

THE HANDBOOK OF MULTISENSORY PROCESSES

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2 Modulations of Visual Perception by Sound

LADAN SHAMS, YUKIYASU KAMITANI, AND SHINSUKE SHIMOJO

Introduction

Perception has traditionally been viewed as a modular function, with the different sensory modalities operating largely as separate and independent modules. To the degree that this thesis holds, it has contributed to progress in both empirical and theoretical research on the perceptual brain, yet to the degree that it has been overemphasized, it has masked the need for intensive research on cross-modal interactions. Perhaps for this reason multisensory integration has been one of the least studied areas of research in perception. As a result, prior to the very recent surge of interest in this topic, knowledge about multisensory integration and cross-modal interactions remained largely at the level of phenomenology. Even at this level, however, many important questions remain unanswered. Because vision has traditionally been viewed as the dominant modality (Howard & Templeton, 1966; Welch & Warren, 1986), most studies have focused on the effects of visual stimulation on perception in other modalities, and consequently the effects of other modalities on vision are not as well understood.

Vision alters other modalities

In normal people, the effects of cross-modal integration are made apparent under cleverly designed artificial conditions. The McGurk effect (McGurk & MacDonald, 1976) exemplifies such a condition. The McGurk effect is a perceptual phenomenon in which vision alters speech perception (for example, a sound of /ba/ tends to be perceived as /da/ when it is coupled with a visual lip movement associated with /ga/). The perceived spatial location of a sound source is also known to be drastically influenced by visual stimulation. This effect is known as the *ventriloquist effect* (Howard & Templeton, 1966) and is a common experience in daily life, such as when one is watching movies on television or at the cinema and voices are perceived to originate from the actors on the screen despite a potentially large spatial discrepancy between the image and the sound source.

It has been shown that tactile location can also be "captured" by visual location (Pavani, Spence, & Driver, 2000; Rock & Victor, 1964). All these effects emphasizing the strong influence of visual signals on other modalities (and a weak or absent reverse cross-modal effect) have been consistent with the commonsense notion that humans are primarily vision-dominant animals.

Sound alters temporal aspects of vision

Some later findings, however, revealed that visual perception could also be altered by other modalities, particularly in the temporal domain. Perceived duration (Walker & Scott, 1981) or rate (Gebhard & Mowbray, 1959; Shipley, 1964; Welch, Duttonhurt, & Warren, 1986) of a visual stimulus was shown to be influenced by accompanying sound signals. A recent study found that visual temporal resolution can be either improved or degraded by sounds, depending on the temporal relationship between the visual and auditory stimuli (Scheier, Nijwahan, & Shimojo, 1999). When two lights were turned on at different locations with a small temporal delay (in the range of -60 to 60 ms), the accuracy of temporal order judgments between the two lights was better with a sound preceding and another sound following the visual stimuli (A-V-V-A time order) than with a no-sound condition. Conversely, the subjects' performance became worse (as compared with the no-sound condition) when two sounds were inserted between the two visual stimuli (V-A-A-V time order). These results are consistent with the findings of another study which found that a flash is perceived earlier when it is preceded by a sound and later when it is followed by a sound, compared with a condition in which they occur simultaneously (Fendrich & Corballis, 2001).

A great body of behavioral findings on the cross-modal interactions summarized above can be accounted for by the modality appropriateness hypothesis (Choe, Welch, Guilford, & Juola, 1975; Fisher, 1968; Howard & Templeton, 1966; Kaufman, 1974; Welch & Warren,

1986). This hypothesis postulates that the modality that is most appropriate or reliable with respect to a given task is the modality that dominates the perception in the context of that task. Vision has a higher spatial resolution, hence its dominance in spatial tasks, whereas audition has a higher temporal resolution, hence its dominance in temporal tasks. The dominance of vision in the ventriloquist effect and the visual capture of tactile stimulation, and the dominance of audition in temporal tasks, are consistent with this hypothesis.

Sound alters other aspects of vision

Alteration of vision by sound, however, turned out to be not limited to temporal aspects of the visual stimuli. Auditory perceptual organization can affect perceptual organization in the visual domain (O'Leary & Rhodes, 1984). A sudden sound can improve the detection of a subsequent flash at the same location (McDonald, Teder-Sälejärvi, & Hillyard, 2000). The perceived intensity of a visual stimulus has recently been shown to be enhanced by the presence of sound (Stein, London, Wilkinson, & Price, 1996). An abrupt sound can improve the identification of a synchronously presented visual target embedded in a series of distractors (Vroomen & de Gelder, 2000).

A recent study has illustrated that the presence of a sound can alter the interpretation of an ambiguous visual motion event (Sekuler, Sekuler, & Lau, 1997). Two identical visual targets moving across each other can be perceived either to bounce off or to stream through each other, since their trajectory would be

nearly identical. Nonetheless, the majority of observers report a perception of streaming, not bouncing motion. However, if a brief sound is added at the moment the targets visually coincide, visual perception is strongly biased in favor of a bouncing motion (Sekuler et al., 1997). The sound has to have a sharp onset to induce this effect (K. Watanabe & S. Shimojo, personal communication). The ecological origin of this phenomenon may be the following: The multisensory experience of collision events in the natural environment could lead to cross-modal associative learning via synchronized stimulation of sensory modalities. Recent studies on this phenomenon have revealed some unexpected properties. For example, a transient sensory stimulus biases visual perception toward bouncing, irrespective of its modality: a brief visual flash and a brief touch were found to induce bouncing perception as well (Watanabe, 2001; Watanabe & Shimojo, 1998).

Auditory "capture" of visual structure

We recently reported a cross-modal effect demonstrating that the alteration of vision by sound is not limited to minor modulation of perceived intensity or situations of ambiguity in the visual stimulus. In the "sound-induced illusory flash," or for short, "illusory flash effect" (Shams, Kamitani, & Shimojo, 2000, 2002), sound radically changes the phenomenological quality of the percept of a nonambiguous visual stimulus. When a single brief visual flash is accompanied by multiple auditory beeps, the single flash is perceived as multiple flashes, as shown in Figure 2.1. Control conditions,

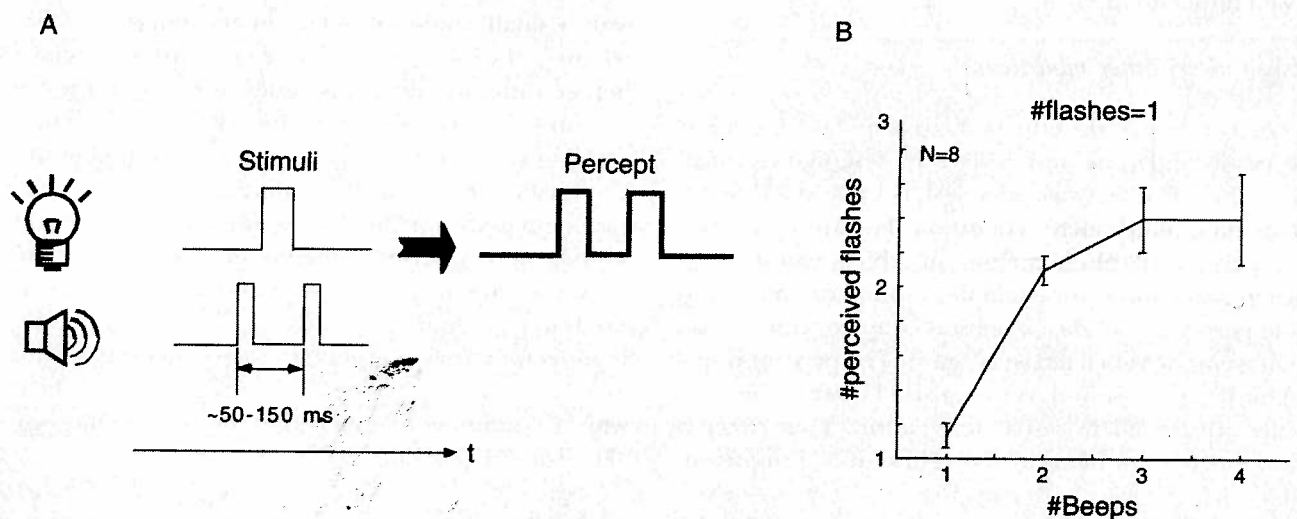


FIGURE 2.1 Sound-induced illusory flash effect. (A) Schematics of the sound-induced illusory flash. When a single flash is accompanied by two (or more) beeps, it is erroneously perceived as two (or more) flashes. (B) The average number of perceived flashes across eight observers is plotted against the number of beeps, for trials in which the visual stimulus consisted of one single flash. Observers reported seeing two or more flashes when the single flash was accompanied by two or more beeps.

catch trials, and many other observations indicate that the illusory flashing phenomenon is indeed a perceptual illusion and is not due to the difficulty of the task or to some cognitive bias caused by sound (Shams et al., 2000, 2002). The illusory double flash is perceptually very similar to a physical double flash. Furthermore, the illusion is not affected by the observer's knowledge about the physical stimulus, and is robust to variations in stimuli parameters. The temporal tuning of this effect was also measured by varying the relative timing of the visual and auditory stimuli. The illusory flash effect declined from 70 ms separation onward; however, it occurred strongly so long as the beeps and flash were within approximately 100 ms (Shams et al., 2002). Also interesting is the fact that the alteration of vision by sound in this study was found to be asymmetrical with respect to the number of events. Alteration of vision by sound occurred strongly only when a single flash was coupled with multiple beeps, but not when multiple flashes were paired with a single beep: multiple flashes were not perceived as one in the presence of a single beep. A similar dependency on the temporal structure of stimuli seems to have been at work in another study, which investigated the effect of vision on hearing (Saldaña & Rosenblum, 1993). A continuous sound (bowing a cello) was modulated by a discontinuous visual stimulus (plucking a cello), whereas a discontinuous sound (plucking) was not affected by the continuous visual stimulus (bowing). These findings, taken together, seem to suggest that cross-modal interactions depend at least partly on the structure of the stimuli.

A later study tackled another question related to the effect of sound on vision in the illusory flash effect: Is the illusory flash effect due to a mere fluctuation in brightness or to the creation of independent visual tokens? The study found that the sound-induced flashes can be perceived at different spatial locations from the real ones, and thus as independent visual tokens, when combined with a visual apparent-motion display (Kamitani & Shimojo, 2001). Two visual objects were flashed at different locations and separated by a temporal interval such that apparent motion was perceived between them. Each visual flash was accompanied by a beep, and another beep was presented between the flashes/beeps. Subjects reported that an illusory flash associated with the second beep was perceived at a location between the real flashes. This is analogous to the cutaneous "rabbit" illusion, in which trains of successive cutaneous pulses delivered to widely separated locations produce sensations at many in-between points (Geldard & Sherrick, 1972). Thus, the illusion can be referred to as sound-induced visual "rabbit."

Because no "rabbit" effect was observed when only visual stimuli were presented in a similar manner, the sound-induced visual rabbit seems to be a uniquely cross-modal effect.

Sound alters vision in motion perception

Perhaps a more direct test of the validity of the modality appropriateness hypothesis is to test the dominance (or nonmalleability) of vision in a spatial task. Motion perception involves an important spatial element and would provide an interesting framework for testing the effects of sound on vision in a spatial task. Whereas many studies have previously investigated cross-modal effects in motion perception, most of them have concentrated on the effects of visual motion on auditory motion perception (Aspell, Bramwell, & Hurlbert, 2000; Mateeff, Hohnsbein, & Noack, 1985; Soto-Faraco, Lyons, Gazzaniga, Spence, & Kingstone, 2002) (see also Soto-Faraco & Kingstone, Chap. 4, this volume) and reported the improvement in the auditory motion detection in the presence of a visual motion in the same direction.

One very recent study reported an influence of auditory motion on visual motion perception (Meyer & Wuerger, 2001). The visual stimulus was a dynamic random dot display in which the degree of motion coherence of the dots was varied, and the auditory stimulus consisted of a binaural tone presented from two speakers that simulated horizontal motion from left to right or vice versa. The investigators found that auditory motion biased the subjects' perceived direction of visual motion of the no-coherent-motion display in a direction consistent with the auditory motion.

Another recent study (Shams, Allman, & Shimojo, 2001) investigated this issue using a different method. Instead of using an ambiguous or subthreshold visual motion display, they used a brief (unambiguous) stationary visual stimulus. Eye movements were monitored during the session so that any artifact related to or created by them could be detected. In a subsequent experiment, other artifacts such as response and cognitive biases were addressed. Taken together, the data indicate that a moving sound does significantly affect visual perception by inducing motion in a stationary visual stimulus. It was also found that the moving flash did not have a significant effect on the percept of the stationary sound. These findings are important, because the observed direction of the cross-modal interactions cannot be uniquely predicted by the modality appropriateness hypothesis. Another theory must be proposed to account for the observations.

Modularity reexamined: Neural evidence

The mechanisms underlying the effects of sound on visual perception are not extensively studied or understood. It is not clear at what level of perceptual processing these cross-modal effects take place. These interactions may occur at subcortical regions, visual cortical areas, or polysensory associative cortical areas.

Event-related potential (ERP) recording provides an appropriate methodology for tackling this question because of its high temporal resolution. Schröger and Widdman (1998) used ERP recording to explore the site of audiovisual interactions. They used an odd-ball paradigm, and found no early interactions between the auditory and visual processes. They interpreted their results as suggesting that audiovisual integration occurs somewhere beyond the modality-specific areas but before the decision-making stage. They pointed out, however, that the lack of evidence for early modulation in their study could have been due to the fact that their task relied on memory mechanisms and thus might not have been appropriate for uncovering early sensory interactions. Giard and Perronet (1999) used ERP recording to tackle the same question using a pattern recognition task. They reported very early cross-modal effects in the occipital area and interpreted these results as a modulation of activity in the "sensory-specific" visual cortical areas by sound. In their study, however, they used two visual deformation patterns (a circle deforming into a horizontal or vertical ellipse) that unfolded over a course of 230 ms, and the subjects were trained in advance to associate each of the two deformation patterns with a specific tone. Therefore, it is not clear whether their results generalize to situations in which subjects are not trained to associate specific visual stimuli with specific auditory stimuli, or where the visual stimulus is a static image as opposed to a deforming pattern.

We recorded ERPs in a framework based on the illusory flash effect in order to examine the locus in the brain associated with alterations of visual perception by sound (Shams, Kamitani, Thompson, & Shimojo, 2001). Unlike the two studies just mentioned, the task used in our study was a simple perceptual task not involving memory. More important, the subjects were not instructed a priori to associate a certain visual stimulus with a certain auditory stimulus. The stimuli were extremely simple—brief tones and flashes. We employed a flash visual-evoked potential (VEP) paradigm and introduced a sound stimulus to examine whether sound would modulate the VEPs. Our prior psychophysical observation had shown that the illusory flash effect is significantly stronger in the periphery than in the fovea.

In order to search for any physiological correlation with this perceptual effect, we recorded VEPs for flashes presented in the fovea and the periphery separately. As can be seen in Figure 2.2, the data indicated extensive and early modulation of VEPs by sound in the illusion trials (the majority of the peripheral trials), in contrast to the lack of modulation of VEPs by sound in the nonillusion trials (the majority of the foveal trials). In a more recent analysis, we compared the time-frequency amplitudes of the illusion trials in the periphery with the no-illusion trials in the periphery and found significant auditory-visual interactions only in the illusion trials (Bhattacharya, Shams, & Shimojo, 2002). These results suggest a clear neurophysiological correlate for the perception of the illusory flash. Modulations of VEPs by sound occurred as early as ~140 ms after the onset of the second beep (or 170 ms after the onset of the flash) (Shams, Kamitani, et al., 2001). Considering that ERPs prior to 200 ms post-stimulus are believed to be due to the activity in the modality-specific pathways (Giard & Perronet, 1999), these modulations appear to occur in the visual pathway. Most interesting is the finding that similar modulations were induced by sound and by an additional physical flash (Shams, Kamitani, et al., 2001). Comparison of the difference waves revealed a striking similarity between the activity associated with an illusory second flash and that of a physical second flash (Fig. 2.2). This similarity suggests that similar brain mechanisms underlie these two percepts. Because the evoked response to a physical flash involves activity in the visual cortex, this implies that the representation of the illusory flash also involves activity in the visual cortex.

The results of this study suggest that sound affects processing at the level of the "visual" cortex. These findings contradict a longstanding modular view of perceptual processing. For a long time—arguably for more than a century—the general belief was that the different modalities operated largely independently of each other, and only at some higher level such as the association cortex did the information from various modalities converge and get combined.

Some recent studies utilizing functional imaging transcranial magnetic stimulation (TMS), or magnetoencephalography (MEG) also have provided evidence that the areas that have traditionally been viewed as modality-specific are modulated by signals from other modalities. For example, Sathian and colleague (Sathian, Zangaladze, Hoffman, & Grafton, 1997; Zangaladze, Epstein, Grafton, & Sathian, 1999) have shown that an area of the extrastriate visual cortex is active during tactile discrimination of grating orientation. Macaluso, Frith, and Driver (2000) have reported

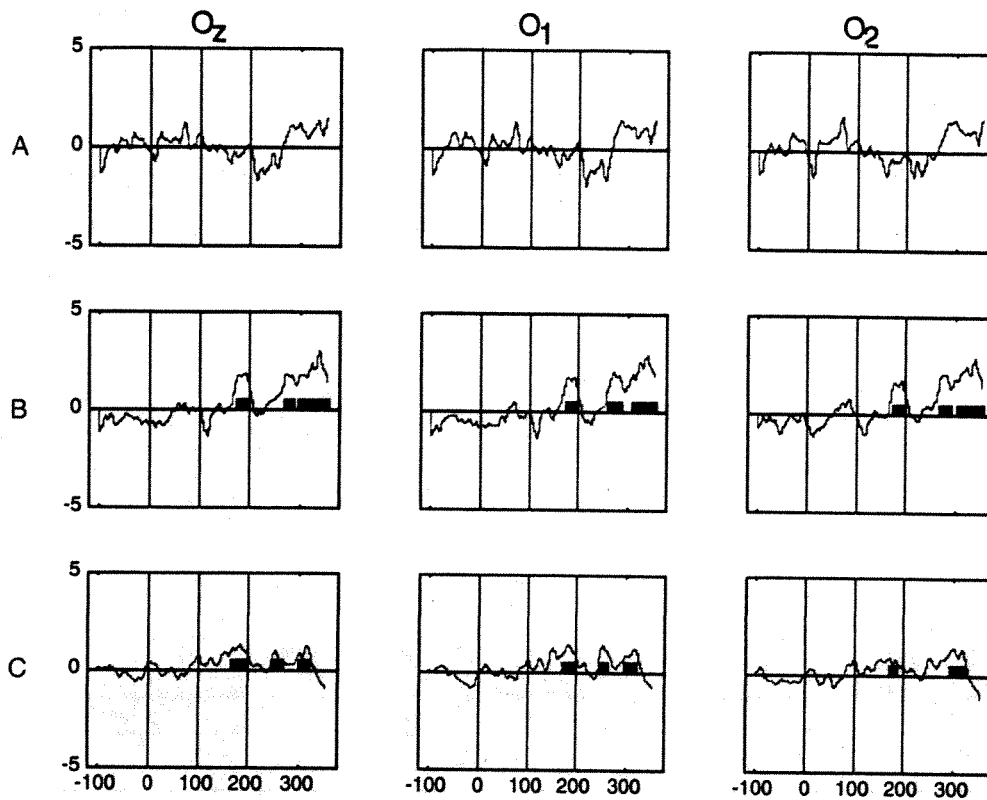


FIGURE 2.2 Auditory-visual interactions reflected in the ERP difference waves. Each row in this figure corresponds to a type of difference waves, and each column corresponds to one electrode. The horizontal and vertical axes denote time in milliseconds with respect to the onset of the (first) flash, and brain potential in μV , respectively. The gray lines represent the mean amplitudes across participants, and the black blocks denote the time intervals in which the amplitudes are significantly different from zero ($P < 0.05$). (A) The difference waves corresponding to subtraction of unimodal conditions from the bimodal condition ($AV - [A + V]$) in the fovea. (B) The difference waves $AV - [A + V]$ in the periphery. (C) The difference waves corresponding to the subtraction of the double flash condition from the single flash condition, both in the periphery.

that activation of the human visual area V5 is enhanced in the presence of accompanying tactile stimulation. Sams et al. (1991) have reported that lipreading syllables that are inconsistent with the auditory syllables (as in McGurk's effect) modifies activity in human auditory cortex. Calvert et al. (1997) have shown that silent lipreading (purely visual) leads to activity in auditory cortical areas BA 41/42. Also, after comparing auditory-visual (bimodal) speech perception with auditory or visual (unimodal) speech perception, they reported enhancement of visual area V5 in the bimodal condition (Calvert et al., 1999). Amedi, Malach, Hendler, Peled, and Zohary (2001) have reported activity in a visual object-related region, the lateral occipital complex, during haptic object recognition.

Interestingly, recent anatomical studies suggest a cortical pathway that may underlie the early cross-modal modulations in visual cortical areas indicated in the ERP studies mentioned above. Very similar findings were reported by two independent laboratories that conducted anatomical studies of projections to

area V1 in monkey (Falchier, Clavagnier, Barone, & Kennedy, 2002; Rockland & Ojima, 2001). One group used anterograde tracers and reported direct projections from auditory parabelt regions to peripheral V1 and V2 (Rockland & Ojima, 2001). In the other study (Falchier et al., 2002), the investigators used retrograde tracers injected separately in foveal and peripheral regions of V1 and found extensive projections from the primary auditory cortex and the caudal parabelt to peripheral V1, in contrast to very sparse projections to foveal V1. They also reported projections from multimodal area STP to peripheral V1. The projections from the auditory cortex and STP to peripheral V1 appeared to constitute a significant proportion of the total projections to V1 (respectively 8% and 41% of that from the visual movement complex to V1). Intriguingly, the difference between the projections to the peripheral and foveal regions reported in these studies are highly consistent with the differential effects between the fovea and periphery that we have observed in our psychophysical and ERP studies. If there are

extensive projections from auditory areas (and to a lesser extent from multisensory areas) to V1 and V2 in the periphery but not in the fovea, then it is not surprising that both the illusory flash effect and the illusory motion effect are strong only in the periphery,¹ and that ERP results suggest a modulation of the activity in visual areas by sound only in the periphery and not in the fovea.

Summary

Vision may be the most important modality in the perceptual world of humans. Nonetheless, visual perception is not exempt from cross-modal influences. Although the effects of sound on vision in temporal tasks² have been documented for a long time, the discovery of cross-modal influences on vision during nontemporal tasks is rather new. A recent study has revealed that vision can be radically altered by sound in a nontemporal task, even when there is no ambiguity in the visual stimulus.

Studies investigating the brain areas involved in multisensory integration have indicated that the activity in areas traditionally considered to be modality-specific can be modulated by cross-modal signals. Again, the visual cortex has not proved an exception to this rule, having been shown to be affected by tactile and auditory stimulation. The majority of the strong cross-modal effects on visual perception occur only or much more strongly when the visual stimulus is in the peripheral visual field. The recent primate neuroanatomical studies reporting direct projections from auditory and multisensory areas to the peripheral representations of early visual areas are consistent with these findings.

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¹The results of various controls and observations reject the possible role of alternative factors such as eye movement or pupillary constriction that may affect perception more strongly in the periphery than in the fovea. For example, the illusory flash effect is stronger with shorter flash durations, persists with very large disk size, and degrades with a decrease in disk contrast (Shams et al., 2002). In the illusory motion effect, no eye movement was detected by EOG, the illusory and nonillusory trials had indistinct EOGs, and the effect persisted even with large disk size.

²Such as judging the duration of a signal, or the temporal order of two signals.

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