed in a repeated-measures analysis of variance (ANOVA) with cued side (left, right) and electrode lateralization (relative to the cued side; contralateral, ipsilateral) serving as within-subject factors. The peak latencies of the C1, P1, N1 and P2 components of the bilateral-target ERP waveform were also determined at posterior electrodes (C1: electrodes P1 and P2; P1, N1 and P2: electrodes PO7 and PO8) and were subjected to a similar ANOVA. Finally, the peak latencies of the P1 and N1 components of the nonsimultaneous target ERP waveforms were measured at posterior electrodes (PO7 and PO8).

Topographical mapping and source localization. Difference waveforms were calculated by subtracting the right-cued from the left-cued simultaneous target ERPs. Topographical maps of the simultaneous-target ERPs and corresponding difference waveforms were constructed by spherical spline interpolation²⁶. The cortical generators of the difference-wave potentials were estimated using Brain Electrical Source Analysis (BESA 2000 version 5.0). The BESA algorithm estimates the location and the orientation of multiple equivalent dipolar sources by calculating the scalp distribution that would be obtained for

a given dipole model (forward solution) and comparing it with the actual scalp-recorded voltage distribution. The algorithm interactively adjusts (fits) the location and orientation of the dipole sources in order to minimize the residual variance (RV) between the model and the observed spatiotemporal ERP distribution.

To investigate the anatomical sources of the attention-induced changes in the amplitude of visual cortical activity, we sequentially fit two pairs of dipoles to distinctive components in the difference waveforms within specified intervals. Each dipole pair was constrained to be mirror-image in location only. The first dipole pair was fit to the left-cued minus right-cued target difference wave topography in the 90–190 ms post-stimulus interval. The second pair was fit over the 220–250 ms interval. The coordinates of each dipole were registered on the standardized finite element model (FEM) of BESA 2000, which was created from an averaged head using 24 individual MRIs in Talairach space.

To investigate the attention-induced changes in the timing of visual cortical activity, we fit separate pairs of dipoles to the occipital P1, N1 and P2 components in the original ERPs (not difference waves) elicited by the simultaneous targets. Dipole pairs were fit within intervals that encompassed these early peaks in the grand-averaged waveforms (P1: 80–120 ms, N1: 150–175 ms and P2: 180–230 ms). Each dipole pair was constrained to be mirror-image in location only. The coordinates of each dipole were registered in Talairach space. The latencies of major peaks in the dipole source waveforms were taken as indices of neural response timing.

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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1. Titchener, E.N. *Lectures on the Elementary Psychology of Feeling and Attention* (Macmillan, New York, 1908).
2. Carrasco, M. & McElree, B. Covert attention accelerates the rate of visual information processing. *Proc. Natl. Acad. Sci. USA* **98**, 5363–5367 (2001).
3. Jaskowski, P. Selective attention and temporal-order judgment. *Perception* **22**, 681–689 (1993).

4. Schneider, K.A. & Bavelier, D. Components of visual prior entry. *Cognit. Psychol.* **47**, 333–366 (2003).
5. Shore, D.I., Spence, C. & Klein, R.M. Visual prior entry. *Psychol. Sci.* **12**, 205–212 (2001).
6. Spence, C., Shore, D.I. & Klein, R.M. Multisensory prior entry. *J. Exp. Psychol. Gen.* **130**, 799–832 (2001).
7. Stelmach, L.B. & Herdman, C.M. Directed attention and perception of temporal order. *J. Exp. Psychol. Hum. Percept. Perform.* **17**, 539–550 (1991).
8. Stone, S.A. Prior entry in the auditory-tactile complication. *Am. J. Psychol.* **37**, 284–287 (1926).
9. Downing, P.E. & Treisman, A.M. The line-motion illusion: Attention or impletion? *J. Exp. Psychol. Hum. Percept. Perform.* **23**, 768–779 (1997).
10. Frey, R.D. Selective attention, event perception and the criterion of acceptability principle: evidence supporting and rejecting the doctrine of prior entry. *Hum. Mov. Sci.* **9**, 481–530 (1990).
11. Pashler, H.E. *The Psychology of Attention* (MIT Press, Cambridge, Massachusetts, 1998).
12. Schneider, K.A. & Bavelier, D. Components of visual prior entry. *Cognit. Psychol.* **47**, 333–366 (2003).
13. Di Russo, F., Martinez, A. & Hillyard, S.A. Source analysis of event-related cortical activity during visuo-spatial attention. *Cereb. Cortex* **13**, 486–499 (2003).
14. Di Russo, F., Martinez, A., Sereno, M.I., Pitzalis, S. & Hillyard, S.A. Cortical sources of the early components of the visual evoked potential. *Hum. Brain Mapp.* **15**, 95–111 (2001).
15. Heinze, H.J., Luck, S.J., Mangun, G.R. & Hillyard, S.A. Visual event-related potentials index focused attention within bilateral stimulus arrays. I. Evidence for early selection. *Electroencephalogr. Clin. Neurophysiol.* **75**, 511–527 (1990).
16. Heinze, H.J. *et al.* Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature* **372**, 543–546 (1994).
17. Luck, S.J., Heinze, H.J., Mangun, G.R. & Hillyard, S.A. Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1 components. *Electroencephalogr. Clin. Neurophysiol.* **75**, 528–542 (1990).
18. Mangun, G.R., Hopfinger, J.B., Kussmaul, C., Fletcher, E. & Heinze, H.J. Covariations in ERP and PET measures of spatial selective attention in human extrastriate visual cortex. *Hum. Brain Mapp.* **5**, 273–279 (1997).
19. Hillyard, S.A. & Anlo-Vento, L. Event-related brain potentials in the study of visual selective attention. *Proc. Natl. Acad. Sci. USA* **95**, 781–787 (1998).
20. Dufour, A. Importance of attentional mechanisms in audiovisual links. *Exp. Brain Res.* **126**, 215–222 (1999).
21. Frassinetti, F., Bolognini, N. & Làdavas, E. Enhancement of visual perception by crossmodal visuo-auditory interaction. *Exp. Brain Res.* **147**, 332–343 (2002).
22. McDonald, J.J., Teder-Sälejärvi, W.A. & Hillyard, S.A. Involuntary orienting to sound improves visual perception. *Nature* **407**, 906–908 (2000).
23. McDonald, J.J., Teder-Sälejärvi, W.A., Di Russo, F. & Hillyard, S.A. Neural substrates of perceptual enhancement by crossmodal spatial attention. *J. Cogn. Neurosci.* **15**, 10–19 (2003).
24. Shimojo, S., Miyauchi, S. & Hikosaka, O. Visual motion sensation yielded by non-visually driven attention. *Vision Res.* **37**, 1575–1580 (1997).
25. Woldorff, M.G. Distortion of ERP averages due to overlap from temporally adjacent ERPs: analysis and correction. *Psychophysiology* **30**, 98–119 (1993).
26. Perrin, F., Pernier, J., Bertrand, O. & Echallier, J.F. Spherical splines for scalp potential and current density mapping. *Electroencephalogr. Clin. Neurophysiol.* **72**, 184–187 (1989).