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Multisensory-mediated auditory localization

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Abstract. Multisensory integration is a powerful mechanism for maximizing sensitivity to sensory events. We examined its effects on auditory localization in healthy human subjects. The specific objective was to test whether the relative intensity and location of a seemingly irrelevant visual stimulus would influence auditory localization in accordance with the *inverse effectiveness* and *spatial rules* of multisensory integration that have been developed from neurophysiological studies with animals [Stein and Meredith, 1993 *The Merging of the Senses* (Cambridge, MA: MIT Press)]. Subjects were asked to localize a sound in one condition in which a neutral visual stimulus was either above threshold (supra-threshold) or at threshold. In both cases the spatial disparity of the visual and auditory stimuli was systematically varied. The results reveal that stimulus salience is a critical factor in determining the effect of a neutral visual cue on auditory localization. Visual bias and, hence, perceptual translocation of the auditory stimulus appeared when the visual stimulus was supra-threshold, regardless of its location. However, this was not the case when the visual stimulus was at threshold. In this case, the influence of the visual cue was apparent only when the two cues were spatially coincident and resulted in an enhancement of stimulus localization. These data suggest that the brain uses multiple strategies to integrate multisensory information.

1 Introduction

There is now a great deal of evidence indicating that perceptual experiences are often shaped by complex interactions between the different senses (see Calvert et al 2004 for a collection of recent reviews). Perhaps the most dramatic evidence of this comes from multisensory illusions, which can be viewed as the flip side of normal sensory experience because they result from disruptions of the cross-modal coherence accompanying most events (Stein 1998). One of the most popular of these illusions is the 'ventriloquism effect', in which a compelling visual stimulus causes a perceptual translocation of a spatially disparate sound (see Bertelson and Aschersleben 1998; also see Bertelson and Radeau 1981; Slutsky and Recanzone 2001; Hairston et al 2003a; Wallace et al 2004; for a review, see Vroomen and de Gelder 2004). This effect of 'visual capture' reflects the dominance of vision when the nervous system deems its information about the location of a multisensory (ie visual – auditory) event most reliable, as is generally the case in normal conditions (Welch and Warren 1980). Although this phenomenon has been very well documented, it is not clear whether it would still be evident if the visual stimulus was only weakly effective. Presumably, the degraded perceptual nature of the visual stimulus would render it incapable of overriding auditory localization judgments and inducing an apparent translocation of the sound. Nevertheless, according to the spatial principle of multisensory integration (see Stein and Meredith 1993), even a weakly effective visual stimulus would be expected to enhance localization of a spatially coincident auditory stimulus (Meredith and Stein 1986a, 1986b; Kadunce et al 2001). Indeed, at cell level spatially coincident audio – visual stimuli interact, thus enhancing the response activity of multisensory neurons in the cat's superior colliculus. Instead, the misalignment of the audio–visual stimuli typically disrupts the multisensory enhancement (the so-called *spatial rule*). Furthermore, the visual induced enhancement of an auditory event would be expected to be proportionately highest when the stimuli to be integrated are weakest (the so-called *inverse effectiveness rule*—Stein and Meredith 1993).

In order to test this hypothesis, hard-to-localize sounds were presented either alone (modality-specific condition) or with a simultaneous visual stimulus (cross-modal condition). The detectability of the visual stimulus was either supra-threshold (experiment 1) or at threshold (experiment 2). In addition, the effect of the spatial arrangement of the visual–auditory stimuli was assessed by systematically varying their spatial disparity. The expectation was that visual stimuli of such differing detectabilities would have substantially different effects with respect to visual capture and adherence to the spatial principle of multisensory integration: visual bias would be evident in experiment 1 regardless of the location of the visual stimulus, but absent in experiment 2, where only a spatially coincident visual stimulus would be effective and, in this case, would enhance correct auditory localization.

2 Experiments

2.1 *Participants*

Eight students (mean age 24 years) from the University of Bologna participated in the study. All subjects had normal or corrected-to-normal vision, as well as normal hearing and all were right-handed. The participants were naive as to the purpose of the experiment and gave informed consent to participate in the study according to the Declaration of Helsinki.

2.2 *Apparatus and stimuli*

The apparatus consisted of a plastic semicircular perimeter device (height 40 cm, length 200 cm) that was fixed to the surface of a table. Eight piezoelectric loudspeakers (0.4 W, 8 Ω) were located horizontally at ear level, at eccentricities of 24°, 40°, 56°, and 72° to the left and right of the central fixation point (0°). They are referred to as A1 to A8 moving from left to right. A black-fabric curtain hid the speakers from view. The auditory stimuli consisted of a 160 ms broadband burst of pure tones (4000 Hz). The intensity range of the auditory stimuli was 76.5–58.5 dB SPL from piezoelectric speakers. The intensity was systematically varied in order to obtain an auditory localization threshold for each subject (see below). The intensity of the background noise was 56.5 dB.

The visual stimuli were generated by single green-light-emitting diodes (LEDs, 90 cd m^{-2}) poking out of the black fabric and were directly presented in front of each loudspeaker (the visual stimuli are referred to as V1 to V8, moving left to right). There were 4 red LEDs (each was 80 cd m^{-2}) arranged in a 1 deg square around each green LED (visual mask). Although never stimulated, other LEDs were located at 32°, 48°, and 64°, to either side of the central fixation (figure 1). They were there to increase uncertainty in the localization task. The exposure time of the visual stimulus and the visual mask was varied in order to obtain a visual threshold for each subject (see below).

All visual and auditory stimuli were 160 ms pulses. Their timing, and response acquisition were controlled by an ACER 711TE laptop computer, provided with a custom program (XGen–Experimental Software, http://www.psychology.nottingham.ac.uk/staff/cr1/) and a custom hardware interface.

2.3 *Procedure*

The experiment was conducted in a dimly lit, sound-attenuated room. The subject sat in front of the apparatus, at a distance of 70 cm. He/she faced directly ahead, with the body aligned with the centre of the apparatus. Before each trial, the subject fixated

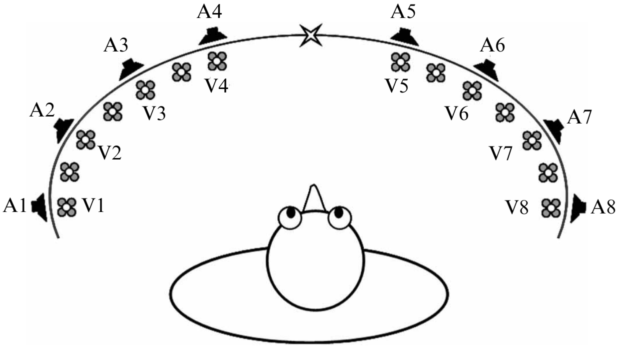

Figure 1. A schematic bird's-eye view of the subject and the experimental apparatus.

a 1-deg-wide white triangle located at 0°. The experimenter stood behind the apparatus, facing the subject and assessed fixation on each trial. Any trials in which fixation was not maintained or was questionable were eliminated from consideration (less than 5%). The experiment was carried out under binocular vision.

2.3.1 *Auditory and visual threshold tests.* Each subject's ability to detect and localize auditory stimuli (auditory threshold) and to detect visual stimuli (visual threshold) was measured at each spatial location. Thus, the auditory stimuli were purposely chosen for each subject to be difficult to localize. Auditory localization threshold was evaluated by assessing their mean localization error (ie the difference between actual and reported location). The criterion for inclusion was as found with a localization error $> 8°$ in 60%–70% of the trials. If a lower percentage of localization errors was obtained, uncertainty was increased by decreasing the intensity of the sound (range, 76.5–58.5 dB).

Visual detection threshold was measured by asking subjects to verbally report when they detected a visual stimulus (ie the target was any one of the 8 green LEDs that was illuminated). After the visual target appeared, the visual mask appeared (ie all 4 red LEDs were illuminated, luminance 80 cd m^{-2} each) at each of the 8 spatial locations. Note that the masking stimulus always appeared simultaneously in all 8 spatial positions, while the visual target appeared in a single location. Catch trials (only the masking stimuli appeared) were also presented.

In order to obtain the visual threshold, the duration of the visual target was gradually reduced from 150 ms to a duration at which the hit rate was 50%, while the duration of the visual mask increased proportionally, so that the visual stimulus complex (visual target + visual mask) always had the same duration (160 ms) (Frassinetti et al 2002a; Bolognini et al 2005a). All subjects were able to detect the visual stimulus (100% of correct responses) when it was presented for 150 ms, regardless of its spatial location.

Possible changes in a subject's thresholds during experimentation were determined by re-measuring them after every four blocks of trials. In the few instances in which such changes were noted, the stimuli were replaced (ie the visual target duration was further reduced, parallel to an increment of the mask duration) to maintain the same relative stimulus effectiveness throughout the experiments.

2.3.2 *Experiments.* Once stimuli were chosen the two experiments began. In the first one, each of the 8 visual stimuli was supra-threshold and was presented for 150 ms followed by a 10 ms visual mask. In the second one, the visual stimuli were at threshold; hence the durations of the visual stimuli were chosen for each subject on the basis of his/her visual detection ability at each location (see previous section). In both experiments the auditory stimuli were below the auditory localization threshold. Each experiment consisted of three sensory conditions:

(i) Modality-specific auditory condition: only the auditory stimulus was presented at one specific location.
(ii) Modality-specific visual catch-trial condition: only the visual masking was presented.
(iii) Cross-modal condition: the auditory stimulus was presented at each location together with a temporally coincident visual stimulus. The visual stimulus (the green target LED) was either spatially coincident (SC) with or spatially disparate (SD) from the auditory target (disparities were 16° or 32° nasal or temporal).

The following trials were presented: 120 modality-specific auditory and 120 modality-specific visual trials (15 for each of the 8 positions); 120 spatially coincident cross-modal trials (15 for each of the 8 positions); and 240 spatially disparate cross-modal trials (15 for each of the 16 cross-modal spatially disparate conditions). Thus, in each experiment the total number of trials was 600, and these were equally distributed in 15 experimental blocks (40 trials each) over two consecutive days.

In both experiments subjects were required to verbally judge sound location. The apparatus was marked in clearly visible 1° steps from left to right and numbered sequentially from 1 to 72. Subjects were instructed to report the number corresponding to the location of the sound, and to ignore any accompanying visual stimulus.

3 Results

Performance was evaluated for responses to auditory stimuli at only four spatial positions: A2, A3, A6, and A7. Auditory stimuli were presented at more peripheral locations (A1 and A8) to increase the subject's uncertainty as regards the location of the auditory stimulus, but were not analyzed. This was because more peripheral localization judgments were not possible in these circumstances and the inclusion of these locations in the analysis would have produced a nasal response bias in the data set. For similar reasons positions A4 and A5 were not considered here (visual stimuli were never presented central to these auditory stimulus locations). No false positives were noted on catch trials.

3.1 *Auditory localization accuracy*

Localization errors were calculated in both modality-specific and cross-modal conditions as the absolute difference, expressed in degrees, between the verbal localization response and the actual target location. Owing to the lack of difference as a function of spatial disparity, data from different locations were collapsed and then analyzed with a repeated-measures analysis of variance (two-way ANOVA) with two main factors: experiment (experiment 1 versus experiment 2) and condition (modality-specific auditory condition versus cross-modal condition). Cross-modal conditions included those in which a visual stimulus was either spatially coincident (SC) with or 16° or 32° disparate from the auditory stimulus (SD-16° and SD-32°, respectively). Pairwise comparisons were conducted by means of the Duncan test.

Significant effects of the main factors, experiment ($F_{1,7} = 6.84$, $p < 0.03$) and condition ($F_{3,21} = 15.39$, $p < 0.0001$) were clearly evident. However, more interesting was the significant interaction between experiment and condition ($F_{3,21} = 8.52$, $p < 0.0006$). In experiment 1, a spatially coincident visual stimulus significantly improved auditory localization accuracy by reducing the localization error from 12.64° (in the modality-specific condition) to 10.33° ($p < 0.008$). In contrast, a disparate visual stimulus increased localization errors to 13.8° in the 16° disparity condition ($p = 0.1$) and to 16.8° in the 32° disparity condition ($p < 0.00008$). In experiment 2, a significant effect of the visual stimulus was evident only in the SC condition. A spatially coincident visual stimulus significantly improved auditory localization accuracy by reducing the localization error from 12.4° (in the modality-specific condition) to 10.7° ($p < 0.03$).

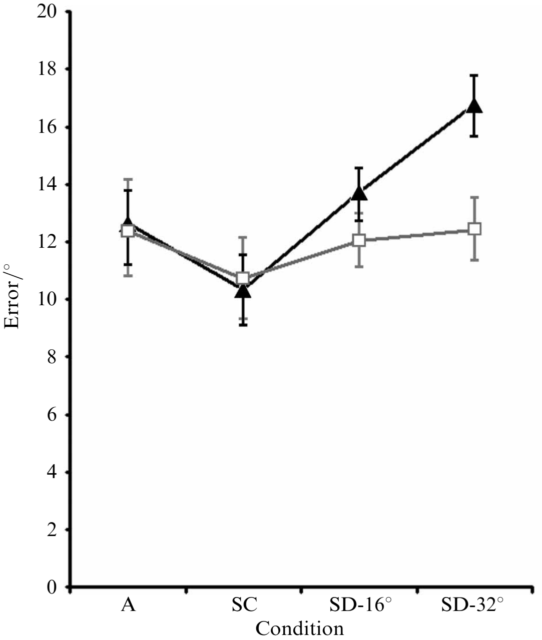

Figure 2. Mean degrees of auditory localization error and standard errors for the modality-specific auditory condition (A) and for the cross-modal conditions: spatially coincident cross-modal condition (SC) and the spatially disparate cross-modal condition (SD) with 16° and 32° of disparity (SD-16° and SD-32°, respectively).

Neither of the cross-modal SD conditions produced any significant change in auditory localization in experiment 2 (SD-16° = 12.06°, $p = 0.6$; SD-32° = 12.4°, $p = 0.9$) (see figure 2).

The increment in localization errors in the SD cross-modal conditions induced by the above-threshold visual stimulus might be explained by the occurrence of a visual bias on judgments of auditory location. Such a visual bias did not occur when the visual stimuli were at threshold. In order to verify this and measure the magnitude of the visual bias, a second analysis was carried out.

3.2 *Visual bias of auditory location*

Here the percentage of visual bias was calculated by subtracting the actual location of the sound from the average location reported, then dividing the difference by the actual visual–auditory disparity and multiplying by 100 (see Hairston et al 2003a; Wallace et al 2004). The resultant percentage of bias represents the degree of 'visual capture' of sound location. Note that visual bias cannot be computed in the absence of disparity. Hence, a score of 100% represents complete bias, wherein the subject localizes the sound at the visual stimulus site, whereas positive scores <100% indicate judgments between the visual and auditory stimuli, and negative scores reflect judgments beyond the visual stimulus (further from the auditory stimulus than is the actual visual stimulus).

Data were collapsed across positions (A2, A3, A6, A7) and then analyzed with a two-way ANOVA. Experiment (experiment 1 versus experiment 2) and spatial disparity (16° versus 32°) were the main factors. A significant main effect was obtained for experiment ($F_{1,7} = 28.92$, $p < 0.001$), showing that the visual bias in sound localization is more evident in experiment 1 (visual bias = 29.3%) than in experiment 2 (visual bias = 2.9%) (see figure 3). In addition, to verify the existence of a real, although small, visual bias in experiment 2, subjects' percentage of visual bias was compared with that of an expected distribution with no visual bias. Exact Fisher test (one-tailed) was not significant ($p = 0.12$), suggesting that subjects' visual capture in experiment 2 did not differ from a condition with no errors.

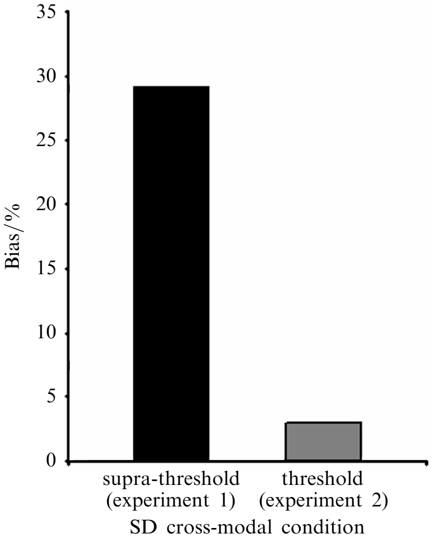

Figure 3. Mean percentage of visual bias in the spatially disparate (SD) cross-modal conditions.

4 Discussion

The present results demonstrate that there is strong synergy between the visual and auditory modalities in enhancing the accuracy of localizing external stimuli. This effect, coupled with the speeded reactions to cross-modal stimulus combinations (Gielen et al 1983; Engelken and Stevens 1989; Frens et al 1995; Hughes et al 1994, 1998; Corneil and Munoz 1996; Goldring et al 1996; Harrington and Peck 1998; Schroger and Widmann 1998; Giard and Peronnet 1999; Colonius and Diederich 2004), underscores the benefits associated with the brain's activity to integrate cross-modal stimuli. In the present context, the influence of a visual stimulus on the localization of an ambiguous sound was dependent on its relative spatial location as well as on its salience.

When the visual stimulus, regardless of its subjective intensity and inherent salience, was at the same location as the auditory stimulus, it improved the accuracy of auditory localization. Interestingly, the spatially coincident visual stimulus affected auditory information processing even when its detectability was so low that it was difficult for subjects to detect its presence. This finding is presumably related to the *inverse effectiveness rule* of multisensory integration, by which weakly effective unisensory stimuli have proportionately greater effects than do stronger stimuli (see Stein and Meredith 1993; Frassinetti et al 2002a, 2002b, 2005; Bolognini et al 2005a, 2005b; Perrault et al 2005; Stanford et al 2005). The observations of Hairston and coworkers (2003b) are in line with the present results. Although these investigators did not manipulate the spatial disparity between the visual and auditory stimuli, they did show that, under conditions of induced myopia, multisensory localization brings significant improvements over localization based on either of the modality-specific component stimuli.

The present results revealed that the interaction between the spatial location of the visual stimulus and its effectiveness has a powerful effect on auditory localization. At supra-threshold intensities, and regardless of spatial location, a strong visual bias was evident. The auditory stimulus appeared shifted toward the location of the visual stimulus: thus, a supra-threshold visual stimulus that was spatially disparate from the auditory stimulus did not provide a generalized positive alerting effect on the task. Rather, it increased errors. This finding is in line with the well-known *ventriloquism effect* (Howard and Templeton 1966; Thurlow and Jack 1973; Bertelson and Radeau 1981; Bertelson and Aschersleben 1998; Spence and Driver 2000; Slutsky and Recanzone 2001; Hairston et al 2003a; Lewald and Guski 2003; Wallace et al 2004; for a review see

Vroomen and de Gelder 2004). Indeed, when the plausibility that a sound originates from a visual event is high, based on the temporal correlation of the stimuli (Jack and Thurlow 1973) and on cognitive factors (Warren et al 1981), visual localization can influence auditory localization even when the stimuli are separated by angular distances of as much as 30° (Jackson 1953; Thurlow and Rosenthal 1976). These findings are also in line with the idea that sensory uncertainty determines the perceptual weight allocated to a given cue during multisensory integration (Ernst et al 2000; van Beers et al 2002; Ernst and Banks 2002; Battaglia et al 2003; Hairston et al 2003a, 2003b; Alais and Burr 2004; Heron et al 2004; Wallace et al 2004).

When, however, the visual cue was weak, and in some cases too weak to be detected, its influence was evident only when the visual and auditory stimuli were spatially coincident. Only spatially coincident stimuli enhanced judgments of auditory location. Surprisingly, this multisensory benefit was as great as it was with supra-threshold visual stimuli. However, when the visual stimulus was weak, the normal visual bias found in the supra-threshold condition disappeared when the cross-modal stimuli were spatially disparate.

The comparable amount of benefit induced by threshold and supra-threshold stimuli suggests that the facilitation with threshold stimuli cannot simply reflect a special case of less powerful visual bias. Otherwise, the spatially coincident threshold stimuli should exert a smaller enhancement of auditory localization compared to that induced by supra-threshold stimuli. But this was not the case. The present findings also suggest that explicit processing is not required for the integration of the visual and auditory stimuli in a spatially specific manner and a specific improvement for auditory localization task can take place in an implicit manner. This is not surprising, if we consider the possibility that this effect is mediated by sub-cortical structures, like the superior colliculus.

Thus, one likely possibility is that the enhancement of auditory localization obtained here with threshold visual stimuli reflected the consequences of multisensory integration in the superior colliculus, a structure that plays an important role in orientation and localization behaviors (see Stein and Meredith 1993). This possibility is supported by the general adherence of the present data set to several fundamental principles of multisensory integration that govern the responses of superior-colliculus neurons. On the other hand, the observation that visual bias occurred only when the visual stimulus was above threshold, and was independent of its location relative to the auditory stimulus, suggests that it might depend on a qualitatively different integrative principle. Whether this also involves the superior colliculus and/or is dependent on other brain areas involved in sensory localization remains to be determined.

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