Temporal Order is Coded Temporally in the Brain: Early Event-related Potential Latency Shifts Underlying Prior Entry in a Cross-modal Temporal Order Judgment Task

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Abstract

■ The speeding-up of neural processing associated with attended events (i.e., the prior-entry effect) has long been proposed as a viable mechanism by which attention can prioritize our perception and action. In the brain, this has been thought to be regulated through a sensory gating mechanism, increasing the amplitudes of early evoked potentials while leaving their latencies unaffected. However, the majority of previous research has emphasized speeded responding and has failed to emphasize fine temporal discrimination, thereby potentially lacking the sensitivity to reveal putative modulations in the timing of neural processing. In the present study, we used a cross-modal temporal order judgment task while shifting attention between the visual and tactile modalities to investigate the mechanisms underlying selective attention electrophysiologically. Our results indicate that attention can indeed speed up neural processes during visual perception, thereby providing the first electrophysiological support for the existence of prior entry. ■

INTRODUCTION

In his attempt to summarize the most important questions in attention research nearly a century ago, Titchener (1908) formulated seven fundamental laws of attention. The fourth law, the law of prior entry, states that attended stimuli come into consciousness more rapidly than unattended stimuli. The law was based on Geiger's (1903) pendulum experiment, whereby participants perceived a pendulum at different locations when a sound was presented depending on whether their attention was directed to the sound or to the sight of the pendulum itself (see also Mollon & Perkins, 1996). Geiger's experiment generated much debate and several different explanations have been put forward. Most notably, contributions of an anticipation bias or physiological factors (auditory processing being faster than visual processing) were proposed, which were refuted by both Titchener and James (see Titchener, 1908). Instead, Titchener suggested that the time of conscious perception of a stimulus could vary within a brief temporal interval depending upon the current focus of an observer's attention. In the century since Titchener formulated his law of prior entry, a great deal of controversy has been generated as to whether attention actually speeds up the processing of stimuli so that they

reach consciousness earlier (e.g., see Zampini, Shore, & Spence, 2005; Schneider & Bavelier, 2003; Spence, Shore, & Klein, 2001).

The law of prior entry has typically been investigated using unspeeded temporal order judgment (TOJ) tasks (see Shore & Spence, 2005, for a recent review). Unlike reaction time (RT) studies, TOJs do not require a speeded response, but instead typically involve participants making nonspeeded perceptual judgments. A typical TOJ trial consists of two stimuli separated in time by a small but variable stimulus onset asynchrony (SOA). On the basis of a participant's decisions about which stimulus appeared first at each SOA, the mean point of subjective simultaneity (PSS) can be calculated. The PSS indicates by how much time one stimulus has to lead the other in order for the two to be judged as occurring simultaneously (i.e., the average SOA at which participants make each response equally often). Because the accuracy of temporal discrimination performance is stressed in TOJ studies rather than the speed of responding, behavioral modulations in the PSS from cuing are thought to result from early perceptual modulations of sensory information processing by attention, making them ideal for the study of prior entry. Early behavioral studies provided mixed evidence for the law of prior entry (see Spence, Shore, et al., 2001, for a comprehensive review). Early research faced extensive criticism, most notably that the prior-entry effects in many studies

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may have stemmed from response biases, changes in decision criteria, or low-level sensory interactions between the attention-modulating cue and target stimuli (e.g., Schneider & Bavelier, 2003; see also Zampini et al., 2005; Spence, Shore, et al., 2001).

Spence, Shore, et al. (2001) highlighted and evaluated a number of the confounds and ambiguities that were present in previous research and reported a series of experiments designed to test for attentional effects upon TOJs while accounting for these confounds. First and foremost, the effects of response bias were identified—the tendency by participants to respond to the stimulus to which they had been instructed to attend. To counteract this bias, Spence and his colleagues used a cuing design in which the participants perceived stimuli from different sensory modalities in different spatial locations, and responded on a dimension that was *orthogonal* to that to which they were instructed to attend (e.g., responding on the basis of the stimulus location that came first while being instructed to attend to a particular sensory modality). While accounting for these potential biases, Spence and colleagues were able to garner support for the veracity of the prior-entry hypothesis. A follow-up experiment by Zampini et al. (2005) also confirmed that attention leads to a shift in the PSS when using a simultaneity judgment task instead.

Although it has proved difficult to arbitrate unequivocally between accounts invoking cognitive biases (Schneider & Bavelier, 2003) or attentional prior-entry effects (Zampini et al., 2005; Spence, Shore, et al., 2001) based solely on the available behavioral evidence, event-related potentials (ERPs) should provide more direct evidence with which to address the issue. Indeed, Dennett (1991, p. 162) suggested that our brains may represent temporal order with primary evoked potentials as a reference point (see also Kelly, 2005; Roache, 1999; Köhler, 1947). ERPs provide a readout of brain activity with real-time resolution, and thus, can reveal the transient modulation of information processing during the perceptual analysis of a stimulus, such as changes in the timing of a particular stage of analysis or in the amount of processing during a particular stage. Therefore, we recorded ERPs during a visuotactile TOJ task using a design based on the work of Spence, Shore, and Klein (2001). Schneider and Bavelier (2003, p. 334) suggest that evaluating the prior-entry hypothesis requires overcoming two major obstacles: "consistently manipulating the attentional states of the observer and demonstrably measuring their perception." We addressed each of these issues, in turn, by using a robust manipulation of selective attention to the visual or tactile sensory modality, and by measuring the electrophysiological correlates of the behavioral prior-entry effect in perceptual processing in cortical areas.

One other recent study has also looked at the attentional modulation of TOJs using ERPs (McDonald, Teder-Sälejärvi, Di Russo, & Hillyard, 2005). Attention

was directed to either side by means of a brief nonpredictive tone presented 100–300 msec before the onset of the TOJ stimuli, and participants had to judge which of two lateralized differently colored light flashes occurred first. The results showed a behavioral prior-entry effect of 68.5 msec, but exogenous spatial attention did not lead to any shift in the latency of early visual potentials. Instead, their gain was modulated, as has commonly been observed in any number of other spatial attention experiments (Anllo-Vento, Schoenfeld, & Hillyard, 2004; Eimer, 1998, 2004; Luck, Woodman, & Vogel, 2000; Hillyard & Anllo-Vento, 1998; Mangun, 1995). The authors concluded that the behavioral shifts in the PSS were not caused by perceptual prior entry, but that they arose instead from modulations of signal strength in early visual–cortical pathways.

The current experiment revisited the possibility that perceptual prior-entry effects may occur under different manipulations of selective attention. Closer to the original observations in Geiger's (1903) pendulum experiment, we manipulated the focus of attention to one sensory modality versus another. We used visual and tactile peripheral stimuli, given that this is the modality pairing that has given rise to the biggest prior-entry effect in previous behavioral work (Spence, Nicholls, et al., 2001; Spence, Shore, et al., 2001). Using an orthogonal cuing task (based on Spence, Shore, et al., 2001), participants were cued to attend to either vision or touch and to respond according to the side on which the first stimulus occurred. The orienting of attention was manipulated in a sustained manner by increasing the proportion of stimuli presented in one modality (attended) and by task instruction. Sustained attention manipulations are often more effective than trial-by-trial manipulations, and therefore might provide a better platform for unveiling mechanisms of attentional modulation.

The task allowed us to identify the stages of perceptual processing of visual stimuli and to investigate their modulation. In particular, we were interested in investigating whether differences in the relative latencies of early visual potentials could be observed as a function of attention being directed to a particular sensory modality in a TOJ task. Latency shifts in early visual potentials would provide the strongest evidence yet in support of the prior-entry hypothesis and would rule out explanations based solely on any direct or indirect changes in response criteria. The task design and parameters were also constructed so as to minimize contributions from any simple sensory effects that were nonattentional in nature.

METHODS

Participants

Seventeen volunteers were recruited from the academic community of students and postdoctoral fellows at the

University of Oxford. Data from two participants were unsuitable for behavioral analysis and were therefore excluded. Analyses of behavioral and electrophysiological data were carried out on the same group of 15 participants (8 women and 7 men, 14 right-handed and 1 left-handed, ages ranging between 18 and 30 years). Participants were paid £20 for their participation. All had normal tactile sensitivity, and normal or corrected-to-normal vision by self-report.

Apparatus and Materials

The experiment took place in a dark, electrically shielded, and sound-attenuated testing booth. Two tactile and two visual stimulators were triggered by Presentation05 (Neurobehavioral Systems, Albany, CA) and a custom-built interface-box connected through the parallel port of a computer. Visual and tactile stimulation was delivered to the dorsal medial phalanges of each of the participant's index fingers (see Figure 1). The visual stimuli consisted of the illumination of a red light-emitting diode (LED) for 10 msec. Tactile stimulation consisted of a tap by a small plastic rod for 10 msec. The plastic rod was driven outward by small custom-built solenoids. The stimulators were suspended by adjustable rods against the participant's fingertips and a set of weights was used to maintain their pressure constant against the participant's fingertips. The participant's hands were placed in a stable position within an anatomically shaped cast.

A central fixation point, consisting of a red LED, was placed 42 cm in front of the participant. The participant's hands were extended 20° to either side of fixation (see Figure 1). In order to mask any sound associated with the operation of the tactile stimulators, white noise [65 dB(A) as measured from the participant's head position] was delivered centrally and ear-
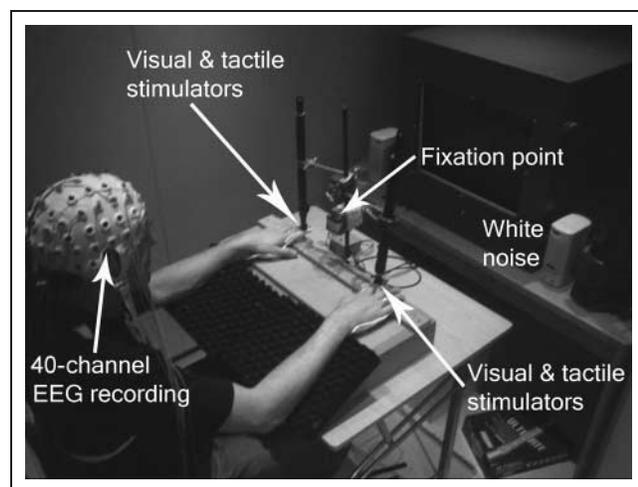

Figure 1. Experimental set-up. Each tactile stimulator was attached to an LED on each side of a central fixation point.

plugs [LaserLite, San Diego CA; noise reduction rate 32dB(A)] were worn. Participants were instructed to maintain central fixation throughout the experiment. Eye movements were monitored by means of an ISCAN ETL-400 eye-tracker (Burlington, MA). Participants responded by lifting either foot off of a footpedal one placed under the toes of each foot.

Design and Procedure

Two peripheral stimuli were presented briefly, one on each side, separated by a variable SOA. Participants had to judge whether the left or right stimulus appeared first, regardless of its sensory modality, and respond by lifting their foot off of the response pedal on the appropriate side. They were instructed to emphasize accuracy over speed. The two stimuli in each trial could either be presented from different sensory modalities (bimodal trials) or else from the same sensory modality (unimodal trials).

The participants were given written instructions at the start of the experiment, as well as a brief practice session consisting of 60 random bimodal trials. Each participant completed 20 blocks of experimental trials. These were divided into two attention conditions, with the order of presentation counterbalanced across participants. The participants were encouraged to take short breaks between blocks of trials within conditions, and a longer break between conditions.

Attention was biased toward the tactile or visual modality by means of verbal instruction and by including a higher frequency of stimuli in that modality (cf. Spence, Nicholls, et al., 2001; Spence, Shore, et al., 2001). In each experimental block, two thirds of the trials were bimodal and one third of the trials were unimodal. Unimodal trials consisted of pairs of stimuli in the "attended" modality, separated by one of five possible SOAs: 0, ±35, and ±150 msec. Bimodal trials also included five SOAs, centered on the PSS established in preliminary behavioral testing ($n = 13$ participants). In this pilot study, the visual stimulus had to lead the tactile stimulus by 60 msec for the PSS to be achieved (cf. Spence, Baddeley, Zampini, James, & Shore, 2003; Spence, Shore, et al., 2001, for similar results). Accordingly, the SOAs used in the bimodal trials of the current experiment were: PSS (60 msec, pilot study PSS), PSS ± 35 msec (95 msec, 25 msec), and PSS ± 150 msec (210 msec, −90 msec). Note that the visual stimuli preceded the tactile stimulus for all but one SOA (−90 msec). Unimodal and bimodal trials, with left and right leading stimuli, at each SOA, were randomly intermixed, and appeared in an unpredictable order.

Participants completed 600 trials in each attention condition, divided into 10 blocks of 60 trials lasting approximately 2–3 min each. There were 400 bimodal trials, equally divided into left-first and right-first trials, but with a greater proportion in the middle three SOAs

(100 trials each) as compared to the outer two SOAs (50 trials each). This translated into 50 left-first trials and 50 right-first trials at the 25, 60, and 95 msec SOAs; and 25 left-first trials and 25 right-first trials at the −90 and 210 msec SOAs. The 200 unimodal trials used a similarly proportioned distribution of trials: 50 trials with the left and right stimuli delivered simultaneously (0 msec SOA); 100 trials with equally distributed left-first and right-first stimuli at an SOA of 35 msec; and 50 trials with left-first and right-first stimuli at an SOA of 150 msec.

Each trial started with the presentation of two stimuli, one on either side of fixation. Participants then responded, indicating which stimulus they thought occurred first. They were told that response accuracy was more important than response speed. The next trial started 1500–2000 msec after the response of the previous trial.

The percentages of bimodal trials in which participants judged that the side on which the visual stimulus was presented first at each SOA were computed and subsequently normalized into z-scores (see Spence, Nicholls, et al., 2001). The PSS for each participant was calculated by fitting the best-fitting straight line through the z-scores across the five SOAs (−90 to 210 msec), and interpolating the value of 50/50 responses (see Cohen, Ward, & Enns, 1999). These values were analyzed using a two-way repeated-measures analysis of variance (ANOVA) with the factors attention (vision, touch) and side of visual stimulation (left, right).

ERP Recordings

Electroencephalogram (EEG) was recorded with Ag–AgCl electrodes from 34 scalp electrodes (Easy Cap, Herrsching-Breitbrunn, Germany; NuAmps digital amplifiers, Neuroscan, El Paso, TX). Additional electrodes served as ground (AFZ), reference, and electrooculogram (EOG) channels (see Figure 2). The right mastoid
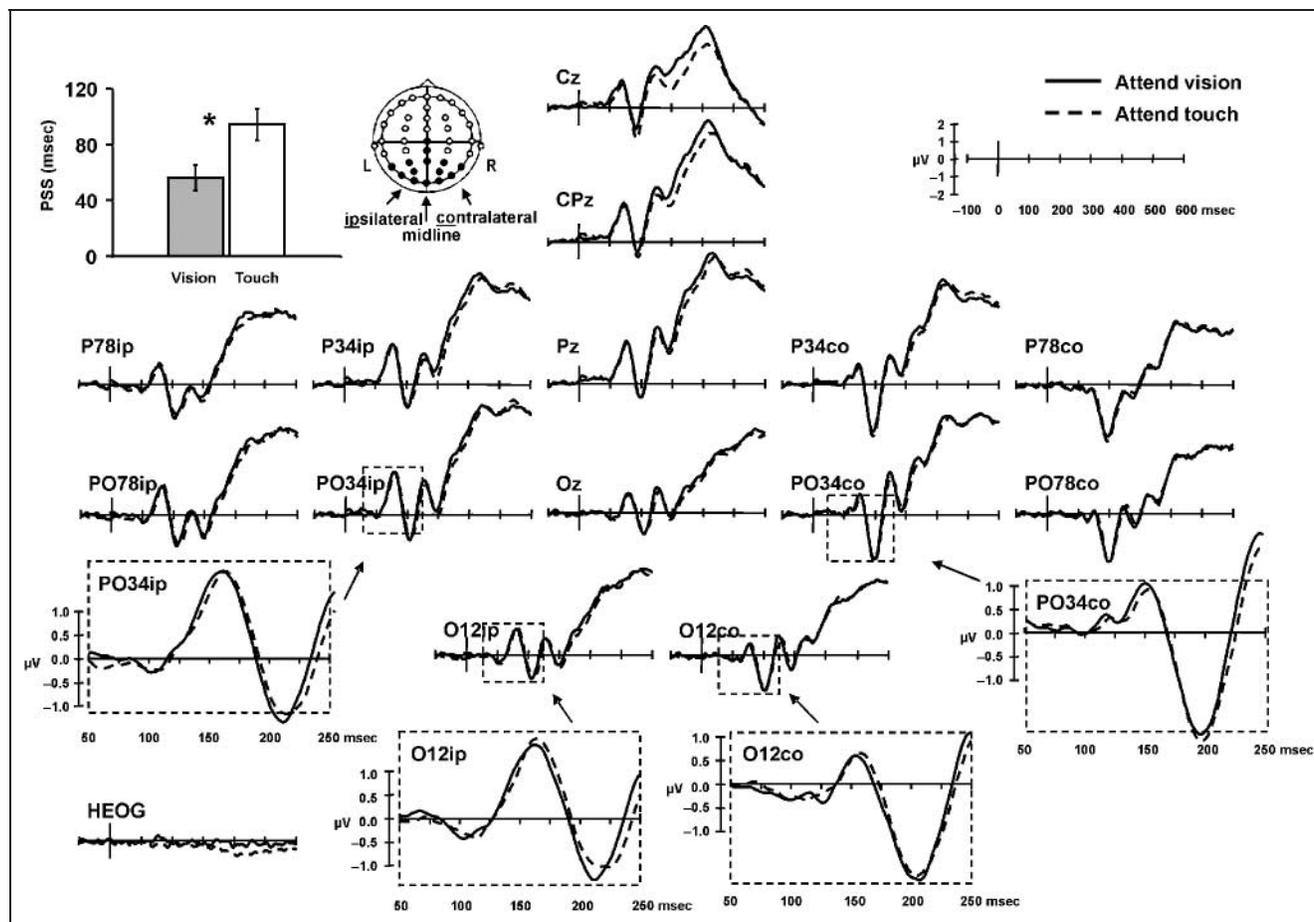

Figure 2. The graph in the upper left corner shows the PSS in the attend-vision and attend-touch conditions, and the significant behavioral prior entry effect. Grand-averaged ERP waveforms for visual stimuli in the attend-vision (attended, solid lines) and the attend-touch (unattended, dashed lines) conditions show latency and amplitude modulations of potentials as a function of the attention condition. A bird's eye view of the electrode montage used in the experiment is shown above. Waveforms are shown for the electrodes used to analyze the visual and P300 potentials, and these are shaded black on the montage schematic. Blow-ups of the early portion of the waveforms at PO3/PO4 and O1/O2 electrodes, where the early prior-entry effects and amplitude modulations were largest, are shown. Positive voltage is plotted upward.

was used during the recordings as the active reference. Subsequently, the data were re-referenced off-line to the average of both mastoids. This choice of reference is the same as that used in the previous TOJ study of McDonald et al. (2005), and was chosen to facilitate direct comparison between the two studies. Electrode impedances were kept below 5 kΩ. The horizontal EOG (HEOG) was recorded from the outer canthi of both eyes and the vertical EOG (VEOG) was recorded from above and below the right eye. All recordings were sampled at a rate of 500 Hz and filtered with a 40-Hz low-pass filter (DC—40 Hz).

The experiment was designed to analyze ERPs elicited by visual stimuli in bimodal trials. Unimodal stimuli were only included in the experimental design to manipulate attention, hence, were not included in the ERP analysis. Because of the smaller amplitudes of potentials associated with tactile as compared to visual stimuli, and the risk of contamination of the tactile potentials by the potentials evoked by preceding visual stimuli in most SOA conditions, analysis of tactile ERPs was not carried out.

EEG and EOG data were processed using Scan 4.3 (Neuroscan). The raw EEG signals were epoched into periods starting 200 msec prior to the onset of the visual stimuli and ending 822 msec after stimulus onset. ERPs were constructed separately for visual stimuli presented in the left and right visual field, at each of the five SOAs, and in each attention condition. The prestimulus period (−200 to 0 msec) was used as a baseline period against which to measure the brain activity evoked by the visual stimulus. Trials including eye blinks or large eye movements, measured as large voltage deflections on the HEOG or VEOG channels (±50 μV), were automatically removed. Additionally, epochs containing potentials above ±150 μV in any channel were also removed to avoid large drifts in the signal. Epochs were also inspected visually to ensure that all eye movements, drift, or excessive alpha activity were eliminated. Because of the subjective nature of TOJs, it was not possible to remove trials according to behavioral errors. After artifact rejection, ERPs for each attention condition, side, and SOA consisted of an average of 41 trials for the three middle SOAs and 20 trials for the two extreme SOA conditions. When stimulus side and SOA were collapsed (see below), the average number of trials was 329, ranging between 231 and 384 across participants.

In order to test for putative amplitude and latency modulations of brain activity as a function of the attention manipulation, the potentials elicited by the visual stimuli were analyzed at electrodes and time periods where they were maximal. As a measure of the amplitude of brain activity, we analyzed the mean amplitudes of the potentials that were reliably identifiable across participants. Mean amplitudes were measured over a relatively narrow band of time around the peak latency of the potential in order to minimize the contributions of activity related to other brain potentials. As a measure of timing of brain activity, the peak latencies of the identifiable potentials were measured. The temporal window was enlarged relative to the mean amplitude window in order to ensure that the peak was reliably identified in each participant. Peak latencies were identified by a simple automated algorithm that found the absolute maximum or minimum value for positive or negative potentials within the temporal window. The results were visually inspected to ensure that the identified peaks were identified correctly, and not contaminated by excessive noise values or drift. Appropriate values of peak latencies were obtained in all cases.

Mean amplitudes and peak latencies of the first identifiable visual potential P1 were analyzed at electrodes O1/2, PO3/4, and PO7/8 between 100 and 200 msec for latencies and between 140 and 160 msec for amplitudes. The later visual N1, P2, and N2 potentials were analyzed at electrodes O1/2, PO3/4, PO7/8, P3/4, and P7/8 in the following ranges for latencies: 150–250 msec (N1), 200–300 msec (P2), 250–350 msec (N2); and in the following ranges for amplitudes: 180–220 msec (N1), 240–360 msec (P2), 280–300 msec (N2). The late P300 potential was identified and analyzed at electrodes C3/Cz/C4, CP3/CPz/CP4, and P3/PZ/P4; between 300 and 600 msec for latencies and between 350 and 450 msec for amplitudes. Effects of the attentional manipulation upon the mean amplitude and latency of the potentials were assessed using repeated-measures ANOVAs, testing for the factors of attention (vision, touch), stimulus side (left, right), SOA (−90, 25, 60, 95, and 210 msec), scalp hemisphere (contralateral, ipsilateral, and midline where relevant), and electrode location. To control for possible violations of sphericity, Greenhouse–Geisser adjustments were applied to the degrees of freedom where necessary.

We were primarily interested in the effects of the attention manipulation. Evidence for prior entry was taken to be constituted by effects of attention upon the latencies of potentials. In order to rule out any influence of possible overlap from tactile potentials upon the latency measures of visual potentials at any given SOA, only effects of attention that did not interact with the SOA factor were considered to be indicators of prior entry. Effects of attention that were independent of the SOA factor were followed up by a simpler analysis, which maximized signal-to-noise. In this additional analysis, ERPs elicited by left and right visual stimuli at each of the five SOAs were combined using weighted averaging according to the number of trials in each condition. Left and right stimuli were combined in a way that preserved the position of the contralateral and ipsilateral electrodes relative to stimulus side. Electrodes were renamed as contralateral or ipsilateral to the stimuli for averaging.

In addition to analysis of the ERPs, a topographical analysis was also carried out in order to examine the onset of stable topographical features associated with the early visual potentials elicited by left and right visual stimuli in the attend-vision and attend-touch conditions. Data were collapsed over the SOA conditions. Brain activity elicited by left and right visual stimuli in the two attention conditions were summarized by an optimum number of segmentation maps using the Cartool software (Functional Brain Mapping Laboratory, Geneva, Switzerland). These segmentation maps represent dissociable stable periods of electrical field patterns, reflecting activity in a unique distribution or weighting of neural generators (Pascual-Marqui, Michel, & Lehmann, 1995; Michel, Henggeler, & Lehmann, 1992; Lehmann, Ozaki, & Pal, 1987). To perform the segmentation analysis, the ERP waveforms were re-referenced to the average reference and normalized by their global field power (Lehman et al., 1987). This measure is calculated as the square root of the mean of the square value recorded at each electrode and is equivalent to the spatial standard deviation of the scalp electric field. The normalized group ERP waveforms were then included in a segmentation process that is similar to a spatial–temporal cluster analysis. In order to investigate the effects of prior entry on early visual potentials, the segmentation was performed between 0 and 300 msec after stimulus onset. To avoid spurious maps, the constraint was imposed that each scalp topography be observed for at least five consecutive data points (more than 10 msec at 500-Hz acquisition rate). The optimal number of maps that best explained the data was defined by a cross-validation criterion (Pascual-Marqui et al., 1995), yielding a sequence of nonoverlapping scalp topographies for each condition.

RESULTS

Two participants had PSS values outside of the range tested (>250 msec) and so were excluded (cf. Spence, Shore, et al., 2001). For the remaining participants, the interval between the visual and tactile stimuli required for the stimuli to be judged as simultaneous was significantly smaller when participants attended to vision than when they attended to touch [$F(1,14) = 15.6$, $p = .001$]. When the participants attended to touch, the visual stimuli had to lead the tactile stimuli by an average of 94 msec in order to be judged as simultaneous. When attention was directed to vision, the visual stimuli had to lead by an average of only 56 msec, giving rise to a mean prior-entry effect of 38 msec. This value is consistent with the findings of previous psychophysical studies of the visuotactile and audiovisual prior-entry effects (e.g., Zampini et al., 2005; Spence, Shore, et al., 2001). There was no main effect of the side of the visual stimulus on

the PSS, nor did it interact with the attention factor (both Fs < 1).

ERP Effects

Peak Latencies

The visual stimuli presented in the bimodal trials elicited clear P1, N1, P2, N2, and P300 potentials. The earlier C1 potential, which originates primarily from the primary visual cortex, was not readily identifiable in the grand-average data nor reliably measured across the participants' data. The successive identifiable visual potentials had a characteristic lateral posterior distribution, and because of the dim and very peripheral nature of the stimulation used, were observed relatively late in this experiment. The P1 potential was largest over the PO3/PO4 electrodes and the N1, P2, and N2 were largest over the more lateral occipito-parietal electrodes. The P300 potential had a broad distribution, which was maximal over the central–posterior region of the scalp over the Pz electrode.

Directing attention to vision rather than to touch resulted in a significant modulation of the peak latency of the visual potentials (see Figure 2). These effects were observed as early as the P1 potential. The attention condition exerted a main effect on P1 latency [$F(1,14) = 5.6$, $p < .05$], revealing that P1 peaked earlier in the attend-vision condition (147 msec) than in the attend-touch condition (151 msec). As expected, the P1 potential peaked significantly earlier over contralateral electrodes (141 msec) than over ipsilateral electrodes (157 msec) [$F(1,14) = 44.7$, $p < .001$], but the effect of attention did not interact with hemisphere. There was a statistical trend towards an interaction between attention and electrode location [$F(1.3,18.1) = 3.3$, $p = .08$], showing the latency effects to be more pronounced over the O1/O2 electrode pair than over the PO7/PO8 and PO3/PO4 electrode pairs.

At the O1/O2 electrode pair, the P1 peaked earlier for attended as compared to unattended visual stimuli in 12 of the 15 participants (3–17 msec difference), remained about the same in 2 participants (0–3 msec, which is within the temporal resolution of the EEG measurement), and was slowed in 1 participant (−6 msec). There was no main effect of stimulus side or SOA, and neither of these factors interacted with the attention condition. Accordingly, the effects of attention on the peak latency of P1 were confirmed by an ANOVA in which the ERPs were averaged across presentation side and SOA [$F(1,14) = 5.6$, $p < .05$]. A correlation analysis tested whether there was a linear relationship between the difference in peak latencies of the P1 potential and the PSS values in the attend-vision versus attend-touch conditions. Differences in P1 peak latencies for left and right visual stimuli at O1/O2, the electrodes where the potential was largest, were significantly positively

correlated with differences in the PSS [$r(28) = .36$, $p < .05$].

The peak latency of the N1 potential was also earlier when attention was directed to vision (198 msec) than when it was directed to touch (201 msec) [$F(1,14) = 7.6$, $p < .05$]. As for the P1, the latencies for the N1 potential were observed significantly earlier contralaterally (197 msec) than ipsilaterally (203 msec) [$F(1,14) = 6.5$, $p < .05$], but once again the effect of attention did not interact with hemisphere. There was no interaction between attention and electrode for the N1 potential. The effect of attention did not interact with the SOA factor, but did interact with stimulus side [$F(1,14) = 11.4$, $p < .05$]. A larger anticipation of the peak latency occurred for stimuli appearing on the left as compared to on the right. The main effect of attention on the peak latency of N1 was confirmed by the ANOVA in which ERPs were averaged across presentation side and SOA [$F(1,14) = 7.63$, $p < .05$], and the effect did not interact with electrode hemisphere or position.

No significant effect of attention condition was observed on the P2 peak latency that was independent of SOA. There was a trend for an interaction between attention condition, SOA, and electrode hemisphere [$F(3.2,44.2) = 2.68$, $p = .06$]. Therefore, although the analysis suggests a tendency for a prior-entry effect at this stage of neural processing, it was not possible to rule out contamination from the overlap of tactile potentials as a cause for the effect.

Attention condition again affected the peak latency of the N2 potential, which was earlier when attention was directed to vision (289 msec) than when attention was directed to touch (293 msec) [$F(1,14) = 4.76$, $p < .05$]. The effect was more pronounced over ipsilateral (6 msec) than contralateral electrodes (2 msec) [Attention × Hemisphere: $F(1,14) = 8.55$, $p < .05$]. The attention effect interacted with both stimulus side and SOA in a complex manner [$F(3.3,45.5) = 3.30$, $p < .05$]. The largest effects of attention condition occurred for the more extreme SOAs, and at the contralateral electrodes.

Latency effects were also seen for the late P300 potential (see Figure 2). The P300 potential peaked earlier when attention was directed to vision (435 msec) than when attention was directed to touch (449 msec) [$F(1,14) = 4.8$, $p < .05$]. The P300 potential was most pronounced over the central scalp region, peaking earliest over Cz and flanking electrodes than over the more posterior electrodes analyzed [main effect of hemisphere: $F(2.0,27.7) = 16.8$, $p < .001$; main effect of electrode: $F(1.4,19.3) = 23.4$, $p < .001$; Hemisphere × Electrode interaction: $F(3.0,42.2) = 9.2$, $p < .001$]. The effect of attention was widespread over the central–parietal scalp region and did not interact with hemisphere or electrode location. The effect of attention upon P300 peak latency did not interact with SOA, but there was a trend toward an interaction between attention and stimulus side [$F(1,14) = 4.5$, $p = .05$], suggesting

that the attention effects tended to be larger for stimuli presented in the left visual field than in the right visual field. In the analysis of the combined data, there was a main effect of attention condition [$F(1,14) = 4.84$, $p < .05$], which did not interact with electrode hemisphere or location.

Mean Amplitudes

In addition to changing the timing of ERPs, the manipulation of attention also affected the amplitude of the ERPs (see Figure 2). The mean amplitudes of visual potentials P1 and N1 were enhanced over selected scalp locations. Analysis of P1 showed a significant modulation of attention by electrode [$F(1.7,23.6) = 4.9$, $p < .05$], with enhanced effects over PO3/PO4. This effect of attention did not interact with either stimulus side or SOA.

Amplitude effects after the P1 potential were difficult to interpret because of possible interactions with effects of SOA. Analysis of N1 showed an interaction between attention and electrode hemisphere [$F(1,14) = 5.4$, $p < .05$], with N1 amplitude enhanced over the ipsilateral, but not the contralateral, electrodes. However, there was also an interaction between attention condition and SOA at specific electrodes [$F(4.7,65.7) = 2.76$, $p < .05$]. Mean amplitudes of the N2 potential were also significantly larger for attended as compared to unattended visual stimuli [$F(1,14) = 6.9$, $p < .05$], but the effect of attention tended to interact with SOA [$F(2.5,34.3) = 2.7$, $p = .07$]. The mean amplitudes of P2 and P300 were not significantly affected by attention in a way that was independent of SOA.

Topographies

Figure 3 shows the topographical summary of the identifiable ERPs elicited by left and right visual stimuli in the attend-vision and attend-touch conditions. Segmentation between 0 and 300 msec resulted in seven topographical maps. The topographies during the identifiable visual potential (P1–N2) did not differ between attention conditions. However, the topographies relating to the P1 and N2 potentials were different depending on the side of the visual stimulus. The segmentation shows that stable topographical states corresponding to the P1, N1, P2, and N2 started and ended earlier for attended as compared to unattended visual stimuli presented in the left visual field. A similar pattern of results occurred for the onset of the N1 and P2 states for stimuli presented in the right visual field. For these stimuli, the P1 and N2 states were found to onset at the same time. The peaks within the global field power waveforms provided an alternative measure of the timing of information processing within each of the stable topographical periods. The latencies of the peaks of global field power within the topographies corresponding to

Figure 3. Global field power (GFP) waveforms for left and right visual stimuli in the attend-vision and attend-touch conditions over the group of participants, with colors indicating the duration of stable topographical states, and the corresponding topographical maps. The waveforms are shown during the period of identifiable early visual potentials (120–300 msec). The visual potentials associated with the topographies shown are labeled above (P1, N1, P2, and N2). The latency for the onset of each topographical state is indicated below each waveform, and the latency for the peak of the GFP within each topographical state, when identified, is shown within the waveform.
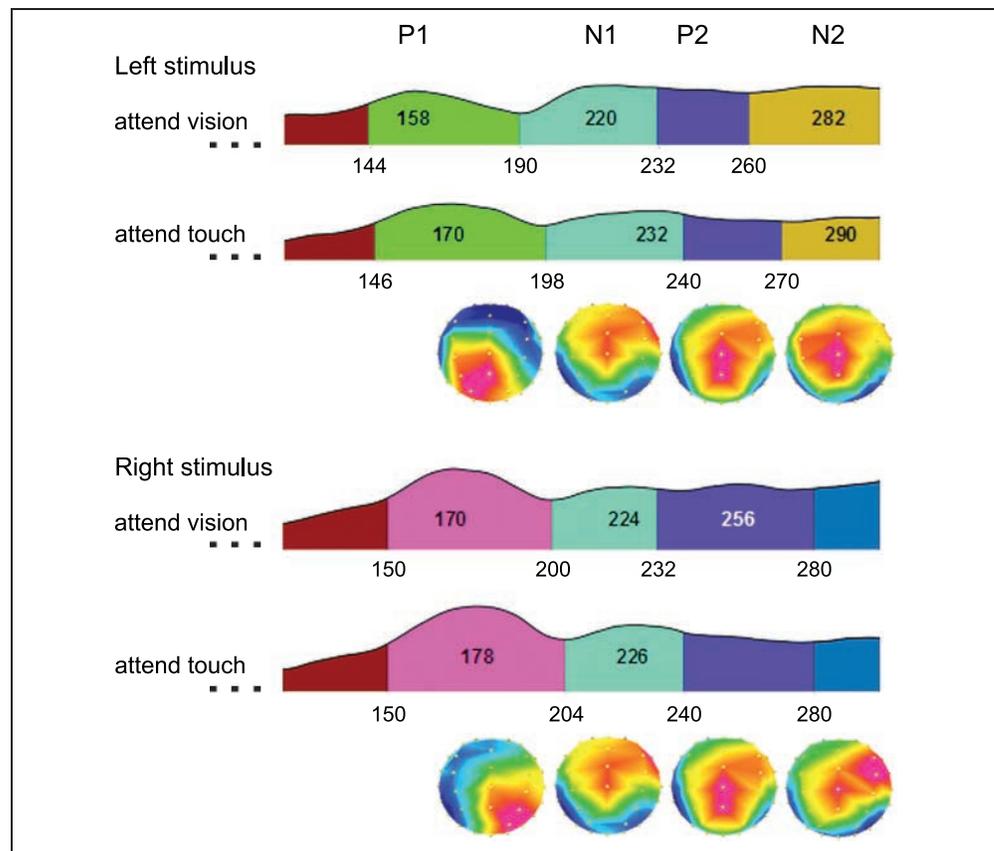
the visual P1 and N1 potentials were consistently earlier for attended as compared to unattended stimuli from both visual fields. In the case of the P2 potential, it was not always possible to identify a peak of the global field power within the corresponding interval. The segmentation ceased before the peaks of the global field power could be reliably identified for the N2 potential in the elicited right visual stimuli.

DISCUSSION

These findings provide the first clear evidence that selective attention can change the timing of perceptual analysis in visual areas using a TOJ task. The behavioral data revealed a shift in the perceived relative latency of visual and tactile stimuli depending upon which sensory modality participants directed their attention toward. The critical new result to emerge from the present study was that these behavioral measures were accompanied by shifts in the latencies of early visual ERPs, reflecting a shift in the perceptual stimulus analysis in the brain.

The attention manipulation and task procedures were adapted from previous behavioral TOJ studies by Zampini et al. (2005) and Spence, Shore, et al. (2001) for investigating the modulation of visual ERPs. The pro-

cedures avoid or minimize effects of response bias by using a response criterion (spatial location) that is orthogonal to the attention manipulation (sensory modality). The sustained attention manipulation by instruction and by the larger proportion of trials from one modality is also likely to be more effective than trial-by-trial attention manipulations. Finally, the procedures avoid the possible effects of low-level sensory interactions between exogenous cue and target stimuli. The resultant behavioral prior-entry effect of 38 msec fits with earlier work (Zampini et al., 2005; Spence, Shore, et al., 2001). These behavioral effects were accompanied by electrophysiological effects starting from relatively early perceptual stages of stimulus processing. In addition to amplitude enhancements of visual potentials, which are typically observed in visual selective attention experiments, the results in our TOJ experiment showed changes in the timing of perceptual stages of analysis as well.

Latency shifts occurring during perceptual stages of stimulus processing, which can be revealed by ERPs, provide the most convincing evidence yet for the existence of prior entry (Titchener, 1908). In the current experiment, the first reliably measurable potential elicited by the peripheral visual LED stimuli was the visual P1, and was followed by the visual N1. The P1 and N1 are widely believed to reflect successive stages of perceptual analysis of visual stimuli across several ven-

tral and dorsal extrastriate areas (Foxe & Simpson, 2004; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Schroeder et al., 1995; Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994). The timing of these potentials was significantly anticipated by sustaining attention to the visual versus tactile modality, as indicated by significant effects of the attention manipulation upon the peak latency of each potential. The peak latency of a potential may not hold any special intrinsic value about the neural computations reflected by a given potential, but it at least provides a temporal landmark that is systematically related to the potential that can be compared across conditions to assess changes in the timing of the underlying neural states. Importantly, these peak latency effects were independent of the specific intervals between the visual and tactile stimuli, and therefore, were unlikely to result from artifacts related to overlap between the potentials evoked by the two types of stimuli. Further evidence for the functional relationship between the shifts in the timing of early neural processes and behavioral shifts in the PSS was provided by a significant correlation between these two effects. The difference in the latency of the P1 potential in the two attention conditions covaried with the difference in the PSS latency.

Converging evidence for the speeding-up of perceptual processes related to the P1 and N1 potentials was obtained from topographical segmentation. Stable topographical states were identified, which corresponded to the P1 and N1 potentials. Selective attention did not alter the topographies, suggesting that the underlying neural processes when attention was directed to vision versus touch could not be distinguished in kind. Instead, the peak in global field power within the P1 and N1 maps, which represent another systematic temporal landmark in these stages of processing, occurred earlier when attention was directed to vision rather than to touch. The P1 and N1 topographical states also started earlier for left visual stimuli when attention was directed to vision rather than to touch. For right visual stimuli, the onset of the N1 state was also earlier, but the onset of P1 did not differ.

Shifts in the timing of subsequent potentials were also observed. Significant differences in peak latencies occurred for the N2 and P300 potentials. The modulation of the N2 latency interacted with the interval between the visual and tactile stimuli, and therefore, it may be imprudent to draw too many conclusions as the result could be contaminated by fortuitous effects of overlap from tactile potentials. Modulation of the P300 was independent of stimulus interval, and therefore, is more readily interpretable as a result of prior entry. Notably, the latency shift of the P300 potential was much larger in magnitude (14 msec) than the shift of the early visual P1 and N1 potentials (3–4 msec). This suggests that the prior-entry effects increase as neural processing proceeds from perceptual to later cognitive and motor-

related processes. In comparison with the 38-msec behavioral prior-entry effect, however, the electrophysiological latency shifts may appear substantially smaller. However, a couple of qualifications should be borne in mind. As mentioned earlier, the peak latency is a rather arbitrary temporal landmark and may not be the optimal measure with which to correlate behavioral measures. Furthermore, temporal overlap between successive potentials elicited by visual stimuli may itself influence the peak latency measures and dilute the ability to obtain a measure of the underlying brain activity. Finally, as latency shifts increase between early visual potentials and the P300, further increases can occur between the P300 and motor-related activity in motor areas and in the muscles of the response effectors.

There are some, possibly insurmountable, difficulties in inferring changes in the timing of brain activity from the peak latencies of ERPs. As described above, temporal overlap between potentials may diminish the information provided by peak latencies. For example, no effect of attention was measured on the P2 peak latency. On the other hand, the onset of the topographical map associated with the P2 occurred earlier when attention was directed to vision rather than to touch. The peak value for global field power within this map was also earlier when attention was directed toward the visual modality. Another problem arises because potentials are complex macroscopic measures of the underlying brain activity. Even relatively early potentials, such as P1, most likely reflect activity in multiple brain areas, and possibly with different underlying time-courses. It is always possible, therefore, that a shift in the apparent peak latency of a potential reflects instead the amplitude modulation of activity in some brain area(s) that contributes to the potential measured at the scalp. However, in this case, given the modulation of multiple potentials and the increase in the latency shifts across the ERP waveform, the most plausible explanation is that the shifts in latency peaks and of the onset of topographical maps do represent changes in the timing of underlying brain activity.

It is difficult to determine the extent to which there are causal links between the shifts in latency of the successive potentials. In principle, it is possible that the potentials measured in the task (P1, N1, P2, N2, and P300) represent interdependent successive stages of information processing. On the other hand, there could be some degree of independence between the neural processing reflected by certain of these potentials. Furthermore, the modulation of the timing of early potentials may have cascaded and accumulated through the various stages of information processing. On the other hand, it is also very likely that our selective attention manipulation may have biased multiple stages of information processing in different ways. There is ample evidence for dissociations in the modulation of potentials in visual selective attention tasks (e.g., see

Anllo-Vento et al., 2004; Luck, 1995, for reviews) Arbitrating between these different possibilities was not possible within the context of the current experiment.

In sum, ERPs recorded during the visuotactile TOJ task yielded convincing evidence for the existence of prior-entry effects. The main criticism of earlier prior-entry research, which holds that the effects reflect nothing more than direct or cognitively mediated response biases (e.g., Zampini et al., 2005; Spence, Shore, et al., 2001), was clearly refuted by the early nature of the effects within the processing pathway. However, the additional top-down cognitive factors may also have contributed, especially as one moves toward the later modulations. In addition, local sensory interactions between cue and target stimuli were ruled out by the blocked attentional manipulation of the task and by the absence of any cuing stimuli.

Finding latency shifts of early visual potentials is unusual in ERP experiments of selective attention, and provides further insight into the multiple mechanisms behind attentional modulation of cortical activity. Most selective attention studies have reported relative enhancement of the amplitude of potentials evoked by attended relative to unattended stimuli, in the absence of any latency modulations (e.g., Anllo-Vento et al., 2004; Eimer, 1998, 2004; Luck et al, 2000; Hillyard & Anllo-Vento, 1998; Mangun, 1995). These findings have suggested a relative gating and sensory gain control mechanism as the main means for attentional biasing (Hillyard & Anllo-Vento, 1998; Hillyard, Vogel, & Luck, 1998; Hillyard & Mangun, 1987). Typically, the attentional tasks used have directed attention to a spatial location for stimulus identification or discrimination. However, similar amplitude modulations have also been observed when attention is directed toward a specific sensory modality (e.g., De Ruiter et al., 1998; Eimer & Schröger, 1998; Woods et al., 1992). The manipulation of attention between sensory modalities is, therefore, unlikely to provide the sole explanation for the unmasking of these latency differences in our experiment.

The determining factor in disclosing changes in timing of neural processing may have been the very strong temporal demands placed by the TOJ task, which was combined with a strong and sustained manipulation of selective attention toward a specific sensory modality. The present experiment was different in that it used a highly demanding temporal discrimination task. Timing was therefore at center stage of the task goals, and in many trials, participants were operating at the limits of their perceptual abilities. In this manner, it was possible to unveil an additional mechanism by which attention can bias information processing. The strength and type of the attentional manipulation may also have contributed to the ability to reveal these subtle temporal modulations in neural processing. It was also critical to use a high sampling rate to measure brain activity (500 Hz), without which the small but reliable effects upon the

early visual potentials would have been missed. Our findings therefore support the availability of multiple mechanisms to bias cortical activity, depending on the task demands and the types of stimulus dimensions used in the attentional manipulation (Nobre, 2004).

Placing high temporal demands upon performance, however, may not be sufficient to induce changes in the timing of early visual potentials. In their recent TOJ study, McDonald et al. (2005) reported amplitude enhancements rather than any latency shifts in the early visual potentials. Latency shifts were observed only for the P2 potential, but they were unable to correlate this effect unambiguously with behavioral performance. Their inability to detect any evidence for an early latency shift could stem from their use of a lower sampling rate than appropriate for detecting small changes in the latencies of perceptual potentials (250 Hz). The type of attentional manipulation or the way in which it was induced on a trial-by-trial basis may also have determined the effects they observed.

Drawing attention to sensory modalities instead of to spatial locations might more readily enable the speeding-up of information processing in modality-specific sensory areas. The types of sensory processing available for modulation by spatial versus modality-based information may differ to some extent (Spence, Shore, et al., 2001), and studies comparing both types of attention in target-detection tasks have occasionally highlighted differences in patterns of modulation (e.g., Hotting, Rosler, & Roder 2003; Talsma & Kok, 2001; Eimer & Schröger, 1998). A direct comparison between ERP effects in equivalent TOJ tasks, in which attention was directed either to a sensory modality or to a spatial location, would be very useful in addressing this possibility.

The sustained nature of our attentional manipulation may also have been important in enabling the measurement of latency shifts of the P1 potential. Sustained attention often results in a stronger modulation of perceptual potentials compared to trial-by-trial attentional orienting (Eimer, 1998). Manipulating attention in a tonic way also avoids any possible sensory interactions between cue and target stimuli, which may be especially problematic when these two types of stimuli occur in very close temporal succession. In the study by McDonald et al. (2005), a brief nonpredictive auditory cue preceded the visual array by very short intervals (100–300 msec SOA, 17–217 msec interstimulus interval). Under these conditions, low-level cross-modal sensory interactions may have contributed to their behavioral as well as electrophysiological effects (see Driver & Spence, 2004; Spence, McDonald, & Driver, 2004). Whereas some aspects of such cross-modal capture effects may occur through top-down spatial biasing effects, others may represent more stimulus-driven, bottom-up sensory interactions. Studies of cross-modal attentional capture have shown that when the intervals between stimuli presented in different sensory modalities is very short, the stimuli may be

integrated, and this can sometimes evoke additional (superadditive) effects (e.g., Calvert, Spence, & Stein, 2004), therefore also potentially relying on different mechanisms (see Schneider & Bavelier, 2003, on this issue). The possible conflation of these types of effects was avoided in our sustained attention manipulation.

Our results suggest the existence of multiple mechanisms by which attention can bias perception. When strong competition occurs within the temporal domain, modulation of neural timing may play a role in biasing information processing, at least when the different stimuli occur in different sensory modalities. These changes in the temporal dynamics can co-occur with the more established changes in the amount of information processing taking place at different stages, as proposed by gain-control accounts (e.g., Hillyard et al., 1998). The modulation of neural timing has also been observed when the appearance of stimuli can be temporally predicted. In temporal-orienting ERP experiments, the latency of postperceptual potentials is enhanced for temporally predicted relative to unpredicted stimuli (Correa, Lupianez, Madrid, & Tudela, 2006; Doherty, Rao, Mesulam, & Nobre, 2005; Griffin, Miniussi, & Nobre, 2002; Miniussi, Wilding, Coull, & Nobre 1999). Single-unit recording studies have also shown modulation of neural timing by the temporal predictability of stimuli in both visual areas (V4, Ghose & Maunsell, 2002) and multisensory parietal areas (LIP, Janssen & Shadlen, 2005). Multiple types of attentional mechanisms may therefore cooperate to enhance perception, and their relative importance may be determined by task goals and affordances (Nobre, 2004).

Almost a century ago, Titchener (1908) claimed that attended stimuli come into consciousness earlier than unattended stimuli (the law of "prior entry"). Our study provides the first empirical support for the ability of early latency shifts of perceptual potentials to provide a potential mechanism for prior entry (cf. Köhler, 1947). Behavioral results suggest that attention can speed up perception, and ERP data support this finding by showing significant shifts in the P1, N1, and P3 potentials. Thus, the finding of early perceptual modulation by attention to sensory modalities provides the first electrophysiological support for the law of prior entry and indicates that both latency and amplitude differences can underlie attentional orienting in the human brain.

Acknowledgments

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