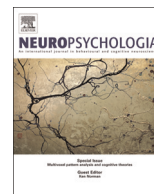




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Cross-modal orienting of visual attention

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ABSTRACT

This article reviews a series of experiments that combined behavioral and electrophysiological recording techniques to explore the hypothesis that salient sounds attract attention automatically and facilitate the processing of visual stimuli at the sound's location. This cross-modal capture of visual attention was found to occur even when the attracting sound was irrelevant to the ongoing task and was non-predictive of subsequent events. A slow positive component in the event-related potential (ERP) that was localized to the visual cortex was found to be closely coupled with the orienting of visual attention to a sound's location. This neural sign of visual cortex activation was predictive of enhanced perceptual processing and was paralleled by a desynchronization (blocking) of the ongoing occipital alpha rhythm. Further research is needed to determine the nature of the relationship between the slow positive ERP evoked by the sound and the alpha desynchronization and to understand how these electrophysiological processes contribute to improved visual-perceptual processing.

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1. Visual stimuli influence auditory perception, and vice versa

The auditory and visual systems interact in many ways, perhaps most strikingly in the ventriloquist illusion (a visual event biases the perceived location of a concurrent sound) and the McGurk effect (visual image of speaker's mouth alters perception of speech sounds) (Calvert et al., 2004; Murray and Wallace, 2012). Conversely, auditory events can produce dramatic alterations in visual perception, such as when two sounds surround a single flash and produce the percept of two flashes (Shams et al., 2000). Insights into the neural bases of these well-known cross-modal interactions have emerged from electrophysiological and neuroimaging studies. Vision-induced modulations of neural activity in auditory cortical regions have been demonstrated for the ventriloquist (Bonath et al., 2007) and McGurk (Baart et al., 2014; Ganesh et al., 2014) illusions, and auditory-induced activity in the visual cortex has been associated with the Shams double-flash illusion (Mishra et al., 2007).

It is well-documented that selectively attending to the location of a stimulus in one modality not only facilitates the processing of that stimulus but also of stimuli of other modalities that occur at

the attended location (Spence and Driver, 2004; McDonald et al., 2012). This cross-modal property of spatial attention was demonstrated early on in electrophysiological studies in which auditory and visual stimuli were presented in random order at left and right locations, and observers attended to one modality at one location at a time; it was found that event-related brain potentials to all stimuli at the attended location were enhanced, both for the relevant and (to a lesser extent) the irrelevant modality (Hillyard et al., 1984; Eimer and Schröger, 1998; Teder-Sälejärvi et al., 1999). Similarly, behavioral studies have shown that when attention is cued to a specific location in space the observer's response to a subsequent target is facilitated regardless of the modalities of the cue and target stimuli (Driver and Spence, 2004). Such facilitation was observed both for endogenous cueing (observers voluntarily direct attention to the location symbolically indicated by the cue) and exogenous (involuntary) cueing (the cue is salient and attracts attention, but its location is not predictive of target location). The present article reviews a series of studies carried out over the past 15 years that explore the behavioral and neural mechanisms by which a non-predictive auditory stimulus facilitates the processing of a subsequent visual event at the same location. By making non-invasive recordings of ERPs and EEG during task performance, our recent studies have identified auditory-evoked patterns of neural activity in the visual cortex that are closely coupled with the cross-modal facilitation of visual processing.

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2. Salient sounds capture visual attention

Several lines of research converge on the hypothesis that a salient sound naturally attracts attention to its location and facilitates the processing of a subsequent visual event at the same location (McDonald et al., 2012; 2013a). The basic design of these studies presents an initial sound (the cue) from a free-field speaker situated to the left or right of the midline, which is followed after a short interval (from one to several hundreds of milliseconds) by a visual stimulus (the target) that occurs either at the same location as the sound or at a mirror-image location in the opposite visual field (or in some studies, at both locations simultaneously). Critically, the left-right position of the cue is non-predictive of the location(s) of the subsequent target event(s), so that any location-specific influence of the cue on target processing must be purely involuntary.

In our first study of this type McDonald et al. (2000) used a signal detection paradigm in which the auditory cue (brief noise burst) was followed after an SOA (stimulus-onset asynchrony) of 100–300 ms by a flashed array of LEDs presented at the same or opposite-field location on an unpredictable basis. The task was to report whether or not a faint, threshold-level target flash preceded the brighter LED array, which served both as a mask and as a post-cue that defined the location to be reported. It was found that the perceptual sensitivity (d') for detecting the faint target was greater when the target+mask array was presented at the same location as the preceding auditory cue than when the array appeared in the opposite visual field. Similar effects of auditory cues on visual target detection were reported by Dufour (1999) and Frassinetti et al. (2002). McDonald and colleagues proposed that the lateralized auditory cue attracted attention to its location involuntarily, which resulted in enhanced perceptual processing of a subsequent visual target at the sound's location. ERP recordings showed that this cross-modal facilitation of visual processing was associated with an increased neural response in the ventral extrastriate visual cortex elicited by the target/mask complex, which may be mediated by a feedback projection from the polymodal region of the superior temporal lobe (McDonald et al., 2003).

A subsequent experiment investigated whether the cross-modal cueing of attention by an auditory cue would speed up the perceived onset time of a co-localized visual event (McDonald et al., 2005). Previous studies had used time-order judgment (TOJ) tasks to demonstrate that when attended and unattended visual stimuli are presented simultaneously, the attended stimulus appears to onset earlier in time (Shimojo et al., 1997; Shore et al., 2001). Using a TOJ paradigm, McDonald et al. (2005) presented observers with a lateralized auditory cue followed by a pair of brief flashes, one at the location of the sound and the other in the opposite visual field. The time offset between the two flashes was varied unpredictably over a small range from trial to trial, and the observer was charged with reporting which flash appeared to occur first. The prior auditory cue produced a dramatic effect, such that the flash on the cued side was judged to occur earlier on the majority of trials (including 79% of the simultaneous-flash trials). Only when the flash on the uncued side preceded the cued-side flash by around 70 ms were the two flashes judged to be simultaneous.

To study the neural basis of this strong cross-modal cueing effect, McDonald et al. (2005) examined ERPs elicited by the paired flashes on trials when they were actually presented simultaneously. The paired flashes elicited an early positivity (starting at 90–100 ms) that was enlarged over the visual cortex contralateral to the side of the auditory cue, but there were no differences in the timing of the peaks of the visual ERP that corresponded to the 70 ms shift in perceived timing. This suggested that the apparent temporal precedence of the flash on the cued

side was due to an enlarged neural response in the contralateral visual cortex rather than to a speeding of neural transmission in the visual pathways. Moreover, the finding of an enhanced visual cortex ERP associated with the speeded perception of the flash on the cued side provided evidence that this TOJ effect was truly an effect of the cue on visual perception rather than a biasing of the post-perceptual decision in favor of the cued side (Schneider and Bavelier, 2003; Santangelo and Spence, 2008).

Another striking example of how the cross-modal cueing of attention influences the timing of visual perception can be seen in the “illusory line motion” (ILM) effect (Hikosaka et al., 1996). When a horizontal line is briefly flashed following a cue to attend to one end of the line, the observer typically reports that the line grows from the cued end to the uncued end, even though the entire line was flashed simultaneously. The ILM illusion appears to be closely related to the aforementioned TOJ effect, since the observer's perceptual report is that the cued end of the line is seen first. McDonald and colleagues (2013a) investigated the neural basis of the ILM illusion in a situation where a brief sound preceded a horizontal line flashed on a video screen with a variable SOA of 100–300 ms; the sound was presented unpredictably from a speaker that was situated either near the right or the left end of the line. A psychophysical analysis using graded line growths in either direction showed that the observers judged a fully stationary line to grow from the cued end on 76% of the trials. Concurrent ERP recordings showed that this ILM illusion, like the TOJ effect, was associated with an enlarged positive component elicited by the line that was localized to ventral visual cortex contralateral to the auditory cue and began about 90–100 ms after the onset of the line. This visual cortex modulation provided further evidence that the influence of the auditory cue on visual timing judgments is a sensory-perceptual effect rather than a consequence of post-perceptual response bias.

3. Auditory cues alter visual appearance

A long-debated question in psychology is whether directing attention to a visual stimulus can alter its subjective appearance, for example by making it appear brighter or higher in contrast than when unattended (James, 1890). Carrasco et al. (2004) obtained an affirmative answer to this question in an experiment where attention was cued by briefly flashing a black dot at a left or right location on a video screen, and this cue was followed immediately by a pair of Gabor patches, one at the cued location and the other in the opposite visual field. On trials when the two patches actually had the same physical contrast, observers judged the patch at the pre-cued location as being higher in contrast. Carrasco et al.'s conclusion that attention can alter appearance was quickly challenged by proponents of alternative explanations; chief among these were proposals that the apparent increase in contrast may have been due to purely sensory interactions between the visual cue and the visual target (Schneider and Komlos, 2008) or to a decision-level response bias in favor of the cued location (Prinzmetal et al., 2008).

In light of the aforementioned evidence that salient sounds can capture visual attention, Störmer et al. (2009) investigated whether an auditory cue might also modulate the perceived luminance contrast of a subsequent visual target. In a cross-modal version of Carrasco et al.'s experiment, an auditory cue (noise burst) was presented unpredictably at a right or left location, followed immediately (SOA of 150 ms) by a bilateral pair of Gabor patches that varied in their relative contrasts (Fig. 1A). On trials where the patches were physically identical, it was found that the patch at the auditorily cued location was judged to be higher in contrast than the patch in the opposite visual field (55% vs 45%) (Fig. 1B).

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