
Crossmodal links in spatial attention are mediated by supramodal control processes: Evidence from event-related potentials

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Abstract

Crossmodal links in spatial attention were studied in an experiment where participants had to detect peripheral tactile or visual targets on the attended side, while ignoring all stimuli on the unattended side and in the currently irrelevant modality. Both relevant locations and relevant modalities were specified on a trial-by-trial basis by auditory precues. Spatial orienting in the cue–target interval was reflected in anterior negativities and occipital positivities contralateral to the cued side, either when vision or touch was cued as relevant. These effects resembled previously reported ERP modulations during shifts of visual attention, implicating supramodal mechanisms in the control of spatial attention and demonstrating their independence of cue modality. Early effects of spatial attention on somatosensory and visual ERPs were of equivalent size for currently relevant and irrelevant modalities. Results support the idea that crossmodal links in spatial attention are mediated by supramodal control mechanisms.

Descriptors: Visual-spatial attention, Tactile-spatial attention, Crossmodal attention, Attentional control, Event-related brain potentials

In many situations, the adaptive control of behavior requires the integration and coordination of information about relevant objects and events that originates from different input modalities, but from overlapping spatial locations. This type of crossmodal coordination could be mediated by spatial synergies (or crossmodal links) in the attentional processing of information across sensory modalities. The questions of whether there are such crossmodal links in spatial attention, which mechanisms are responsible for the presence of any such links, and how the processing of sensory information within different modalities is affected by crossmodal links have recently become a major focus in research on selective attention (see Driver & Spence, 1998, for an overview).

Several behavioral studies (e.g., Spence & Driver, 1996; Spence, Pavani, & Driver, 2000) have found evidence for crossmodal interactions in endogenous (voluntary) spatial attention between vision and audition, and vision and touch. In these experiments, participants had to direct their attention to the expected location of target stimuli within one (primary) modality. On a minority of trials, stimuli of a different (secondary) modality were presented, but these stimuli were more likely to be presented on the side opposite to the expected location in the primary modality. Superior

performance for stimuli at the expected location in the primary modality was observed not only for that primary modality, but also for secondary modality stimuli, thus demonstrating that the focus of attention within one modality influences the processing of information in other modalities.

Although these behavioral results demonstrate crossmodal interactions in endogenous spatial attention between vision, audition, and touch, they do not provide any direct insight into the neural processes associated with such interactions. The observation that crossmodal links in spatial attention influence behavioral performance does not allow firm conclusions with respect to which stages in the processing of visual, auditory, and somatosensory information are affected by such links. Performance benefits for secondary modality stimuli at locations attended for the primary modality could, in principle, result from effects of crossmodal attention on perceptual processes, or from attentional modulations of later, postperceptual stages. Another issue that cannot be resolved exclusively on the basis of behavioral measures concerns the nature of attentional control mechanisms involved in crossmodal links. Crossmodal interactions in spatial attention may reflect the activity of a single supramodal system that controls attentional orienting processes in different modalities (Farah, Wong, Monheit, & Morrow, 1989). Alternatively, such links could result from spatial synergies between “separable-but-linked” modality-specific attentional control systems (Spence & Driver, 1996).

To investigate these issues, a number of studies have examined neural correlates of crossmodal attentional interactions, using ERP (e.g., Eimer & Driver, 2000; Eimer & Schröger, 1998; Hillyard,

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Simpson, Woods, VanVoorhis, & Münte, 1984; see Eimer & Driver, 2001, for review) or hemodynamic measures (e.g., Macaluso, Frith, & Driver, 2000a, 2000b). Eimer and Schröger investigated ERP effects of crossmodal attention between vision and audition in a study where attention had to be directed to the left or right within one relevant modality (vision or audition), while the other modality could be entirely ignored. Effects of spatial attention on sensory-specific N1 components were observed not only for the currently relevant modality, but also for stimuli in the entirely irrelevant modality. However, these effects were larger in amplitude for the relevant modality (see also Hillyard et al., 1984, and Teder-Sälejärvi, Münte, Sperlich, & Hillyard, 1999, for related findings). Similar results were recently obtained by Eimer and Driver in an ERP study of crossmodal links between vision and touch, with the exception that touch can apparently be “decoupled” from spatial orienting in vision when all tactile events are entirely task irrelevant throughout a block of trials. Analogously, Eimer, Van Velzen, and Driver (2002) used ERP measures to investigate crossmodal links in spatial attention between audition and touch and found crossmodal effects of spatial attention on the auditory N1 when attention was directed to the location of relevant tactile stimuli, but no attentional modulations of somatosensory ERPs when audition was task relevant, and all tactile stimuli could be completely ignored.

Overall, these ERP results suggest that relatively early stages of visual, auditory, and tactile information processing (i.e., stages traditionally considered to be “unimodal”) can be affected by crossmodal interactions (see Eimer, 2001, and Eimer & Driver, 2001, for a more comprehensive evaluation of these findings and their implications). They are however inconclusive with respect to whether crossmodal links in spatial attention reflect the activity of a supramodal system, or are caused by spatial synergies between separable modality-specific attentional control systems. The effects of attentional shifts within one modality on sensory-specific ERP components elicited by stimuli in another modality could suggest that locations are initially selected at a multimodal level of spatial representation, with this selection then feeding down to influence unimodal sensory processes for incoming stimuli. Alternatively, spatial selection may arise primarily within a given task-relevant modality, and then spread to affect other modalities.

A closer look at the literature on crossmodal links in spatial attention reveals that some findings seem to support a supramodal account, whereas other results may appear more consistent with the idea that attentional control systems are modality specific and separable. Farah et al. (1989) based their hypothesis that spatial attention is controlled by a supramodal mechanism on results of spatial cueing experiments for patients with right-parietal lesions. The detection of visual targets presented on the contralesional (left) side was substantially delayed when these stimuli were preceded by spatially uninformative cues on the right, indicating an impaired disengagement of attention from the ipsilesional side. Importantly, this delay was independent of the modality of the cue (visual or tactile), suggesting that parietal lobe mechanisms responsible for allocating attention are based on multimodal spatial representations. Additional evidence for supramodal attentional control mechanisms was recently found by Eimer et al. (2002), who studied covert control processes involved in anticipatory shifts of spatial attention, on the basis of ERPs elicited in response to central, symbolic cue stimuli directing attention to the left or right side. In this study, participants were instructed to shift attention to the side indicated by a visual precue in order to detect infrequent auditory or tactile targets at the cued side. The relevant

modality (audition or touch) was varied between blocks, and irrelevant modality stimuli were to be entirely ignored. Attentional control processes activated in the cue–target interval were reflected in lateralized ERP modulations sensitive to the direction of spatial orienting. An enhanced anterior negativity contralateral to the cued side (“anterior directing attention negativity”) was followed by an enhanced contralateral positivity at posterior sites (“late directing attention positivity”). Importantly, these effects were elicited both when attention had to be directed to the location of relevant auditory events, and when attention was directed to the location of relevant tactile events. These lateralized effects also closely resembled ERP modulations previously observed during shifts of *visual* attention (Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Hopfinger, Jha, Hopf, Girelli, & Mangun, 2000; Mangun, 1994; Nobre, Sebestyen, & Miniussi, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994, 1995). The observation that similar ERP modulations sensitive to the direction of spatial orienting are elicited during shifts of attention to the location of relevant visual, auditory, or tactile stimuli is entirely in line with the hypothesis that unitary supramodal mechanisms are responsible for allocating attention to task-relevant locations and that the same processes are involved regardless of whether attention is shifted to visual, auditory, or tactile events.

However, other aspects of previous findings appear more consistent with the idea that attentional control systems are separable but linked than with an entirely supramodal account. First, behavioral effects of crossmodal links are typically larger for primary modalities than for secondary modalities (Spence & Driver, 1996; Spence et al., 2000). Second, effects of spatial attention on early modality-specific ERP components are also generally larger in amplitude for the task-relevant modalities than for currently irrelevant modalities (cf., Hillyard et al., 1984; Eimer & Schröger, 1998). For example, although effects of spatial attention on the visual N1 have been observed both when vision was task relevant and touch could be ignored and when touch was the relevant modality and visual stimuli were to be ignored, attentional N1 modulations were significantly larger when vision was relevant (Eimer & Driver, 2000). Third, attentional modulations of ERPs elicited by irrelevant-modality stimuli are usually absent beyond 200 ms poststimulus, as attentional negativities in this time range are typically only found for task-relevant modalities (Eimer & Driver, 2000; Eimer & Schröger, 1998). Finally, touch can apparently be “decoupled” from spatial attention in other modalities when entirely task irrelevant (Eimer & Driver, 2000; Eimer et al., 2002). These observations do not support the idea of a unitary supramodal attentional control system. If attentional shifts were controlled supramodally, one would expect to find equivalent attentional effects within different modalities, regardless of whether a specific modality is currently relevant or irrelevant.

In summary, recent results from studies of crossmodal attention are inconclusive with respect to the question of whether attentional control processes are supramodal or modality specific. If the allocation of attention was based on supramodal mechanisms (as suggested by the similarity of ERP modulations observed during attentional shifts towards relevant visual, auditory, or tactile events), behavioral and electrophysiological effects of spatial attention should be equivalent for primary/relevant and secondary/irrelevant modalities. In contrast, if attentional control processes were modality specific (as indicated by differences in the effects of spatial attention for primary and secondary modalities), this should be reflected in systematic differences between ERPs recorded during shifts of visual, auditory, and tactile attention.

To account for these inconsistencies between experimental results, we have recently argued that a hybrid account, which combines aspects of both the supramodal and the “separable-but-linked-systems” approaches, may be needed to provide a full explanation of the control processes underlying crossmodal links in spatial attention (Eimer & Driver, 2001; Eimer et al., 2002). According to this account, the *phasic* selection of relevant locations typically operates in a supramodal manner, is reflected by ERP modulations observed during shifts of spatial attention, and will influence processing in task-relevant as well as in other modalities. On the other hand, the extent of the influence from such supramodal spatial selection on stimulus processing within a particular modality may also depend on the *tonic* state of activity in that modality. Activity levels vary with task relevance (see also Ward, McDonald, & Golestani, 1998, for suggestions along similar lines) and will generally be high when a given modality is relevant, and low when a modality can be ignored for an extended period of time. Such “baseline shifts” in overall activity have recently been uncovered in several functional imaging studies of selective attention (e.g., Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; see Driver & Frith, 2000, for review). Effects of spatial attention for any given modality may be modulated by such modality-specific differences in activation level. Attentional effects will be larger when tonic baseline activity is high, and will be attenuated when activity levels are reduced.

In previous investigations of crossmodal links in spatial attention that have found results in favor of the hypothesis that attentional control mechanisms are modality specific, relevant/primary modalities remained constant for a series of successive blocks. This fact may have resulted in systematic tonic baseline shifts in the overall activation level within modality-specific areas for currently relevant and irrelevant modalities. Thus, any difference in the size of attentional effects between relevant and irrelevant modalities may have been due to systematic differences in modality-specific activation levels. For example, a “decoupling” of touch from crossmodal spatial attention might, in principle, be achieved simply by reducing overall activity levels for touch during blocks where tactile stimuli are irrelevant.

The primary aim of the present study was to investigate this hybrid account by studying effects of crossmodal links in spatial attention between vision and touch under conditions where relevant and irrelevant modalities did not remain constant for an extended period of time (as in all previous experiments), but were varied on a trial-by-trial basis. The present experiment was similar to our previous ERP study on crossmodal links in spatial attention between vision and touch (Eimer & Driver, 2000). As in this earlier study, participants’ task was to detect and respond to infrequent targets in a currently relevant modality (vision or touch) when these targets were presented at a cued (attended) location and to ignore all stimuli at uncued locations as well as all stimuli (regardless of their location) in the currently irrelevant modality. The crucial new manipulation of the present experiment was that not only relevant locations but also *relevant modalities* were now cued on a trial-by-trial basis. At the beginning of each trial, an auditory cue was presented which was characterized by two distinct attributes. Cues were high-pitch (1500 Hz) or low-pitch (500 Hz) sounds of two highly discriminable instruments (flute and marimba). The relevant modality for any given trial (vision or touch) was indicated by the instrument, and the relevant location (left or right) was indicated by the pitch. Instrument/modality and pitch/location assignments were counterbalanced across participants. To allow participants to learn a specific instrument/modality

and pitch/location assignment, several training blocks were run prior to the start of the experimental blocks. To provide sufficient time for the decoding of the cue sound and subsequent shifts of attention to relevant modalities and locations, both the cue duration (300 ms) and the cue–target interval (800 ms) were longer than in our previous study (Eimer & Driver, 2000).

Our hybrid account assumes that ERP effects of crossmodal links in spatial attention are attenuated or (in the case of touch only) absent for modalities that are irrelevant for an extended period of time because of tonic baseline shifts in the overall activation level within modality-specific areas. We propose that no such baseline shifts will be present when modalities cannot be ignored continuously, because relevant modalities are cued at the beginning of each trial and thus change from trial to trial. These hypotheses lead to two specific predictions for the present experiment. First, and in contrast to the results found by Eimer and Driver (2000) and Eimer et al. (2002), effects of spatial attention on somatosensory ERPs should now be observed under conditions where another modality is relevant and tactile stimuli can be entirely ignored. Second, and more generally, early effects of spatial attention on modality-specific visual and somatosensory ERP components should be equivalent in size regardless of which modality is relevant on a given trial.

In addition to studying the effects of crossmodal links in spatial attention on visual and somatosensory ERPs under conditions where relevant locations as well as relevant modalities are specified on a trial-by-trial basis, the present cueing procedure also allowed follow-up of the results reported by Eimer et al. (2002) for ERPs recorded in the cue–target interval. In this study, lateralized ERP effects sensitive to the direction of an attentional shift were strikingly similar when attention was directed to the location of relevant tactile and auditory targets and also very similar to the effects previously observed during shifts of visual–spatial attention. But a potential confounding factor in this earlier study was that the central cues were always visual (left-pointing and right-pointing arrows presented on a computer screen). The similarity of ERP correlates of spatial orienting across modalities in the cue–target interval might thus, at least in part, be an artefact of the modality of the cue. Because the present experiment used *auditory* cues to direct spatial attention to the location of relevant visual or tactile events, this criticism does not apply. A second aim of the present study thus was to investigate ERP modulations in the cue–target interval sensitive to the direction of attentional shifts elicited by auditory symbolic central cues, separately for trials where vision or touch are relevant. If the anterior directing attention negativity and late directing attention positivity effects observed by Eimer et al. (2002) reflected supramodal mechanisms involved in the control of attentional orienting, similar results should be obtained in the present study in response to auditory cues, even though the cueing procedure was more complex than in previous studies.

Methods

Participants

Twenty paid volunteers participated in the experiment. One of them had to be excluded due to a large number of eye blinks during trials, and 3 were excluded because of insufficient eye fixation control in the cue–target interval (see below). Thus 16 participants (11 women), aged 19–31 years (mean age: 23.2 years) remained in the sample. All participants were right-handed, and all had normal or corrected-to-normal vision.

Stimuli and Apparatus

Participants sat in a dimly lit experimental chamber, with a head-mounted microphone positioned in front of the mouth, and facing a dark computer screen. A small white fixation cross was continuously present at the center of this screen throughout the experimental blocks. Tactile stimuli were presented using two 12-V solenoids that drove a metal rod with a blunt conical tip through a small hole on to the outside of the index fingers, making contact with the pad of the participants' index fingers whenever a current was passed through the solenoid. The rods and fingertips were occluded, so that participants could not see the rod movements. White noise (62 dB SPL) was presented from a central loudspeaker positioned on the top of the computer screen throughout the experimental blocks to mask any sounds made by the operation of the tactile stimulators. Visual stimuli were presented by illuminating an ensemble of green LEDs on the left or right side. Each ensemble consisted of six LEDs arranged in a circle plus one central LED element. The angular size of each LED was 0.65° , the diameter of the circle was 2.4° . Four different types of tones served as cue stimuli. To generate these tones, the sound of one of two instruments (flute; marimba) was selected from the Sound Blaster Instrument Bank file to present one of two MIDI notes (high: 1500 Hz; low: 500 Hz). All cue sounds were presented at 72 dB SPL simultaneously from two loudspeakers located on the left and right side. The two tactile stimulators, the two LED ensembles, and the two loudspeakers were placed on a table in close spatial register, each 25° to the left or right of the central fixation cross, at a viewing distance of about 45 cm from the participant's eyes.

All auditory cue stimuli were presented for 300 ms. Tactile nontarget stimuli consisted of one rod tip contacting the participants' index finger for 200 ms. The less frequent tactile target stimuli had a gap, where this continuous contact was interrupted for 10 ms after a duration of 95 ms. Visual nontarget stimuli consisted of the continuous illumination of one LED ensemble for 200 ms. For the less frequent visual target stimuli, which like the tactile targets included a gap, the LED ensemble was illuminated for 75 ms, turned off for 50 ms, and illuminated again for 75 ms. This difference in "gap size" between tactile and visual targets was chosen to account for the fact that tactile stimulation offsets appear more abrupt and thus as more salient than LED offsets. Vocal response onset times were measured with a voice key.

Procedure

The participants' task was to respond vocally (by saying "yes") whenever a gap target was presented in the relevant modality (vision or touch) and at the relevant location (left or right). Relevant modalities and relevant locations changed independently from trial to trial, and were indicated by the four different cue types (flute-high; flute-low; marimba-high; marimba-low). The stimulus modality relevant for a given trial (vision or touch) was specified by the instrument delivering the sound (flute; marimba); the relevant location (left or right) was indicated by the pitch of the sound (low: 500 Hz; high: 1500 Hz). The mapping of instrument to relevant modality and of pitch to relevant location was counterbalanced across participants. The experiment consisted of eight experimental blocks of 124 trials each. After 62 trials of each block, participants were given a rest period, and could initiate the next run of 62 trials by pressing a response key. Each trial started with a 300-ms presentation of an auditory cue stimulus, which was followed after an empty interval of 800 ms by a visual or tactile stimulus

(200-ms duration). The intertrial interval was 1,000 ms. All four cue types were presented in random order and with equal probability. In 96 trials per block, visual or tactile nontarget stimuli were presented with equal probability on the left or right side. Each of these stimuli was preceded with equal probability by one of the four cue types, resulting in a total of six trials per block for each combination of cued modality (vision versus touch), cued location (left versus right), actual stimulus modality (vision versus touch), and stimulus location (left versus right). In the remaining 28 trials per block, visual or tactile gap targets were presented with equal probability on the left or right side. Sixteen of these trials (eight visual and eight tactile trials) contained gap targets in the relevant modality and at the relevant location, as indicated by the preceding cue, and only these stimuli required a vocal response. In the remaining 12 trials (six visual, six tactile), the modality and/or the location of the gap target was irrelevant, and responses had to be withheld to these stimuli.

Participants were instructed to respond as quickly and accurately as possible only to gap stimuli on the cued side in the cued modality, and to maintain central eye fixation throughout the blocks. A gradual training procedure was used prior to the first experimental block to enable participants to acquire the specific cue/modality and cue/location mappings. This training started with two blocks (36 trials each) where the instrument/modality mapping was introduced. Here, marimba or flute sounds were presented at an intermediate frequency (1000 Hz), and participants had to detect and respond to cued modality targets regardless of their location. Cue duration was 500 ms, cue-target interval was 1,000 ms, and intertrial interval was 1,500 ms. In training Blocks 3 and 4 (76 trials each), location cueing was added, so that the cueing procedure was identical to the subsequent experimental blocks, except that the timing of events was as in the first two training blocks. The final training block (76 trials) was identical to the subsequent experimental blocks. Eye movements were closely monitored during these training blocks. Whenever the horizontal EOG revealed that participants did not maintain central eye fixation, they were reminded again of the necessity of continuously fixating the central cross throughout an experimental block.

Recording and Data Analysis

EEG was recorded with Ag-AgCl electrodes and linked-earlobe reference from Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, and Oz (according to the 10-20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG (HEOG) was recorded bipolarly from the outer canthi of both eyes. The impedance for all electrodes was kept below 5 k Ω . The amplifier band-pass was 0.1 to 40 Hz, and no additional filters were applied to the averaged data. EEG and EOG were sampled with a digitization rate of 200 Hz and stored on disk. Voice onset times were measured for each vocal response.

EEG and HEOG were epoched off-line into 1,800-ms periods, starting 100 ms prior to cue onset and ending 600 ms after the onset of the subsequent peripheral stimulus. Separate averages were computed for ERPs recorded in the cue-target interval (relative to a 100-ms baseline preceding cue onset), and for ERPs in response to subsequent peripheral stimuli (relative to a 100-ms baseline preceding the onset of these stimuli). Trials with eyeblinks (Fpz exceeding $\pm 60 \mu\text{V}$ relative to baseline), horizontal eye movements (HEOG exceeding $\pm 30 \mu\text{V}$ relative

to baseline), or other artefacts (a voltage exceeding $\pm 60 \mu\text{V}$ at any electrode location relative to baseline) were excluded from analysis. This procedure resulted in a mean trial exclusion rate of 38% (trial exclusion rates for individual participants ranging from 15% to 52%). Averaged HEOG waveforms in response to auditory cues directing attention to the left versus right side were scored for systematic deviations of eye position, indicating residual tendencies to move the eyes towards the cued location. A residual HEOG deviation exceeding $\pm 2 \mu\text{V}$ led to the disqualification of three participants.

The EEG obtained in the cue–target interval was averaged for all combinations of cued modality (vision versus touch) and cued direction (left versus right). Mean amplitude values were computed at lateral anterior sites (F7/8, F3/4, FC5/6), lateral central sites (T7/8, C3/4, CP5/6), and lateral posterior sites (P7/8, P3/4, OL/R) within different latency windows relative to cue onset, and these values were analyzed separately for anterior, central, and posterior electrodes by repeated measures ANOVAs for the factors of electrode site, cued modality, cued direction, and hemisphere (left vs. right). Additional analyses were run for ERPs obtained in the cue–target interval at midline electrodes, omitting the factor hemisphere.

The EEG obtained in response to peripheral visual and tactile stimuli was averaged for nontarget events (stimuli without gaps) only, to avoid contamination by vocal responses. Trials where false positive vocal responses were recorded on nontarget trials were excluded from analysis. Separate averages were computed for visual and tactile nontarget stimuli for all combinations of cued modality, cued direction, and stimulus side (left vs. right), resulting in 16 average waveforms for each participant. Mean amplitude values were computed for early visual and somatosensory ERPs within different latency windows measured relative to onset of the peripheral stimulus (visual P1: 90–130 ms, at lateral occipital sites; visual N1: 160–200 ms; somatosensory P100: 80–120 ms, at lateral central sites; somatosensory N140: 120–170 ms). Later effects of attentional cueing were analyzed separately for visual and somatosensory ERPs within two successive 100-ms analysis windows between 200 and 400 ms poststimulus. In addition, effects of modality cueing were also analyzed within the P2 time range (200–260 ms poststimulus). Mean amplitude values obtained for visual and somatosensory ERPs at lateral anterior sites, lateral central sites, lateral posterior sites, and at midline electrodes (Fz, Cz, Pz) were submitted to separate ANOVAs with the factors electrode site, cued modality, spatial attention (stimulus at cued location vs. stimulus at uncued location), stimulus side, and hemisphere (this latter factor was omitted in the analysis of midline electrodes). When appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were performed, and the adjusted p values are reported. Nonsignificant terms and results due trivially to stimulus and anatomical laterality are not reported. Whenever interactions between attention and electrode site were found (for brevity, these are not all reported in full), additional analyses were conducted for single electrode sites. For vocal responses, repeated measures ANOVAs were performed on response latencies and on arcsin-transformed error rates for the factors of task condition and target location (left vs. right).

Results

Behavioral Performance

Vocal response times ($\pm SD$) to relevant visual and somatosensory target stimuli were 668 (± 71) ms and 661 (± 75) ms, respectively,

and these values did not differ significantly.¹ Participants missed 9.6% ($\pm 8.1\%$) of all relevant visual targets and 9.8% ($\pm 8.1\%$) of all relevant tactile targets. The rate of false alarms to irrelevant gap targets was 3.1% ($\pm 2.9\%$) (2.5% and 3.6% for visual and tactile stimuli, respectively). None of these differences in error rates was significant. The rate of false alarms to nontargets (stimuli without gaps) was below 0.3%.

ERP Correlates of Anticipatory Spatial Orienting in the Cue–Target Interval

Figure 1 shows ERPs elicited in the interval between cue onset and the onset of the subsequent peripheral stimulus in response to cues directing attention to the left versus right side. Waveforms are shown for anterior, central, and posterior electrode pairs over the left and right hemispheres, separately for cue directing attention to the location of relevant visual stimuli (top) or tactile stimuli (bottom). ERP lateralizations sensitive to the direction of attentional shifts are visible in both sets of waveforms. At frontal electrodes, a negativity contralateral to the direction of an attentional shift (anterior directing attention negativity; ADAN) can be observed, in particular over the right hemisphere. In contrast, a contralateral positivity is elicited at lateral posterior sites (late directing attention positivity; LDAP). Importantly, these lateralized effects appear to be present both when vision was the cued task-relevant modality (top) as well as when touch was cued (bottom).

Statistical analyses were used to confirm that the effects shown in Figure 1 were indeed related to systematically different ERP patterns over the left and right hemispheres in response to auditory cues directing attention to the side of relevant visual or tactile events. No systematic ERP modulations related to the direction of attentional shifts were observed within the first 300 ms following cue onset. The anterior directing attention negativity was analyzed within two successive 400-ms windows (300 to 700 ms and 700 to 1,100 ms after cue onset; corresponding to -800 to -400 ms and -400 to 0 ms relative to the onset of the subsequent peripheral stimulus). In the earlier time interval, a significant Hemisphere \times Cued Direction interaction was present at anterior sites, $F(1, 15) = 6.6$, $p < .021$, reflecting a trend for contralaterally increased negativities. However, when effects of cued direction were analyzed separately for left and right anterior electrodes, no significant main effects of cued direction were observed. In the last 400 ms of the cue–target interval (700 to 1,100 ms after cue onset), a significant Hemisphere \times Cued Direction interaction was present at lateral anterior electrodes, $F(1, 15) = 10.7$, $p < .005$, as well as at C3/C4, $F(1, 15) = 23.7$, $p < .001$, reflecting enhanced frontocentral negativities contralateral to the direction of an attentional shift. Importantly, no three-way interactions (Cued Modality \times Hemisphere \times Cued Direction) were obtained, all $F < 1$, indicating that this effect was elicited regardless of whether attention was directed to the location of relevant visual or tactile events. In line with this observation, significant Recording Site \times Cued Direction interactions were present at frontal electrode pairs and at C3/C4 both when vision was relevant as well as when touch was relevant, all

¹When defined relative to the onset of the target-defining gap, response times (RTs) to tactile stimuli were significantly faster than RTs to visual stimuli, presumably due to the fact that the offset of tactile stimulation not only appeared more abrupt, but was, in fact, faster than the more gradual offset of the LEDs. To compensate for this difference in the response characteristics of the stimulation devices used, and to equate overall task difficulty across modalities as much as possible, visual targets had a much wider gap than tactile targets.

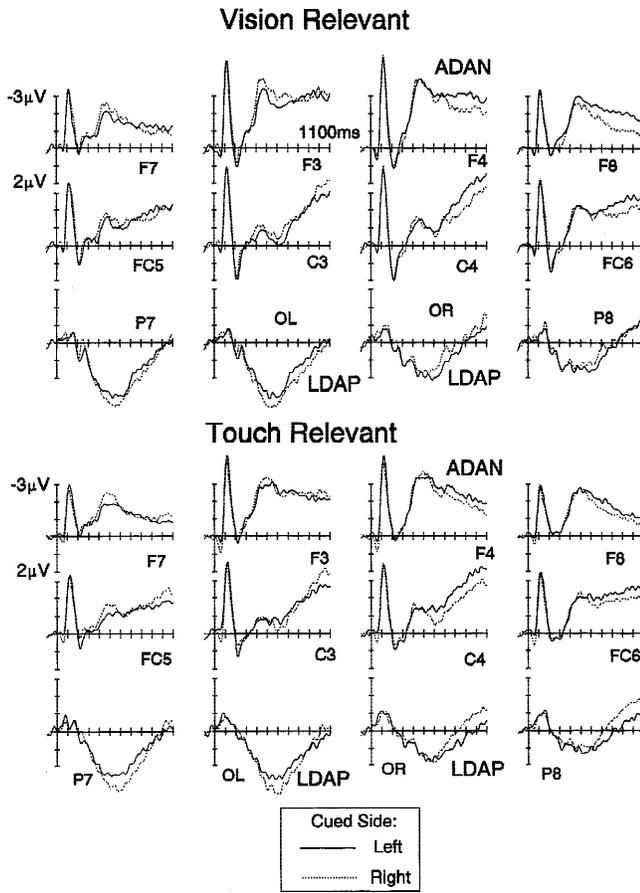


Figure 1. Grand-averaged ERPs elicited at anterior, central, and posterior lateral electrodes in the interval between cue onset and the onset of the subsequent peripheral stimulus in response to auditory cues directing attention to the left side (solid lines), or cues directing attention to the right side (dashed lines). Top: ERPs elicited in trials where vision was the relevant modality. Bottom: ERPs elicited in trials where touch was the relevant modality. ERPs reveal a right-lateralized frontocentral negativity (anterior directing attention negativity; ADAN) and a posterior positivity (late directing attention positivity; LDAP) contralateral to the direction of an attentional shift.

$F(1,15) > 5.3$, all $p < .036$. When these effects were analyzed separately for left and right electrodes, significant main effects of cued direction emerged over the right hemisphere, all $F(1,15) > 6.4$, all $p < .023$. In contrast, no significant effects of cued direction were found at left frontocentral electrodes, indicating that the anterior directing attention negativity was primarily lateralized over the right hemisphere (see also Figure 1).

The posterior late directing attention positivity was analyzed within a 500-ms time interval between 500 and 1,000 ms after cue onset (-600 to -100 ms relative to target onset). At lateral posterior sites, the Hemisphere \times Cued Direction interaction only approached significance, $F(1,15) = 4.4$, $p < .053$, but a significant Recording Site \times Hemisphere \times Cued Direction interaction was obtained, $F(2,30) = 12.6$, $p < .001$, $\epsilon = .956$. Follow-up analyses revealed significant Hemisphere \times Cued Direction interactions at OL/OR, $F(1,15) = 11.0$, $p < .005$, and at P7/P8, $F(1,15) = 5.2$, $p < .037$, but not at P3/P4. At lateral occipital electrodes OL and OR, significant Hemisphere \times Cued Direction interactions were

present regardless of whether vision or touch was relevant on a given trial, both $F(1,15) > 7.5$, both $p < .015$, indicating that an enhanced occipital positivity contralateral to the direction of an attentional shift (late directing attention positivity) was present when attention was oriented to the location of relevant tactile as well as visual events. Accordingly, no three-way interaction (Cued Modality \times Hemisphere \times Cued Direction) was obtained at lateral occipital electrodes, $F < 1$. Additional analyses conducted separately for electrodes OL and OR revealed significant main effects of cued direction, both $F(1,15) > 4.7$, both $p < .047$, suggesting that a late directing attention positivity was present over both hemispheres (see Figure 1). A similar pattern of results was obtained for P7/P8, except that the Hemisphere \times Cued Direction interaction was reliable only when touch was relevant, $F(1,15) = 5.7$, $p < .03$, and just approached significance on trials where vision was relevant, $F(1,15) = 3.4$, $p < .084$.

Effects of Spatial Orienting on Visual ERPs

ERPs elicited in response to peripheral visual nontarget stimuli at cued and uncued locations are shown in Figure 2, separately for trials where the auditory cue indicated that vision was relevant (left), and for trials where touch was the cued modality (right). As can be seen from this figure, spatial attention had pronounced effects on visual ERPs in both task conditions, and attentional modulations of early ERP components seem to be largely independent of which modality was cued as relevant on a given trial.

These observations were confirmed by statistical analyses. A significant effect of spatial attention on P1 amplitudes (90–130 ms poststimulus) was present at lateral occipital electrodes, $F(1,15) = 4.5$, $p < .05$, reflecting enhanced P1 components for visual stimuli at cued locations. No sign of any Cued Modality \times Spatial Attention interaction was present, $F < 1$, suggesting that these P1 modulations were elicited regardless of the task relevance of visual stimuli (see Figure 2). A similar pattern of results was obtained for the subsequent N1 component (160–200 ms poststimulus). Here, significant effects of spatial attention were present at lateral posterior, central, and anterior electrodes as well as at midline sites, all $F(1,15) > 23.5$, all $p < .001$, and Cued Modality \times Spatial Attention interactions never even approached significance at any site, all $F < 2.3$. Reliable effects of spatial attention on N1 amplitudes were obtained at all recording sites not only when vision was relevant, all $F(1,15) > 13.0$, all $p < .003$, but also on trials where the cue indicated that touch was the currently task-relevant modality, all $F(1,15) > 17.3$, all $p < .001$. At lateral posterior electrodes, a Spatial Attention \times Hemisphere \times Stimulus Side interaction was present, $F(1,15) = 12.6$, $p < .003$, reflecting the fact that attentional N1 modulations were larger over the hemisphere contralateral to the visual field of stimulus presentation (see Figure 2). No such three-way interactions were found at lateral anterior or central electrode pairs.

In the two subsequent analysis windows (200–300 ms and 300–400 ms poststimulus), main effects of spatial attention were again found over all regions, all $F(1,15) > 10.0$, all $p < .006$, reflecting enhanced negativities elicited by visual stimuli at cued locations (Figure 2). Although Cued Modality \times Spatial Attention interactions failed to reach significance between 200 and 300 ms poststimulus, these interactions were reliable at lateral anterior, lateral central, and at midline electrodes in the 300–400-ms interval, all $F(1,15) > 5.5$, all $p < .034$, indicating that effects of spatial attention were more pronounced in trials where vision was relevant relative to trials where touch was the relevant modality (see Figure 2). Additional analyses were conducted separately for

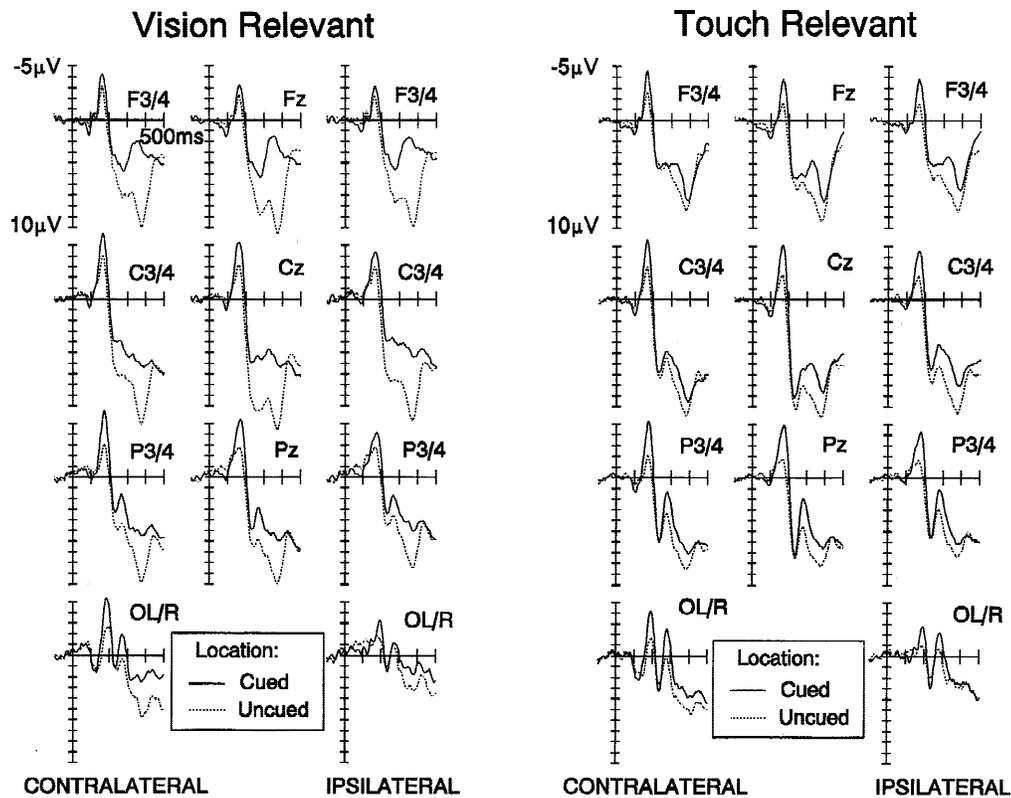


Figure 2. Grand-averaged ERPs elicited at midline electrodes and at sites contralateral and ipsilateral to the side of stimulus presentation by visual nontarget stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 500-ms interval following stimulus onset in trials where vision was relevant (left) and in trials where touch was relevant (right).

vision-relevant and touch-relevant trials. When vision was relevant, effects of spatial attention were significant over all regions within both analysis windows, all $F(1,15) > 7.7$, all $p < .014$. Although smaller, similar sustained attentional negativities were also reliably present in trials where touch was the relevant modality, all $F(1,15) > 5.1$, all $p < .039$.²

Effects of Spatial Orienting on Somatosensory ERPs

ERPs elicited in response to peripheral tactile nontarget stimuli at cued and uncued locations are shown in Figure 3, separately for trials where the auditory cue indicated that touch was relevant (left) and for trials where vision was the relevant modality (right). Similar to the effects observed for visual ERPs, spatial attention had pronounced effects on somatosensory ERPs not only when touch was the cued modality, but also when vision was cued. Attentional modulations of early somatosensory ERP components seem to be clearly present in trials where vision was task relevant, and these effects appear to be comparable in size to the effects observed for trials where touch was the relevant modality.

No reliable effects of spatial attention or any Cued Modality \times Spatial Attention interactions were obtained in the P100 time range (80–120 ms poststimulus). In contrast, spatial attention had pronounced effects on the N140 component (120–170 ms poststimu-

lus), with larger N140 amplitudes elicited in response to tactile stimuli at cued relative to uncued locations. This was reflected in significant effects of spatial attention at lateral central electrodes, $F(1,15) = 15.8$, $p < .001$. No indication of any Cued Modality \times Spatial Attention interaction was obtained, $F < 1$, indicating that the enhancement of lateral central N140 components for tactile stimuli at cued versus uncued locations was equivalent in trials where touch was relevant and in trials where vision was the task-relevant modality (see Figure 3). This was confirmed by analyses conducted separately for these two task conditions, which revealed significant effects of spatial attention on N140 amplitudes not only when touch was relevant, $F(1,15) = 7.4$, $p < .016$, but also in trials where the auditory cue indicated vision was task relevant, so that tactile stimuli could be entirely ignored, $F(1,15) = 6.1$, $p < .026$. Effects of spatial attention on somatosensory ERP amplitudes in the N140 time range were also present at lateral posterior and anterior sites as well as at midline electrodes, all $F(1,15) > 5.7$, all $p < .031$. These effects were accompanied by significant Spatial Attention \times Electrode Site interactions, and subsequent analyses revealed that effects of spatial attention on somatosensory ERPs were absent at OL/R, P7/8, and F3/4, but present at all other recording sites. Again, no indication of any Cued Modality \times Spatial Attention interactions were observed at any site, all $F < 1$.

In the subsequent 200–300-ms poststimulus analysis window, significant effects of spatial attention were found only at midline electrodes Fz and Cz and at C3/C4, all $F(1,15) > 4.6$, all $p < .047$, reflecting enhanced negativities for tactile stimuli at cued

²The only exception to this general pattern was found at lateral anterior electrodes in the 200–300-ms analysis windows, where spatial attention failed to significantly affect visual ERPs when touch was the currently relevant modality.

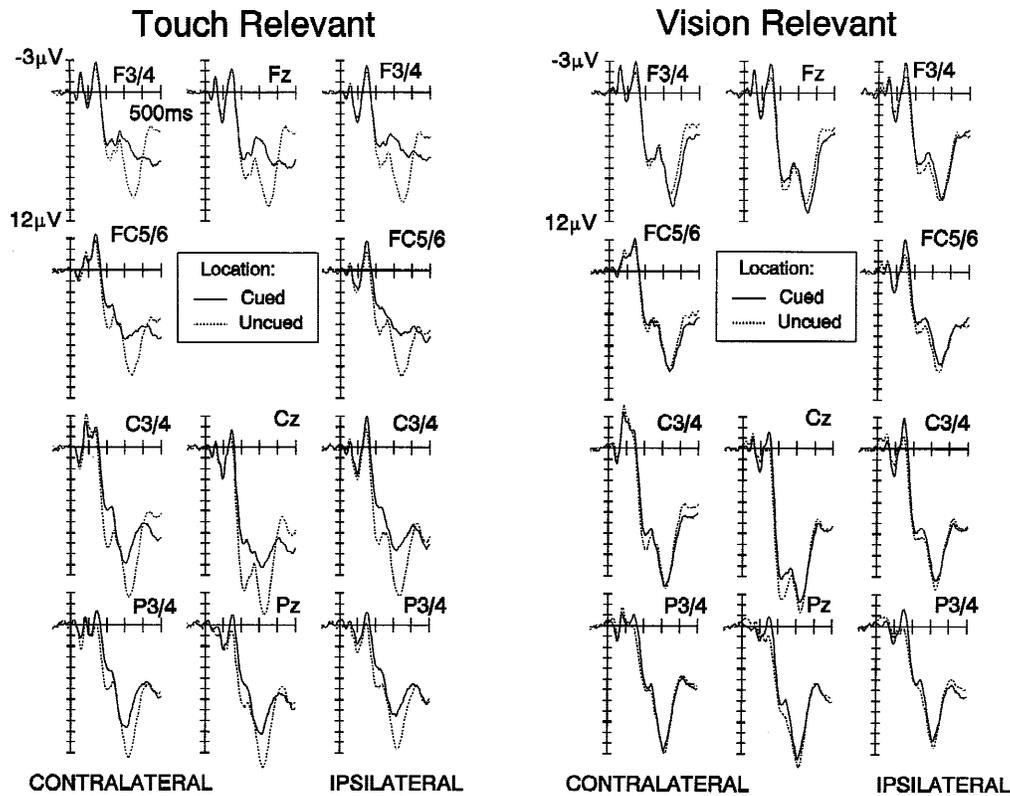


Figure 3. Grand-averaged ERPs elicited at midline electrodes and at sites contralateral and ipsilateral to the side of stimulus presentation by tactile nontarget stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 500-ms interval following stimulus onset in trials where touch was relevant (left) and in trials where vision was relevant (right).

locations. Although Cued Modality \times Spatial Attention only approached significance at these sites, all $F(1, 15) > 3.4$, all $p < .085$, subsequent analyses revealed significant effects of spatial attention when touch was relevant, all $F(1, 15) > 7.0$, all $p < .018$, but not in trials where vision was relevant.³ In the subsequent analysis window (300–400 ms poststimulus), main effects of spatial attention at all sites, all $F(1, 15) > 6.5$, all $p < .022$, were accompanied by significant Cued Modality \times Spatial Attention interactions, all $F(1, 15) > 9.6$, all $p < .007$. Whereas broadly distributed enhanced negativities were elicited by tactile stimuli at cued locations when touch was relevant, all $F(1, 15) > 14.0$, all $p < .002$, these effects were entirely absent in trials where vision was the relevant modality and tactile stimuli could be ignored, all $F < 1$ (see Figure 3).

Effects of Modality Cueing

ERP modulations sensitive to which modality (vision versus touch) was cued as relevant on a given trial are discussed separately for

the cue–target interval, and for ERPs elicited in response to subsequent visual and tactile nontarget stimuli. No Hemisphere \times Cued Modality interactions were obtained in the cue–target interval, indicating that modality cueing did not result in any systematic lateralizations. The only reliable difference of cue–target ERPs elicited by vision-relevant and touch-relevant cues was observed in the 400-ms interval prior to the onset of a peripheral stimulus. Here, ERPs in response to cues specifying vision as relevant were more negative at midline electrodes than ERPs elicited by cues indicating touch as task relevant for the current trial, $F(1, 15) = 5.6$, $p < .032$. This difference is illustrated in Figure 4 for Cz and Pz.

Figure 5 shows ERPs elicited by peripheral visual (top) and tactile (bottom) nontarget stimuli at midline sites and at electrodes contralateral and ipsilateral to the side of stimulus presentation, recorded in trials where the current stimulus modality was either relevant or irrelevant. Note that these waveforms combine trials where stimuli were presented at cued and uncued locations, and thus represent the net effect of modality cueing, independently of spatial attention effects. Early effects of cued modality were found at posterior electrodes in the visual P1 and somatosensory P100 windows, both $F(1, 15) > 7.4$, both $p < .016$, for both visual and somatosensory ERPs, reflecting enhanced negativities in trials where vision was cued relative to trials where touch was cued (see Figure 5). These posterior differences were not lateralized, and are thus likely to reflect the continuation of systematic differences between vision-relevant and touch-relevant trials observed during later phases of the cue–target interval (Figure 4), rather than

³The only two electrodes where spatial attention effects on somatosensory ERPs approached significance in the 200–300-ms analysis window when vision was relevant were Cz and Pz, $p < .09$ (see Figure 3, right). To study whether any enhanced negativities for tactile stimuli at cued locations were present at all beyond 200 ms poststimulus when touch was irrelevant, an additional analysis was run on ERP mean amplitudes obtained in the P2 latency range (200–260 ms poststimulus). Here, significant effects of spatial attention were present for somatosensory ERPs at Cz and Pz when vision was the relevant modality, both $F(1, 15) > 4.8$, both $p < .044$.

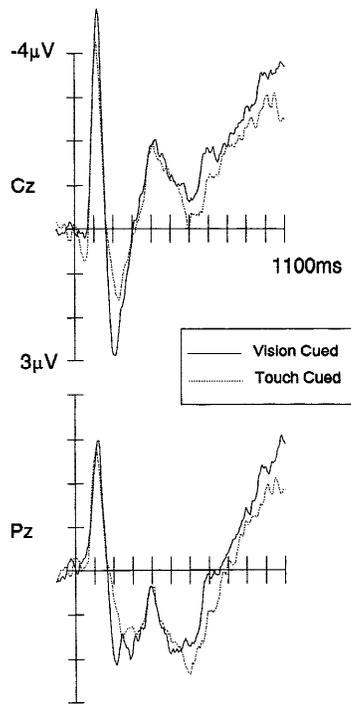


Figure 4. Grand-averaged ERPs elicited at Cz and Pz in the interval between cue onset and the onset of the subsequent peripheral stimulus, in response to auditory cues specifying vision (solid lines) or touch (dashed lines) as the relevant modality for the current trial.

genuine effects of modality cueing on the processing of visual or tactile stimuli. Effects of modality cueing on somatosensory ERPs were also observed in the P100 window at lateral central electrodes C3/C4, $F(1,15) = 18.4, p < .001$. In contrast to the posterior differences observed within the same latency range, a significant Cued Modality \times Hemisphere \times Electrode Side interaction was obtained, $F(1,15) = 6.1, p < .026$, reflecting the fact that P100 enhancements in trials where touch was relevant were more pronounced contralateral to the side of stimulus presentation (see Figure 5, bottom, for C3/4). The visual N1 component elicited at posterior electrodes was enhanced in trials where vision was relevant, $F(1,15) = 11.4, p < .004$. Again, a significant Cued Modality \times Hemisphere \times Electrode Side interaction, $F(1,15) = 8.6, p < .01$, indicated that these N1 enhancements were more pronounced at posterior electrodes contralateral to the visual field of stimulus presentation (see Figure 5, top, for OL/R).

Subsequent effects of modality cueing were present for visual as well as somatosensory ERPs in the P2 time window (200–260 ms poststimulus). Here, ERPs elicited in trials where the current modality was relevant were more negative than ERPs observed when a given modality was irrelevant (Figure 5). The scalp distribution of these effects appears to show modality-specific differences. For visual ERPs, significant effects of modality cueing were present at lateral posterior and central electrodes as well as at Cz and Pz, all $F(1,15) > 6.0$, all $p < .027$, but were entirely absent at lateral anterior sites, $F < 1$. For somatosensory ERPs, modality cueing effects in the P2 time range were significant at lateral anterior sites as well as at C3/C4, Fz, and Cz, all $F(1,15) > 8.7$, all $p < .011$, but were absent at lateral posterior sites, $F < 1$. In the 300–400 ms latency window, reliable effects

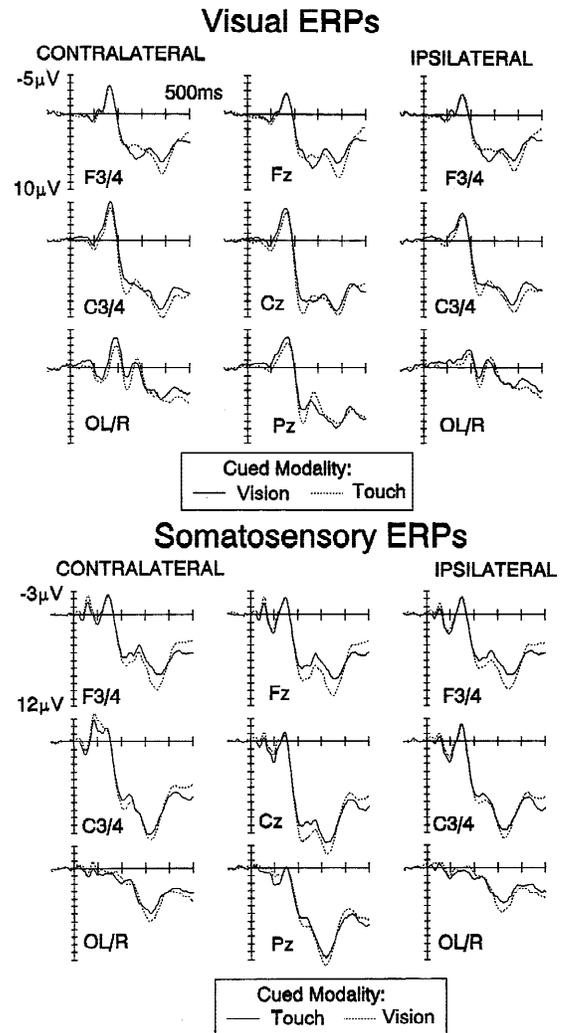


Figure 5. Grand-averaged ERPs elicited in the 500-ms interval following stimulus onset at midline electrodes and at sites contralateral and ipsilateral to the side of stimulus presentation by visual nontarget stimuli (top) and by tactile nontarget stimuli (bottom) in trials where the current stimulus modality was either relevant (solid lines) or irrelevant (dashed lines).

of modality cueing on somatosensory ERPs were found at lateral anterior sites and at Fz, all $F(1,15) > 4.7$, all $p < .045$. In contrast, no significant modality cueing effects were observed for visual ERPs within this latency range.

Discussion

The primary aim of this study was to investigate the nature of attentional control processes responsible for the existence of crossmodal links in spatial attention. Attentional orienting might be mediated by a single supramodal mechanism that controls attentional shifts within different modalities (Farah et al., 1989). According to this view, crossmodal links in spatial attention are an immediate consequence of the supramodal control of attentional orienting. Alternatively, attentional shifts in vision, audition, and touch may be controlled by separate modality-specific mechanisms, with crossmodal links reflecting spatial synergies between these otherwise separate attentional control processes (Spence &

Driver, 1996). In previous ERP studies of crossmodal links in spatial attention between vision, audition, and touch (cf. Eimer & Driver, 2000; Eimer & Schröger, 1998; Hillyard et al., 1984; Teder-Sälejärvi et al., 1999), effects of spatial attention tended to be larger for the currently relevant modality than for the modality that could be ignored. In addition, touch can apparently be decoupled from attentional orienting in other modalities when entirely task irrelevant (Eimer & Driver, 2000; Eimer et al., 2002). Although these findings appear most in line with the idea that attentional control processes within different modalities are separable but linked, other recent observations show that ERP modulations sensitive to the direction of anticipatory attentional shifts, elicited in response to cues indicating the side of an upcoming task-relevant event, are similar regardless of whether a visual, auditory, or tactile event is expected (Eimer et al., 2002). This finding suggests that shifts of spatial attention are controlled by supramodal processes.

Advocates of a separable but linked account might argue that the similarities of ERP correlates of spatial orienting across modalities observed by Eimer et al. (2002) simply reflect the fact that in their study, task-relevant locations were always indicated by *visual* cues. It is conceivable that attentional shifts in response to visual cues will always be anchored in coordinates of visual space, even when relevant locations have to be selected for other modalities. The ERP modulations observed in the present study in response to *auditory* cues directing attention to the side of relevant tactile or visual events provides clear-cut evidence against this hypothesis. Similar to previous findings from studies investigating visual–spatial orienting (Harter et al., 1989; Hopf & Mangun, 2000; Hopfinger et al., 2000; Mangun, 1994; Nobre et al., 2000; Yamaguchi et al., 1994, 1995) and attentional orienting to auditory or tactile events (Eimer et al., 2002), spatial cueing was reflected in a frontocentrally enhanced negativity (anterior directing attention negativity) as well as a posterior positivity (late directing attention positivity) contralateral to the direction of an attentional shift. The anterior directing attention negativity may reflect supramodal control processes within an “anterior attention system” (Posner & Petersen, 1990), whereas the late directing attention positivity might indicate the activation of posterior attention systems involved in spatial selectivity (e.g., LaBerge, 1995) and in the integration of information from different sense modalities (e.g., Andersen, Snyder, Bradley, & Xing, 1997). Importantly, these effects were very similar regardless of whether attention was directed to the location of relevant visual or tactile events (Figure 1), thus suggesting the implication of supramodal processes. In contrast to all previous studies investigating ERP correlates of spatial orienting in the cue–target interval, the present experiment used auditory rather than visual cues, thus demonstrating that the presence of these effects and their similarity across different task-relevant modalities is not restricted to attentional shifts initiated in response to visual cues. The anterior directing attention negativity was found to be strongly lateralized over the right hemisphere, which is consistent with several previous observations during shifts of visual attention (Hopf & Mangun, 2000; Hopfinger et al., 2000; Mangun, 1994; Nobre et al., 2000), although no such lateralization was observed in our previous study (Eimer et al., 2002). Although the latency of the posterior late directing attention positivity was comparable to previous observations, the frontal anterior directing attention negativity was substantially delayed in the present experiment. In contrast to earlier studies (Eimer et al., 2002; Nobre et al., 2000), where the anterior directing attention negativity preceded the late directing attention positivity, these two

effects were elicited in parallel in the current experiment (see Figure 1). This delay of the frontal anterior directing attention negativity may be related to the complex demands of the cueing procedure used, which required participants to detect and interpret two simultaneously presented attributes of the cue stimulus (instrument and pitch).

We have recently proposed that although the selection of relevant locations typically operates in a supramodal manner, the effects of spatial selection on stimulus processing within a particular modality also depends on the tonic state of activity within that modality (Eimer & Driver, 2001; Eimer et al., 2002). Tonic differences in the overall activation level of modality-specific visual, auditory, or somatosensory areas may emerge when participants attend to a relevant modality, and ignore irrelevant modality stimuli for several successive blocks of trials. Effects of spatial attention can be attenuated within currently irrelevant modalities as a result of such tonic baseline shifts of modality-specific activation levels. To test this hypothesis, the present experiment investigated ERP correlates of crossmodal links in spatial attention under conditions where not only task-relevant locations, but also task-relevant modalities were cued on a trial-by-trial basis. When task-relevant modalities change from trial to trial, no tonic baseline shifts of modality-specific activation levels should be induced. Accordingly, ERP effects of spatial attention should be of equivalent size for the currently relevant modality and for the modality that is to be ignored on a given trial. This pattern of results should not only be observed for visual ERPs, but also for somatosensory ERPs, indicating that touch is not decoupled from attentional orienting to the location of relevant visual events on trials where tactile stimuli can be ignored (unlike the results found by Eimer & Driver, 2000, when the relevant modality was blocked rather than cued on a trial-by-trial basis).

The effects of spatial attention on visual and somatosensory ERPs observed in this study fully confirmed these new predictions. For visual ERPs, spatial attention resulted in enhancements of posterior P1 and N1 components, as well as broadly distributed enhanced negativities for visual stimuli at cued locations in the N1 time range and in two subsequent time windows between 200 and 400 ms poststimulus. No significant Cued Modality \times Spatial Attention interactions were obtained at any site in the first 300 ms after stimulus onset, indicating that these effects were very similar in trials where vision was relevant and in trials where touch was relevant and visual stimuli could be ignored. In contrast to our previous ERP study investigating visual/tactile crossmodal links (Eimer & Driver, 2000), where attentional modulations of visual N1 components were reduced when visual stimuli were irrelevant for several successive experimental blocks, no such attenuation of spatial attention effects as a consequence of task relevance were observed in the present experiment. This is illustrated in Figure 6 (left), where mean cued location – uncued location difference amplitudes obtained in the N1 time range at OL/OR, P3/4, and Pz are displayed separately for trials where either vision or touch were relevant. There was not even a trend for attentional N1 modulations to be smaller when vision was irrelevant, and none of the differences between cued modality and uncued modality trials shown in Figure 6 (left) even approached significance, all $t(15) < 1$. It should also be noted that in contrast to previous crossmodal ERP experiments (cf. Eimer & Driver, 2000; Eimer & Schröger, 1998), effects of spatial attention on visual ERPs were clearly present beyond 200 ms poststimulus when vision was irrelevant. Even in the 300–400-ms analysis interval, where Cued Modality \times Spatial Attention interactions indicated that effects of spatial cueing were

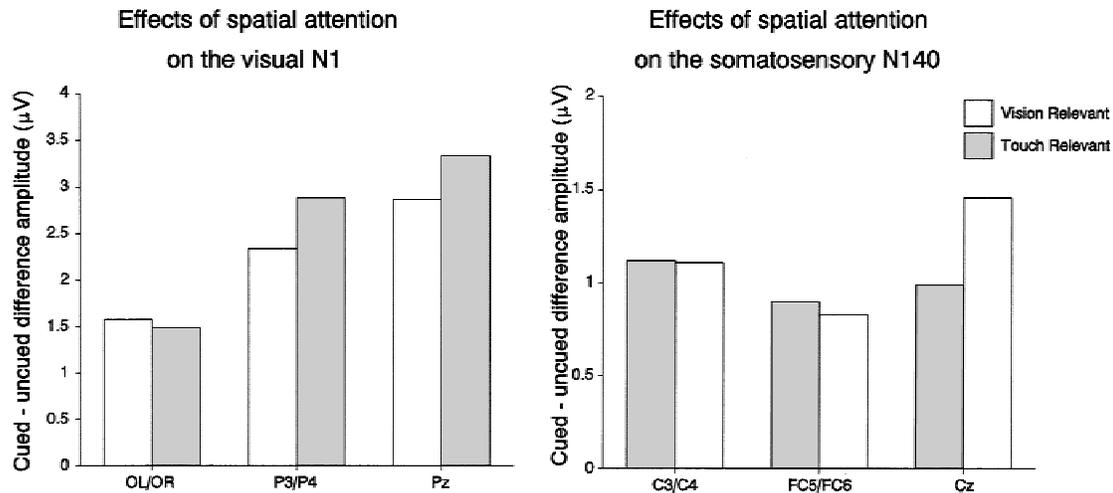


Figure 6. Effects of spatial attention on the visual N1 component (left) and the somatosensory N140 component (right), displayed separately for trials where vision was relevant (white bars) and trials where touch was relevant (gray bars). Mean difference amplitude values are shown that were obtained by subtracting ERPs in response to stimuli at uncued locations from ERPs in response to stimuli at cued location. Left: Difference amplitudes obtained for visual ERPs in the N1 latency window (160–200 ms poststimulus) at posterior electrodes OL/OR, P3/P4, and Pz. Right: Difference amplitudes obtained for somatosensory ERPs in the N140 latency window (120–170 ms poststimulus) at central electrodes C3/C4, FC5/FC6, and Cz.

larger on vision-relevant trials, reliably enhanced negativities were still elicited by visual stimuli at cued locations when these stimuli could be completely ignored.

A similar pattern of results was found for somatosensory ERPs. Most importantly, systematic effects of spatial attention were clearly present for somatosensory ERPs on trials where tactile stimuli were task irrelevant. In other words, there was no evidence that tactile processing could be decoupled from attentional orienting when attention was directed to the location of relevant visual events and all tactile stimuli could be ignored. Similar to previous results (Eimer & Driver, 2000; García-Larrea, Lukaszewicz, & Mauguière, 1995), larger N140 components were elicited by tactile stimuli at attended locations when touch was relevant. Essentially the same spatial attention effect was observed on trials where touch was irrelevant. This is illustrated in Figure 6 (right), where mean cued location – uncued location difference amplitudes obtained in the N140 time range at C3/4, FC5/6, and Cz are displayed separately for trials where touch or vision were relevant. Similar to the pattern observed for the visual N1, there was not even a trend for effects of spatial attention on the somatosensory N140 component to be larger in touch-relevant trials. This was reflected in the absence of any Cued Modality \times Spatial Attention interaction in the N140 latency window, and the fact that none of the differences between cued modality and uncued modality trials shown in Figure 6 (right) approached significance, all $t(15) < 1$. These findings contrast with the results by Eimer and Driver (2000) and by Eimer et al. (2002), who found no evidence for visual–tactile links or for auditory–tactile links under conditions where touch was irrelevant for several successive blocks. The current findings provide clear evidence for the existence of crossmodal links in spatial attention from vision to touch under conditions where tactile information can be entirely ignored, provided that relevant modalities can change across trials. The lateral central somatosensory N140 is assumed to be generated in secondary somatosensory cortex (Frot, Rambaud, Guénot, & Mauguière, 1999), thus suggesting that crossmodal links in spatial attention from vision to touch can affect

modality-specific stages in the processing of tactile information. In contrast to the results observed for vision, effects of spatial attention beyond 200 ms poststimulus were largely confined to trials where touch was relevant. This may reflect a residual asymmetry between crossmodal effects on visual and somatosensory processing. Later stages of somatosensory processing seem to be largely unaffected by attention directed to the location of visual events, whereas later visual processing stages were apparently modulated by spatial attention in trials where touch was relevant.

One might argue that early spatial attention effects were equivalent for currently relevant and irrelevant modalities for the simple reason that participants failed to use the auditory cues to direct attention to a specific modality relevant for a given trial. This possibility is unlikely for several reasons. First, auditory cue stimuli were specifically designed to make the difference in sound quality (flute vs. marimba), which was mapped to relevant modalities, at least as salient as the difference in pitch, which served as location cue.⁴ Second, directing attention to the cued modality was necessary to avoid false alarms to targets in the currently irrelevant modality, and very few such errors were observed. Third, modality cueing did result in systematic ERP modulations during the cue–target interval. In the 400-ms interval prior to the onset of peripheral stimuli, midline ERPs were more negative in trials where cues specified vision as relevant modality (see Figure 4). Because

⁴The physical difference between “flute” and “marimba” cues also resulted in substantial differences in early auditory components elicited by these cues, with larger N1 and P2 amplitudes in response to sounds delivered by the marimba relative to sounds produced by the flute. Taking into account the unavoidable between-participant variability in auditory N1 and P2 amplitudes, and the fact that instrument-modality mappings were varied between participants, this fact can also account for the differences in auditory N1 and P2 components in response to vision-relevant and touch-relevant cues which can be seen in Figure 6. Accordingly, these differences did not even approach significance, both $F < 1$ for N1 amplitudes (measured between 100 and 150 ms after cue onset) and P2 amplitudes (measured between 180 and 280 ms after cue onset).

CNV-like waves elicited in the interval between cues and targets are sensitive to anticipated task difficulty (McCallum, 1988), this difference may reflect the fact that in spite of our efforts to equate the difficulties of visual and tactile discrimination tasks, participants may have still perceived the visual task as more demanding. But the important point is that reliable ERP differences in response to cues specifying vision or touch as task-relevant modality were apparent even before the onset of a peripheral stimulus, demonstrating that participants did not simply ignore those attributes of the cue that were to be used for modality selection. Finally, effects of modality cueing were also observed for ERPs in response to subsequent visual and tactile nontarget stimuli. Early differences between vision-relevant and touch-relevant trials found for visual and somatosensory ERPs (Figure 5) are difficult to evaluate. Enhanced CNV-like negativities elicited in the cue–target interval in trials where vision was cued may have continued to affect ERP waveforms even after the onset of peripheral stimuli, and thus have contributed to modality cueing effects observed for the somatosensory P100 and the visual N1. The fact that these early effects were larger contralateral to the side of stimulus presentation, whereas the differential effects of modality cueing in the cue–target interval were not lateralized, may indicate that they are at least in part genuine effects of modality cueing on the early processing of visual and tactile stimuli. Modality cueing had clear and unequivocal effects on visual and somatosensory ERPs in the P2 latency window, with enlarged negativities elicited when a given stimulus modality was currently relevant (Figure 5). The scalp distribution of these modality cueing effects was modality specific (posterior for visual ERPs, frontocentral for somatosensory ERPs), confirming earlier observations from ERP studies investigating selective attention to relevant modalities (Eimer & Schröger, 1998; Woods, Alho, & Algazi, 1992).

Overall, the ERP effects of modality cueing observed in these studies are inconsistent with the idea that participants failed to use the information provided by the cues to direct their attention to the

modality relevant for a given trial. Thus, the observed effects of spatial attention on ERPs elicited by visual or tactile stimuli on trials where this modality was irrelevant not only provide further evidence for the existence of crossmodal links in spatial attention but also supports the hybrid account of the control processes underlying such crossmodal links that was outlined above. Crossmodal attention effects are mediated by supramodal attentional control mechanisms, but they can be attenuated as a consequence of tonic differences in the overall activation level of modality-specific areas, which will result when one modality is task relevant for an extended period of time. Eliminating such tonic baseline shifts by cueing relevant modalities on a trial-by-trial basis should therefore eliminate this influence of modality relevance. That was exactly what was found in the present study, suggesting that the observed ERP effects of crossmodal links in spatial attention between vision and touch are mediated primarily by a supramodal attentional control system.

In summary, the ERP results observed in the cue–target interval and the effects of spatial attention on visual and somatosensory ERPs provide clear and consistent evidence for the role of supramodal attentional control systems in crossmodal links in spatial attention. The observation that ERP modulations sensitive to the direction of anticipatory attentional shifts were similar when attention was directed to the location of relevant visual, tactile, or auditory events (see also Eimer et al., 2002), even when relevant locations were indicated by auditory rather than visual cues, supports the hypothesis that shifts of spatial attention are controlled by supramodal processes. The fact that spatial cueing effects on early visual and somatosensory ERP components were unaffected by the task relevance of visual or tactile stimuli lends further support to the idea that supramodal mechanisms play an important part in the control of spatial orienting and that the existence of crossmodal links in spatial attention is a direct consequence of this supramodal control.

REFERENCES

- Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representations of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, *20*, 303–330.
- Driver, J., & Frith, C. (2000). Shifting baselines in attention research. *Nature Reviews Neuroscience*, *1*, 231–232.
- Driver, J., & Spence, C. (1998). Attention and the crossmodal construction of space. *Trends in Cognitive Sciences*, *2*, 254–262.
- Eimer, M. (2001). Crossmodal links in spatial attention between vision, audition, and touch: Evidence from event-related brain potentials. *Neuropsychologia*, *39*, 1292–1303.
- Eimer, M., & Driver, J. (2000). An event-related brain potential study of cross-modal links in spatial attention between vision and touch. *Psychophysiology*, *37*, 697–705.
- Eimer, M., & Driver, J. (2001). Crossmodal links in endogenous and exogenous spatial attention: Evidence from event-related brain potential studies. *Neuroscience and Biobehavioral Reviews*, *25*, 497–511.
- Eimer, M., & Schröger, E. (1998). ERP effects of intermodal attention and cross-modal links in spatial attention. *Psychophysiology*, *35*, 313–327.
- Eimer, M., Van Velzen, J., & Driver, J. (2002). Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, *19*, 254–271.
- Farah, M. J., Wong, A. B., Monheit, M. A., & Morrow, L. A. (1989). Parietal lobe mechanisms of spatial attention: Modality-specific or supramodal? *Neuropsychologia*, *27*, 461–470.
- Frot, M., Rambaud, L., Guénot, M., & Maugière, F. (1999) Intracortical recordings of early pain-related CO₂-laser evoked potentials in human second somatosensory (SII) area. *Clinical Neurophysiology*, *110*, 133–145.
- García-Larrea, L., Lukaszewicz, A. C., & Maugière, F. (1995). Somatosensory responses during selective spatial attention: The N120-to-N140 transition. *Psychophysiology*, *32*, 526–537.
- Harter, M. R., Miller, S. L., Price, N. J., LaLonde, M. E., & Keyes, A. L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience*, *1*, 223–237.
- Hillyard, S. A., Simpson, G. V., Woods, D. L., Van Voorhis, S., & Münte, T. F. (1984). Event-related brain potentials and selective attention to different modalities. In F. Reinoso-Suarez & C. Ajmone-Marsan (Eds.), *Cortical integration* (pp. 395–414). New York: Raven Press.
- Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, *111*, 1241–1257.
- Hopfinger, J. B., Jha, A. P., Hopf, J. M., Girelli, M., & Mangun, G. R. (2000). Electrophysiological and neuroimaging studies of voluntary and reflexive attention. In S. Monsell & J. Driver (Eds.), *Attention and performance XVII* (pp. 125–153). Cambridge, MA: MIT Press.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*, 751–761.
- LaBerge, D. (1995). *Attentional processing*. Cambridge, MA: Harvard University Press.
- Macaluso, E., Frith, C., & Driver, J. (2000a). Selective spatial attention in vision and touch: Unimodal and crossmodal mechanisms revealed with PET. *Journal of Neurophysiology*, *83*, 3062–3075.

- Macaluso, E., Frith, C. D., & Driver, J. (2000b). Modulation of human visual cortex by crossmodal spatial attention. *Science*, *289*, 1206–1208.
- Mangun, G. R. (1994). Orienting attention in the visual fields: An electrophysiological analysis. In H.-J. Heinze, T. F. Münte, & G. R. Mangun (Eds.), *Cognitive electrophysiology* (pp. 81–101). Boston: Birkhäuser.
- McCallum, W. C. (1988). Potentials related to expectancy, preparation, and motor activity. In T. W. Picton (Ed.), *Human event-related potentials. EEG Handbook* (Vol. 3, pp. 427–534). Amsterdam: Elsevier.
- Nobre, A. C., Sebestyen, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related brain potentials. *Neuropsychologia*, *38*, 964–974.
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.
- Spence, C., & Driver, J. (1996). Audiovisual links in endogenous covert spatial attention. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 1005–1030.
- Spence, C., Pavani, F., & Driver, J. (2000). Crossmodal links between vision and touch in covert endogenous spatial attention. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 1298–1319.
- Teder-Sälejärvi, W. A., Münte, T. F., Sperlich, F.-J., & Hillyard, S. A. (1999). Intra-modal and cross-modal spatial attention to auditory and visual stimuli: An event-related brain potential (ERP) study. *Cognitive Brain Research*, *8*, 327–343.
- Ward, L. M., McDonald, J. J., & Golestani, N. (1998). Cross-modal control of attention shifts. In R. D. Wright (Ed.), *Visual attention* (pp. 232–268). New York: Oxford University Press.
- Woods, D. L., Alho, K., & Algazi, A. (1992). Intermodal selective attention. I. Effects on event-related potentials to lateralized auditory and visual stimuli. *Electroencephalography and Clinical Neurophysiology*, *82*, 341–355.
- Yamaguchi, S., Tsuchiya, H., & Kobayashi, S. (1994). Electroencephalographic activity associated with shifts of visuospatial attention. *Brain*, *117*, 553–562.
- Yamaguchi, S., Tsuchiya, H., & Kobayashi, S. (1995). Electrophysiologic correlates of age effects on visuospatial attention shift. *Cognitive Brain Research*, *3*, 41–49.

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