RESEARCH ARTICLE

Auditory facilitation of visual-target detection persists regardless of retinal eccentricity and despite wide audiovisual misalignments

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Abstract It is well established that sounds can enhance visual-target detection, but the mechanisms that govern these cross-sensory effects, as well as the neural pathways involved, are largely unknown. Here, we tested behavioral predictions stemming from the neurophysiologic and neuroanatomic literature. Participants detected near-threshold visual targets presented either at central fixation or peripheral to central fixation that were sometimes paired with sounds that originated from widely misaligned locations (up to 104° from the visual target). Our results demonstrate that co-occurring sounds improve the likelihood of visual-target detection (1) regardless of retinal eccentricity and (2) despite wide audiovisual misalignments. With regard to the first point, these findings suggest that auditory facilitation of visual-target detection is unlikely to operate through previously described corticocortical pathways from auditory cortex that predominantly terminate in regions of visual cortex that process peripheral visual space. With regard to the second point, auditory facilitation of visual-target detection seems to operate through a spatially non-specific modulation of visual processing.

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Introduction

Several studies have now demonstrated that sounds facilitate the detection of simultaneously presented visual targets (Lippert et al. 2007; Noesselt et al. 2008, 2010; Odgaard et al. 2003; Stein et al. 1996; Van der Burg et al. 2008a, b), but the neural mechanisms and pathways underlying this well-established behavioral effect are still being investigated. Here, we manipulated the spatial properties of co-occurring sounds and visual targets to test specific hypotheses based on previously reported neurophysiologic and neuroanatomic findings.

Two primary anatomic models of cortical multisensory integration have been proposed. In one model, unisensory information is first processed extensively in unisensory cortex, with these well-elaborated unisensory representations then converging in so-called higher-order multisensory association areas such as the superior temporal sulcus (Calvert et al. 2001). In the other model, unisensory information begins to interact in early sensory cortices near the onset of stimulus processing (Foxe et al. 2000; Foxe and Schroeder 2005). Whereas it was once thought that only the first of these models was anatomically plausible, neuroanatomic data now also exist to support the second model (Cappe and Barone 2005; Falchier et al. 2002, 2010; Rockland and Ojima 2003). Falchier et al. (2002), for example, described direct projections from auditory cortical regions to primary visual cortex. These corticocortical projections terminated most prominently in the areas of visual cortex that process peripheral visual space (i.e., the areas of cortex that process the visual field 10–20° from central fixation), suggesting that audiovisual interactions

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that occur via this neural pathway might serve to specifically bolster the processing of peripheral stimuli. This is an attractive finding in that it suggests the possibility of an early warning system, whereby potentially threatening stimuli that arise outside central vision are more likely to be detected. We took advantage of this important anatomic detail to test whether these previously described corticocortical projections are involved in auditory facilitation of visual-target detection (Fig. 1). Specifically, we tested whether improvements in detection are greater when a visual target paired with a co-occurring sound is presented peripheral to central fixation, relative to when the same bisensory pairing is presented at central fixation.

To further probe the neural substrates underlying the auditory facilitation of visual-target detection, we manipulated audiovisual spatial alignment. Previous research has revealed that early auditory–somatosensory interactions in low-level sensory cortices occur despite wide peripersonal separations (100° along the horizontal meridian; Murray et al. 2005). Here, we tested whether a co-occurring sound enhances performance in a visual-target detection task, even when the spatial representations of the sound and the visual target are widely misaligned (by up to 104° along the horizontal meridian; Fig. 1). It is well established that multisensory neurons typically have overlapping unisensory receptive fields (i.e., the spatial rule of multisensory integration), such that these neurons respond most strongly to stimuli that arise from the same location (e.g., Meredith and Stein 1986). If auditory facilitation of visual-target detection occurs despite wide spatial misalignments, it would suggest an underlying neural mechanism that operates through a spatially diffuse modulation of visual responses. It would also exclude brain areas where the spatial rule of multisensory integration is known to

dominate, such as the superior colliculus, as the source of these multisensory effects.

Methods

Participants

Twelve neurologically normal volunteers participated in the experiment (mean age 31 ± 6.2 years; 4 women; 2 left handed). The Institutional Review Board of the City College of CUNY approved the experimental procedures. Written informed consent was obtained from all subjects prior to data collection, in line with the Declaration of Helsinki.

Stimuli and task

Participants, who were positioned 70 cm in front of a 21-inch cathode-ray tube (CRT) monitor, were asked to maintain central fixation and report the occurrence of visual stimuli: sine-wave gratings with 16-ms duration, subtending 2.5° of the visual angle in both the vertical and horizontal planes. These visual targets were equally likely to occur at any of 3 possible target locations: centrally and 2° below central fixation, 14° to the right and 2° below central fixation, and 14° to the left and 2° below central fixation (Fig. 1). Potential target locations were marked with circles to increase the ease with which participants were able to deploy their attention. When a visual stimulus appeared, participants pressed a button corresponding to its location (i.e., the up arrow to indicate a central target, the right arrow for a peripheral target to the right of central fixation, or the left arrow for a peripheral target to the left of central fixation). Participants were instructed to respond

Fig. 1 A schematic of the experimental design for Experiment 1. **a** The experimental display had 3 target locations. Participants were told to respond whenever they saw a visual stimulus (i.e., to press 1 of 3 *arrow keys* corresponding to the target location). **b** There were 4 equiprobable trial types: auditory-alone catch trials (*A*), visual-alone trials (*V*), no-stimulus catch trials (*NS*), and audiovisual trials (*AV*)
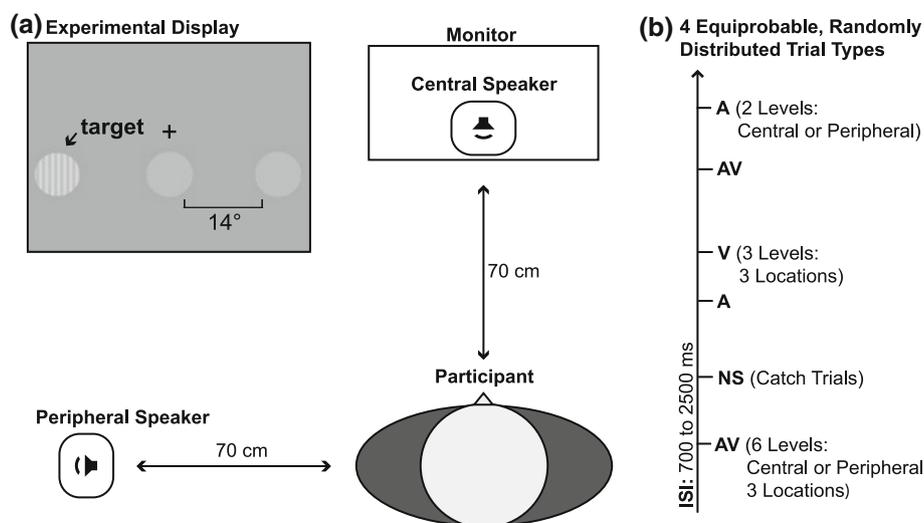
to all visual stimuli, regardless of whether the visual stimuli occurred alone or with a sound. Task-irrelevant sounds (1,000-Hz tone, 16 ms) were presented at a comfortable listening level, either from a BOSE (Companion 2) speaker positioned on top of the monitor or from a BOSE (Companion 2) speaker positioned 90° to the left of central fixation, at a distance of 70 cm from the participant (Fig. 1). The auditory and visual components of the audiovisual stimuli were therefore maximally misaligned by 104°. There were four equiprobable stimulus types: visual alone (three locations), auditory alone (two locations), audiovisual (six combinations of visual and auditory locations), and "no-stimulus trials" (i.e., points in time randomized like other stimulus events in which no stimulus actually occurs). Because auditory alone and audiovisual trials were equiprobable, sounds did not predict the occurrence of a visual stimulus (i.e., a target). To guard against anticipatory or rhythmic responding, the stimulus-onset asynchrony (SOA), which varied randomly throughout the experiment with a rectangular distribution, was 700–2,500 ms. Participants completed twelve blocks. Each block included 252 trials and was broken into 6 mini-blocks (i.e., points at which participants were encouraged to take brief breaks). At the conclusion of each mini-block, hit rates and false alarm rates were calculated online, and participants were given feedback on their performance. Between mini-blocks, the contrast of the visual stimuli was automatically adjusted as necessary—and separately for central and peripheral stimuli—such that each participant's hit rate in response to visual-alone stimuli was maintained at approximately 65%. That is, contrast was increased if participants detected less than 55% of the visual stimuli, and contrast was decreased if participants detected more than 75% of the visual stimuli. The contrast levels of visual-alone and audiovisual stimuli were always kept identical.

Statistical analysis

Location-specific false alarm rates in response to auditory-alone trials and no-stimulus trials were combined with location-specific hit rates in response to audiovisual trials and visual-alone trials, respectively, to calculate d-prime

values (Green and Swets 1966). A button press was considered a hit if it occurred 150–1,000 ms after a visual stimulus. D-prime provided a measure of detectability independent of the potential response bias associated with the inclusion of paired sounds. That is, using d-prime to measure detectability eliminates the alternative hypothesis that improved behavioral performance results from participants simply responding to the occurrence of sounds (see Odgaard et al. 2003). To determine whether it was necessary to use d-prime instead of simply analyzing hit rates, we examined *criterion*, which is a well-established measure of response bias (Macmillan and Creelman 1991).

To test whether there was significant auditory facilitation of visual-target detection and whether this enhancement varied with the visual target's retinal eccentricity or its misalignment with task-irrelevant sounds, a two-way repeated-measures ANOVA was conducted with factors of stimulus type (three levels: visual alone, audiovisual with centrally presented sound, or audiovisual with peripherally presented sound) and target location (three levels: center, right, or left). Following a significant ANOVA, pairwise comparisons were made using planned protected t-tests (Fisher's least significant difference). The same statistical analyses were then repeated with criterion and reaction times as the dependent measure. The alpha level for all statistical analyses was set at 0.05.

Results

Table 1 shows hit rates and false alarm rates for each combination of visual-target location (i.e., left, center, or right) and stimulus type (i.e., visual alone, audiovisual with centrally presented sound, or audiovisual with peripherally presented sound). A quick inspection of these data suggests that pairing a visual target with a sound improved visual-target detection regardless of retinal eccentricity and despite wide audiovisual misalignments; however, a repeated-measures ANOVA with criterion as the dependent measure revealed that response bias (as measured through criterion) was significantly different across the three target locations ($F_{2,22} = 22.7$, $P < 0.001$, $\eta_p^2 = 0.67$). Pairwise comparisons showed that this difference was attributable to

Table 1 Hit rates and false alarm rates by visual-target location and stimulus type (visual alone, audiovisual with a centrally presented sound, or audiovisual with a peripherally presented sound)

	Left target			Center target			Right		
	V (%)	AVC (%)	AVP (%)	V (%)	AVC (%)	AVP (%)	V (%)	AVC (%)	AVP (%)
HR%	70	80	82	67	75	74	67	80	76
FAR%	10	3	6	5	1	1	6	4	2

V visual alone, *AVC* visual paired with sound from the central speaker, *AVP* visual paired with sound from the peripheral speaker
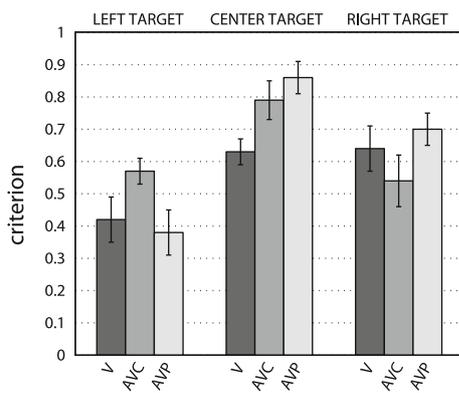
Fig. 2 The criterion for reporting occurrences of visual targets at each of the three target locations, sorted by target type: visual alone (*V*), visual paired with a sound from the central speaker (*AVC*), and visual paired with a sound from the peripheral speaker (*AVP*)

an overall lower criterion for the left-target location, with participants more likely to report having seen a visual target at the leftmost location relative to the central- (*P* = 0.001) and right-target (*P* = 0.001) locations. Participants were also more likely to report seeing a visual target at the rightmost location relative to the central-target location (*P* = 0.03). A statistically significant interaction between visual-target location and sounds ($F_{2,22}$ = 4.3, *P* < 0.005, η_p^2 = 0.28) further revealed that response bias when there was no sound or when there was a sound that occurred at either of the two speaker locations was not uniform across the three visual-target locations (Fig. 2). Because the analysis of criterion revealed significant differences in response bias across our conditions, it was necessary to use a measure of detectability that is independent of response bias to determine whether co-occurring sounds improved the sensitivity of visual-target detection: d-prime.

A repeated-measures ANOVA with d-prime as the dependent measure revealed that co-occurring sounds did indeed significantly improve the detection of visual targets ($F_{2,22}$ = 99.6, *P* < 0.01, η_p^2 = 0.90). Pairwise comparisons further revealed that this multisensory enhancement of visual-target detection was independent of whether the co-occurring sound was presented from the central speaker or from the peripheral speaker (*P* = 0.59). That is, sounds improved the detection of visual targets even when these unisensory components were misaligned by up to 104° along the horizontal meridian (Fig. 3a).

The main effect of target location approached significance ($F_{2,22}$ = 3.3, *P* = 0.06, η_p^2 = 0.23), suggesting that the overall detectability of visual targets at central fixation might be greater than that for visual targets peripheral to central fixation. More importantly for our central hypotheses, the interaction between visual-target location and stimulus type failed to reach significance ($F_{4,44}$ = 1.7,
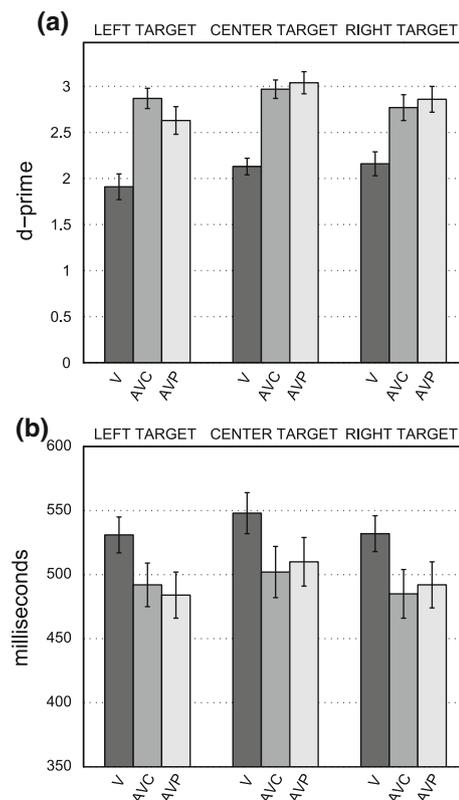

Fig. 3 Auditory facilitation of visual-target detection occurs regardless of retinal eccentricity (*right target*, *center target*, *left target*), and despite wide audiovisual misalignments (as large as 104°). These multisensory effects are demonstrated using both **a** d-prime and **b** reaction times. There were 3 target types: visual alone (*V*), visual paired with a sound from the central speaker (*AVC*), and visual paired with a sound from the peripheral speaker (*AVP*)

P = 0.19, η_p^2 = 0.13), suggesting that auditory facilitation of visual-target detection does not significantly differ with regard to retinal eccentricity (Fig. 3a). Numerically, facilitation was comparable across the three target locations, with d-prime values ranging from 1.9 to 2.2 in response to visual-alone targets and 2.6–3.0 for audiovisual targets (Fig. 3a). Although it is unconventional to examine pairwise comparisons when the *F* value fails to reach statistical significance, we decided based on a reviewer's comments that it was important to further investigate what was driving the interaction's relatively low *P* value (i.e., 0.19). A closer examination of the data confirmed that auditory facilitation of visual-target detection was significant at each target location, regardless of whether the visual target was paired with a sound from the central or the peripheral speaker (all *P values* < 0.003). There was also a potential trend toward lower detectability of visual-alone stimuli at the leftmost target location relative to the central- (*P* = 0.08) and right-target locations (*P* = 0.08), as well as a smaller increase in detectability when a target at the leftmost location was paired with a sound from the

peripheral speaker relative to when it was paired with a sound from the central speaker ($P = 0.06$). None of these potential trends, however, suggest that auditory facilitation of visual-target detection is greater when a visual target is presented peripheral to central fixation rather than at central fixation. These results are therefore inconsistent with what would be predicted based on previously described corticocortical projections from auditory to visual cortex (Falchier et al. 2002). Such projections have been shown to predominately terminate in regions of visual cortex that process the peripheral visual space (Falchier et al. 2002).

A repeated-measures ANOVA with reaction times as the dependent measure mirrored the results from our d-prime analysis, revealing that co-occurring sounds significantly speeded reaction times ($F_{2,22} = 54.8$, $P < 0.01$, $\eta_p^2 = 0.83$). Pairwise comparisons further demonstrated that the influence of co-occurring sounds on reaction times was independent of whether the co-occurring sound was presented from the central speaker or from the peripheral speaker ($P = 0.36$; Fig. 3b). Combined with the results of our d-prime analysis, these findings indicate that the neural mechanism underlying auditory facilitation of visual-target detection can operate in a spatially diffuse manner, such that the location of a sound does not define the area of the visual field that receives enhancement.

With regard to whether retinal eccentricity influences the speed of visual-target detection, there was a significant main effect of target location ($F_{2,22} = 3.5$, $P < 0.05$, $\eta_p^2 = 0.23$), where reaction times in response to peripheral targets were faster than those in response to central targets, regardless of whether the visual target was presented with a co-occurring sound. These findings make sense in the context of the magnocellular and parvocellular visual pathways, where magnocellular projections, which consist of large, rapidly conducting neurons, dominate in the visual periphery (Kaplan 1991; Merigan and Maunsell 1993). In other words, differences between the cell types that populate the central and peripheral retina most likely account for faster reaction times when visual targets are presented in the periphery, relative to when visual targets are presented near central fixation.

Discussion

Although numerous studies have demonstrated auditory facilitation of visual-target detection (Lippert et al. 2007; Noesselt et al. 2008, 2010; Odgaard et al. 2003; Stein et al. 1996; Van der Burg et al. 2008a, b), little is known about the underlying neural substrates. One hypothesis put forth in the literature is that these audiovisual interactions are mediated via direct corticocortical projections from auditory cortices to visual cortex (see Van der Burg et al.

2008a). Here, however, we find no evidence that the spatial characteristics of the behavioral effect fit with what one might predict based on the anatomic data. Falchier et al. (2002) reported that projections from belt and parabelt regions of auditory cortex predominately project to regions of visual cortex that process the periphery (10–20° from central fixation), but our findings show that auditory facilitation of visual-target detection is similar regardless of the retinal eccentricity at which visual targets are presented. Based on these similarities (see Fig. 3), it appears that there is a common mechanism operating across the visual field and that this mechanism therefore does not stem from the previously described direct corticocortical projections (Falchier et al. 2002). It should be noted, however, that future studies could reveal a separate neural pathway that specifically mediates auditory facilitation of visual-target detection near central fixation. The existence of two pathways, one projecting to regions of visual cortex that process stimuli in the periphery and one projecting to regions of visual cortex that process stimuli near central fixation, might also explain these results.

Our findings further demonstrate that auditory facilitation of visual-target detection persists despite wide audiovisual misalignments of up to 104° on the horizontal meridian. Several previous studies have similarly described spatially non-specific multisensory interactions, but within different behavioral contexts (e.g., Gondan et al. 2005; Keetels and Vroomen 2005; Murray et al. 2005; Stein et al. 1996; Teder-Sälejärvi et al. 2005). Van der Burg et al. (2008a), for example, demonstrated that a spatially uninformative sound, simultaneously presented with a target-specific color change, facilitated visual-target detection within a cluttered, continuously changing environment. But here, unlike in the present study, the sound was not clearly misaligned with the visual stimuli, and it is therefore possible that the co-occurring sound selectively enhanced the sensitivity of neurons in an area of visual cortex corresponding to the sound's relatively diffuse spatial representation (i.e., an area of visual cortex that included both the targets and the surrounding distractors). In comparison, we used a widely misaligned speaker—where the spatial representation of the sound clearly came from a location that differed from that of the target. Thus, we are able to specifically to demonstrate that the spatial representation of a co-occurring sound in no way delimits the area of visual space where visual processing is modulated. That is, we find that auditory facilitation of visual-target detection is entirely independent of auditory spatial mapping.

Vroomen and Keetels (2006) likewise used a widely misaligned speaker to demonstrate that some multisensory interactions persist despite the absence of spatial overlap. Their results revealed that sounds influence the sensitivity of visual temporal order judgments, even when presented at

locations that are separated from the visual stimuli by 90° along the horizontal meridian. These misaligned sounds, which occurred both 100 ms before the first visual stimulus and 100 ms after the second visual stimulus, were hypothesized to improve sensitivity through temporal ventriloquism (i.e., an illusion whereby a sound presented in close temporal proximity to a visual stimulus alters the perceived temporal occurrence of that visual stimulus). Misaligned sounds were thus thought to improve the sensitivity of temporal order judgments by increasing the apparent temporal separation of consecutive visual stimuli. In comparison, the present experiment investigated whether a widely misaligned sound enhanced the detectability of a co-occurring, near-threshold visual target. Under these conditions (i.e., spatial misalignment but temporal overlap), we hypothesize that the simultaneous presentation of widely misaligned sounds might have led to an increase in the apparent contrast of the visual targets, thereby improving behavioral performance (see Carrasco et al. 2004).

The persistence of auditory facilitation of visual-target detection despite wide audiovisual misalignments suggests that its underlying multisensory interactions are unlikely to arise from brain regions where spatial overlap of the unisensory components is known to be a prerequisite for multisensory integration (e.g., the superior colliculus). Alternatively, auditory facilitation might result from interactions in brain regions that have traditionally been considered to be modality specific (e.g., Lakatos et al. 2007, 2009; Murray et al. 2005; Noesselt et al. 2008, 2010). Murray et al. (2005), for example, used EEG and behavioral measures to demonstrate that auditory–somatosensory interactions occur despite wide peripersonal separations, where the unisensory components of the stimulus were presented at locations that were approximately 100° apart (along the horizontal meridian). These multisensory effects, which were evident in the ERPs at just 50 ms poststimulus, were localized to auditory cortical association areas (see also Gonzalez Andino et al. 2005). Such evidence suggests that multisensory interactions can occur at approximately the same time that initial afferent activity arrives in the primary sensory cortices (see also Foxe et al. 2000; Giard and Peronnet 1999; Molholm et al. 2002; Schroeder et al. 2004; Wang et al. 2008). Given that auditory facilitation of visual-target detection similarly persists despite wide audiovisual misalignments, it is plausible that its underlying multisensory interactions also occur in the early sensory cortices near the onset of cortical processing.

A possible neural mechanism

Auditory facilitation of visual-target detection despite spatially uninformative (e.g., Van der Burg et al. 2008a) or

widely misaligned sounds (see Fig. 3) suggests that it might be temporal information from the non-target modality, rather than spatial information, that promotes enhanced detection. Several studies have shown that a temporal cue can be used to guide attentional deployment in preparation for a subsequent target, improving reaction times (e.g., Coull and Nobre 1998; Hackley et al. 2007; Miniussi et al. 1999). Such an anticipatory focusing of attentional resources, however, seemingly cannot explain the multisensory effects observed in our data. Here, a short-duration sound (16 ms) was presented simultaneously with a short-duration (16 ms) visual stimulus, not prior to the visual stimulus. It is therefore unlikely that auditory facilitation of visual-target detection resulted from an anticipatory focusing of attentional resources, because the boost in visual processing would need to be more immediate. An alternative hypothesis that better fits with our data has recently been proposed in the neurophysiologic literature that the auditory facilitation of visual-target detection operates through a modulation of the brain's intrinsic oscillations (Lakatos et al. 2009).

Neurophysiologic recordings in non-human primates have demonstrated that a stimulus in one sensory modality can synchronize neural activity across multiple functionally interconnected cortical regions, including the primary sensory cortices (Lakatos et al. 2007, 2009). This synchronization results from the phase reset of ongoing neural oscillations, which are intrinsic fluctuations in the brain's excitability that have been shown to influence perception (e.g., Busch et al. 2009; Busch and VanRullen 2010; Foxe et al. 1998; Lakatos et al. 2009; Mathewson et al. 2009; Monto et al. 2008; Snyder and Foxe 2010; VanRullen et al. 2006, 2007; Worden et al. 2000). In the context of the present experiment, sounds would be hypothesized to reset the phase of ongoing oscillations in visual cortex, such that co-occurring visual targets align with high-excitability phases. By shifting the baseline of neurons in visual cortex closer to their firing threshold (Kayser et al. 2009; Montemurro et al. 2008; Whittingstall and Logothetis 2009), such cross-sensory phase reset would be expected to enhance visual-target detection.

Findings from a recent study in our laboratory provide compelling support for this notion that auditory facilitation of visual-target detection is attributable to cross-sensory phase reset of ongoing neural oscillations (Fiebelkorn et al. under review). Our data demonstrate stimulus-locked periodicity in visual-target detection as a function of when a near-threshold visual target was presented relative to a sound that occurred at the beginning of each trial. Such periodicity in visual-target detection is a predicted outcome of cross-sensory phase reset in visual cortex. That is, if the phase of ongoing oscillations is consistently reset—time locked to the occurrence of a sound at the beginning of

each trial—then high- and low-excitability phases following this consistent reset should align across trials. Whether or not a subsequent visual target is detected should therefore be influenced by where its presentation falls relative to the underlying oscillatory activity (i.e., when it is presented relative to the sound that occurs at the beginning of each trial).

Spatial constraints and multisensory processing

One might ask why it is that multisensory facilitation is observed here for inputs that are so obviously misaligned. Spatial alignment is known to play an important role in other forms of multisensory behavioral facilitation. For example, auditory-driven speeding of saccadic reaction times to a visual target decreases as the spatial disparity between the bisensory stimuli increases (Arndt and Colonius 2003; Frens et al. 1995). This is probably not surprising given the central role of the superior colliculus in mediating saccades, a midbrain structure in which multisensory integration is well known to be dependent upon overlapping receptive fields (see Stein 1998). We suggest that the specific constraints on multisensory integration change depending on the neural mechanisms invoked by the demands of the task at hand. Thus, when the task requires an eye movement to an easily detectable visual target, key multisensory processes will occur in the superior colliculus and be subject to the constraints therein. Alternatively, in the case of auditory facilitation of near-threshold visual targets, the best way to guarantee that the signal exceeds the noise—and will therefore be detected—might be to amplify initial afferent activity in visual cortex, for example in the manner proposed above (i.e., cross-sensory phase reset). A spatially diffuse model of signal enhancement might well be beneficial here, perhaps increasing the likelihood of detection in cases where the location of the target is not predetermined. Once detection has occurred, a saccade might then be initiated to the location of the near-threshold visual target. Of course various mechanisms of multisensory enhancement need not be mutually exclusive.

Concluding remarks

Auditory facilitation of visual-target detection occurs regardless of retinal eccentricity and despite wide audio-visual misalignments. The data presented here thus provide important clues about the neuroanatomic substrates underlying auditory facilitation of visual-target detection. Our results suggest that these multisensory effects might arise from interactions in brain regions that have traditionally been considered to be unisensory (in light of Murray et al. 2005), but do not operate via previously

described corticocortical pathways between these early sensory cortices (in light of Falchier et al. 2002).

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