Sensory modalities are not separate modalities: plasticity and interactions

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Historically, perception has been viewed as a modular function, with the different sensory modalities operating independently of each other. Recent behavioral and brain imaging studies challenge this view, by suggesting that cross-modal interactions are the rule and not the exception in perception, and that the cortical pathways previously thought to be sensory-specific are modulated by signals from other modalities.

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Abbreviations
fMRI functional magnetic resonance imaging
PET positron emission tomography

Introduction

Cross-modal integration is performed on a vast level in the brain and contributes significantly to adaptive behavior in our daily life. Very little is known about how integration is achieved or its underlying neural mechanisms, however, because the overwhelming majority of studies on perception have focused on one sensory modality. Studying perception in an isolated single modality would be justifiable if different modalities processed sensory inputs independently of each other, as separate 'modules'. But are sensory modalities really separate modules? A variety of evidence seems to counter this notion of modularity. In this review, we summarize the evidence for vigorous interaction among sensory modalities.

Plasticity across sensory modalities

Both animal and human studies suggest that sensory modalities in early stages of development are not as inherently distinct and independent as was previously once thought. For example, in a study of cross-modal plasticity Sur *et al.* [1] removed the superior colliculus of both the ferret and the hamster on the day of birth by direct ablation. They also deprived the medial geniculate nucleus or the ventrobasal nucleus from their normal sensory input by sectioning the major input pathways. The retina then invaded these thalamic nuclei, which under ordinary circumstances relay auditory and somatosensory signals to the cortices, respectively. They found that visual responses (i.e. responses triggered by light stimulation on the retina) were elicited from neurons in the auditory or the somatosensory cortex. More recently, Sur and co-workers [2••] reported that these animals interpreted the activation of the rewired auditory cortex as visual sensation, indicating a functional relevance of the rewiring. There is also evidence for a cross-modal postnatal perceptual enhancement by prenatal sensory stimulation. When bobwhite quail chicks were prenatally exposed to an auditory, visual, tactile or vestibular stimuli, their postnatal auditory and visual responsiveness was enhanced, irrespective of the modality of prenatal stimulation [3–6].

Cross-modal plasticity has also been reported in humans that have had sensory deprivation in early life [7–13]. The typical finding in these studies has been that sensory deprivation in one modality starting from an early period of life causes the cortical area that is normally devoted to that modality to be used by some other modality. Early studies reported that visual event-related potentials tend to be enhanced in early onset deaf individuals [7,8].

Auditory-evoked potentials have also been recorded from posterior (occipital) regions in early and late blind subjects [9]. Although suggestive, however, these studies were neither able to identify exactly which part of the brain is responsible for the enhanced activity, nor able to examine functional relevance of the activity.

Studies that use a perceptual task have been more informative in this regard. For example, Uhl *et al.* [10] have provided evidence for posterior DC potentials in blind subjects engaging in a tactile reading task. Similarly, a positron emission tomography study (PET) by Sadato *et al.* [11] indicated the activation of primary and secondary visual cortical areas induced by Braille reading in early blind subjects, but the deactivation of the same areas relative to the rest condition induced by Braille reading in sighted subjects [11]. Simple tactile stimuli that did not require discrimination produced no activation of visual areas in either group.

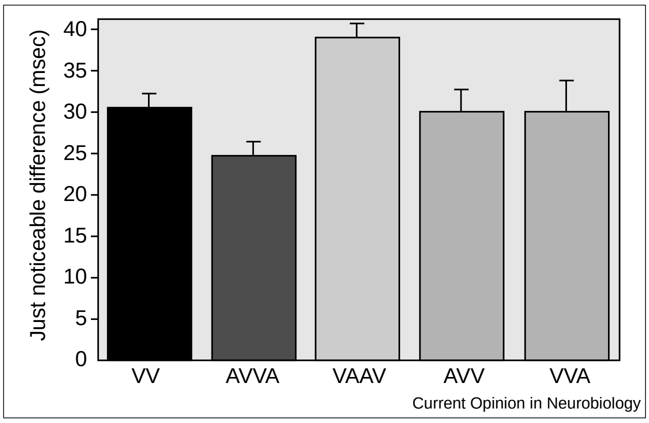
Furthermore, the same researchers applied a train of pulses of transcranial magnetic stimulation to the occipital region of blind subjects engaged in the Braille reading task, and showed that indeed it degraded performance but selective to this task only [12].

Taken together, these animal and human studies indicate a surprising degree of neural plasticity in early stages of life, and clearly argue against the most stringent version of brain segregation and modularity of sensory modalities.

Interaction across modalities

In the phenomenological and psychophysical literature, a wealth of literature on mature perceptual systems indicates

Figure 1



Visual temporal resolution modulated by sounds. Temporal resolution is often expressed in terms of just noticeable differences (JNDs), the smallest temporal gap between two signals at which the two signals are not perceptually fused. JNDs are plotted for conditions of a vision only baseline (V-V), a preceding sound and a following sound (A-V-V-A), two sounds inserted between the two visual signals (V-A-A-V), one sound preceding the two visual signals (A-V-V), and one sound following the two visual signals (V-V-A). During the task, two LEDs were switched on with asynchrony varying from –60 to +60 ms, and the subject had to judge which LED was first. The sounds were always presented through a single speaker located between the two LEDs. The JND is smaller (thus, the visual temporal resolution is better) in the A-V-V-A condition, and larger (worse) in the V-A-A-V condition. The results of the last two conditions, particularly that of the A-V-V condition, indicate that the modulation effect is not due to general warning or arousal effects [22].

that there is vigorous interaction and integration among the sensory modalities — a far greater interaction than what is expected from a 'naive modularity' point of view. One of the most intriguing examples of cross-modal interaction is synesthesia, in which an involuntary conscious sensation (such as color) is induced by a stimulus in another modality (such as sound). Synesthesia can occur in normal, healthy populations, in brain-damaged or sensory-deafferented patients, or in people who are addicted to hallucinogenic drugs [14••].

Vision alters other modalities

In normal people, the effects of vigorous cross-modal integration are made apparent under cleverly designed artificial conditions. The McGurk effect exemplifies such a condition [15]. The McGurk effect is a perceptual phenomenon in which vision alters speech perception (e.g., the sound 'ba' tends to be perceived as 'da' when it is coupled with a visual lip movement associated with 'ga' [15]).

The spatial location of a sound source can also be drastically influenced by visual stimulation. This effect is known as the 'ventriloquist effect' [16], and is experienced frequently in daily life when watching television or movies in which the voices are perceived to originate from the actors on the screen, despite a potentially large spatial discrepancy between the two.

It has been shown that tactile location, such as location of a finger pointing, can also be 'captured' by visual location [17]. All these effects emphasize the strong effect of visual signals on the other modalities, consistent with the commonsense notion that human is primarily a vision-dominated animal.

Sound alters the temporal aspects of vision

Although the best-known cross-modal effects are those of vision influencing other modalities, visual perception can also be altered by other modalities. All the earlier reports of alteration of visual perception by other modalities have been in the temporal domain. For example, the perceived duration [18] or rate [19–21] of a visual stimulus has been shown to be influenced by accompanying sound signals. More recently, Scheier *et al.* [22] have shown that visual temporal resolution can be either improved or degraded by sounds, depending on the temporal relationship. They showed that when two lights are turned on with a small temporal delay (in the –60 to +60 ms range), the accuracy of temporal order judgment is better when a sound precedes and another follows the visual stimuli (the audio-visual-visual-audio [A-V-V-A] time order). In contrast, the subjects' performance becomes worse when two sounds are inserted between the two visual stimuli (V-A-A-V time order), as illustrated in Figure 1.

Sound alters other aspects of vision

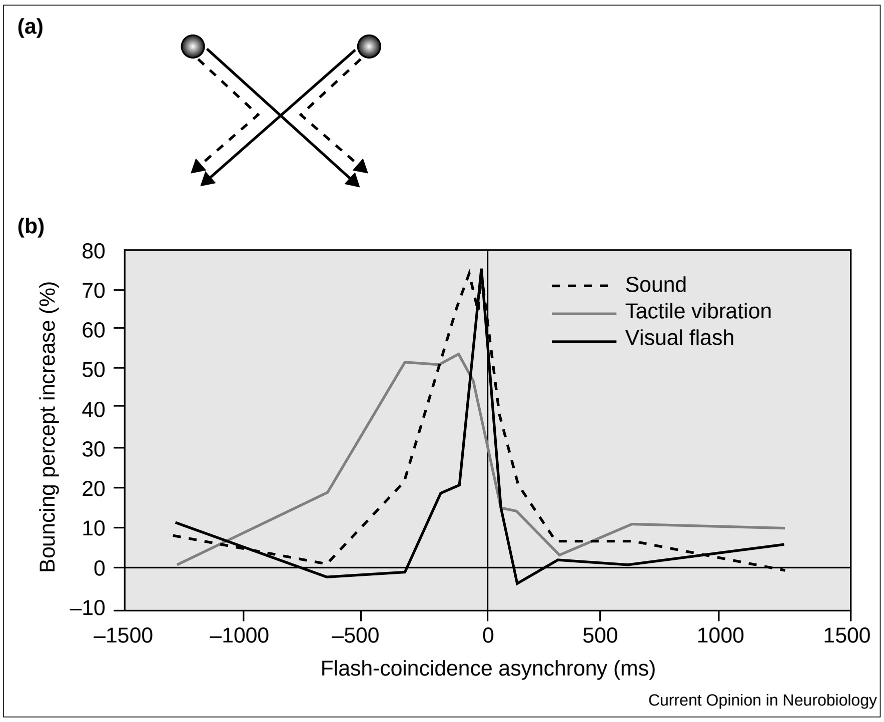
The great body of behavioral findings on cross-modal interactions has been accounted for in a 'modality appropriateness' hypothesis [23]. This hypothesis postulates that the modality that is most appropriate or reliable with respect to a given task is the modality that dominates the perception in the context of that task. Vision has a higher spatial resolution, hence its dominance in spatial tasks (e.g. the ventriloquist effect and visual capture), whereas audition has a higher temporal resolution, hence its dominance in temporal tasks.

Alteration of vision by sound, however, turns out to be not limited to temporal aspects. The perceived intensity of a visual stimulus has been shown recently to be enhanced in presence of sound [24]. Moreover, the quality or structure of visual perception itself can be altered by auditory stimuli, according to the latest psychophysical studies.

Sekuler *et al.* [25] have shown that the presence of a sound can also alter the perceptual interpretation of an ambiguous visual motion event. Two identical visual targets moving across each other can be perceived either to bounce off or to stream through each other, as their trajectories are nearly identical (Figure 2a). Nonetheless, most observers report a perception of streaming, not bouncing motion.

If a brief sound is added at the moment that the targets coincide visually, however, visual perception is strongly biased in favor of bouncing motion [25]. The sound has to have a sharp onset to induce this effect. The ecological origins of

Figure 2



Cross-modal modulation of visual motion perception. **(a)** The ambiguous motion display, in which two objects move across each other. Observers typically perceive an object as streaming with an X-shaped trajectory when there is no accompanying sound or an accompanying sound that is not synchronous with the visual crossing. When there is a sound (or a flash or a tactile vibration) synchronized with visual coincidence, however, the perceptual dominance reverses and most observers now see the objects as bouncing against each other. **(b)** Temporal tuning curves of the bounce-inducing effects of a synchronous transient signal in auditory, visual or tactile modality. The percentage increase in the perception of bounce is plotted against asynchrony between the transient signal in each modality and the visual coincidence. Thus, qualitatively the same effect can be obtained as long as there is a transient sensory stimulus that is approximately synchronized with the critical visual event, regardless of the modality in which the transient stimulus is given.

this phenomenon are intuitively obvious: it should be related to the fact that the majority of collision events in the natural environment yield synchronized cross-modal signals.

Other studies on this phenomenon have revealed some unexpected properties. First, a transient sensory stimulus biases visual perception toward bouncing irrespective of its modality; for example, a brief visual flash or a brief tactile vibration on an observer's finger also induces bouncing perception [26,27]. The stimulus, however, has to be synchronized with the visual coincidence of two objects (the effective time window was found to be in the range of –300 to +200 ms, –600 to +100 ms and –100 to +100 ms for auditory, tactile and vision stimuli, respectively; see Figure 2b).

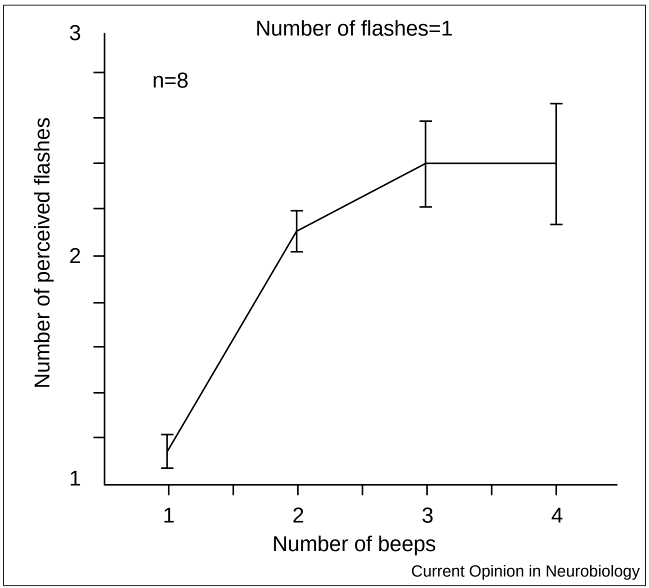
Thus, the same effect can be obtained qualitatively as long as there is a transient sensory stimulus that is approximately synchronized with the critical visual event, regardless of the modality in which the transient stimulus occurs. This type of perceptual modulation may serve as a collision detector at a functional level, yet there is a series of evidence indicating that it is implemented through a more generic and efficient mechanism of spatial attention [26–28]. Developmentally, at five months of age, human infants show behavioral evidence for the adult-like perceptual change caused by a synchronous sound [29–30]; this age is roughly the maturation onset of spatial attention mechanisms.

A recent study has shown that the alteration of vision by sound is not limited to the situations of ambiguity in the visual stimulus. The 'illusory flash effect' reports that an illusion in which a radical change in the phenomenological quality of perceiving a non-ambiguous visual stimulus is induced by sound [31•]. When a single brief visual flash is accompanied by multiple auditory beeps, the single flash is perceived as multiple flashes (see Figure 3). Control conditions, 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 some cognitive bias (caused by sound).

The illusory double flash is perceptually very similar to the physical double flash. Furthermore, the illusion is very robust to the observer's knowledge about the physical stimulus, and to variations in stimuli parameters. The temporal tuning of this effect was also measured by varying the relative timing of visual and auditory stimuli. The illusory flashing effect decreased at separations greater than 70 ms; however, illusory flashing occurred as long as the beeps and flash were within about 100 ms — consistent with the integration time of polysensory neurons in the brain [32,33]·

The alteration of vision by sound in this experiment was found to be asymmetrical: alteration occurred strongly only when a single flash was coupled with multiple beeps, and not when multiple flashes were paired with a single beep. In other words, strong alteration of vision by sound occurs only when sound is more discontinuous and structured than the visual stimulus. A similar phenomenon seems to be at work in a study that investigated the effect of vision on hearing [34]. Saldaña and Rosenblum's [34] data suggest that only the discontinuous visual stimulus has a strong effect on the perception of the sound.

Figure 3



Sound-induced illusory flashing. The number of flashes reported by the observers is plotted against the number of beeps that accompanied the visual stimulus, in trials where the visual stimulus comprises only one flash. Observers report seeing two or more flashes, when a single flash is accompanied by two or more beeps.

Cross-modal interactions depend on stimuli structure

The direction of cross-modal interactions has been thought to be determined by the relative appropriateness of the modalities involved in the task, as mentioned above. The evidence discussed above, however, seems to indicate that the direction of cross-modal interactions depends, at least in part, on the structure of the stimuli; that is, the modality that carries a signal which is more discontinuous (and hence more salient) becomes the influential or modulating modality. Such a hypothesis would also account for the findings of streaming/bouncing motion studies discussed above, in which the transient, hence more discontinuous and structured, stimulus alters the perception of a continuous visual stimuli regardless of its modality (auditory, tactile or visual) [25–30].

Neural mechanisms

At what point along the perceptual processing pathway do these cross-modal interactions take place? Recent data from brain imaging studies suggest that they occur at brain sites that used to be considered as modality-specific. For example, Calvert *et al.* [35] carried out a functional magnetic resonance imaging (fMRI) study that showed that the primary auditory cortex is activated when a talking face is viewed in the absence of sound. The activation was observed specifically in speech or pseudo-speech type of lip movements, but not in other type of lip movements.

The same research group has also reported that activity in visual (V5) and auditory (BA 41/42) cortices after exposure to bimodal (audio-visual) speech is enhanced relative to activity after a unimodal stimulus [36•]. The enhancement was found to be contingent on congruency between the audio and visual signals. But as these studies deal only with speech perception, would their findings generalize to other types of stimuli?

Two very recent studies may have more general implications. An fMRI study has shown that tactile stimulation of a hand enhances activity in the visual cortex when the touched hand is on the same side as the visual stimulus [37••]. Likewise, an event-related potential (ERP) study also suggests that activity in the visual cortical areas is modulated by sound [38]. The modulation was found as early as 100 ms after the visual stimulus onset. This study used a brief flash and a brief beep as visual and auditory stimuli.

In contrast to speech stimuli, which inherently hinge on some higher level matching process (such as congruency detection), the stimuli used in the last two studies are very simple, and thus the results may have more general implications. In particular, the results of the ERP study, unlike any of the other findings discussed above, may have very general implications because they do not require congruency between the stimuli in the two modalities and do not seem to involve spatial attention mechanisms.

Together, the results of the studies summarized in this review challenge the common belief that 'modality-specific' cortices function in isolation from other modalities.

Conclusions

We have discussed a wide variety of evidence against the notion of strict modularity of sensory modalities. Both animal studies and human-deprivation cases provide evidence for a surprising degree of cross-modal plasticity in cortical processing. Psychophysical data indicate that interaction between modalities is the rule as opposed to the exception in brain function, and brain imaging and recording studies provide evidence against modularity and for interaction in areas traditionally thought to be unimodal.

Motivated by some of the recent psychophysical findings, we put forth a new hypothesis for multisensory interactions. We propose that the transient/discontinuous signals possess a special status in determining the direction of cross-modal interactions, with the transient stimulus strongly influencing the multimodal perception, regardless of the modality in which it occurs.

Acknowledgements

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

• of special interest
•• of outstanding interest

1. Sur M, Pallas SL, Roe AW: **Cross-modal plasticity in cortical development: differentiation and specification of sensory neocortex.** *Trends Neurosci* 1990, 13:227-233.

2. von Melchner L, Pallas SL, Sur M: Visual behaviour mediated by
•• retinal projections directed to the auditory pathway. *Nature* 2000, 404:871-876.

The authors investigate whether activity in the auditory cortex, which has been rewired to receive input normally projected to the visual cortex, is interpreted by the animal as auditory or visual sensation. They find that the activation of rewired auditory cortex is interpreted as visual stimulation, which suggests that the modality of a neocortical area is intrinsic and can be significantly influenced by its extrinsic input.

3. Sleigh MJ, Lickliter R: Augmented prenatal auditory stimulation alters postnatal perception, arousal, and survival in bobwhite quail chicks. *Dev Psychobiol* 1997, 30:201-212.

4. Sleigh MJ, Lickliter R: Timing of presentation of prenatal auditory stimulation alters auditory and visual responsiveness in bobwhite quail chicks (***Colinus virginianus***). *J Comp Psychol* 1998, 112:153-160.

5. Carlsen R, Lickliter R: Augmented prenatal tactile and vestibular stimulation alters postnatal auditory and visual responsiveness in bobwhite quail chicks. *Dev Psychobiol* 1999, 35:215-225.

6. Casey MB, Lickliter R: Prenatal visual experience influences the development of turning bias in bobwhite quail chicks (***Colinus virginianus***). *Dev Psychobiol* 1998, 32:327-338.

7. Neville HJ, Schmidt A, Kutas M: Altered visual-evoked potentials in congenitally deaf adults. *Brain Res* 1983, 266:127-132.

8. Neville HJ, Lawson D: Attention to central and peripheral visual space in a movement detection task: an event-related potential and behavioral study. II. Congenitally deaf adults. *Brain Res* 1987, 405:268-283.

9. Kujala T, Alho K, Huotilainen M, Ilmoniemi R J, Lehtokoski A, Leinonen A, Rinne T, Salonen O, Sinkkonen J, Standertskjold-Nordenstam CG, Naatanen R: Electrophysiological evidence for cross-modal plasticity in humans with early- and late-onset blindness. *Psychophysiology* 1997, 34:213-216.

10. Uhl F, Franzen P, Lindinger G, Lang W, Deecke L: On the functionality of the visually deprived occipital cortex in early blind persons. *Neurosci Lett* 1991, 124:256-259.

11. Sadato N, Pascual-Leone A, Grafman J, Ibanez V, Deiber MP, Dold G, Hallett M: Activation of the primary visual cortex by Braille reading in blind subjects. *Nature* 1996, 380:526-528.

12. Cohen LG, Celnik P, Pascual-Leone A, Corwell B, Falz L, Dambrosia J, Honda M, Sadato N, Gerloff C, Catala MD, Hallett M: Functional relevance of cross-modal plasticity in blind humans. *Nature* 1997, 389:180-183.

13. Hamilton R, Pascual-Leone A: Cortical plasticity associated with Braille learning. *Trends Cogn Sci* 1998, 2:168-174.

14. Grossenbacher, PG, Lovelace, CT: Mechanisms of synesthesia:
•• cognitive and physiological constraints. *Trends Cogn Sci* 2001, 5:36-41.

The authors review recent findings on synesthesia obtained from cognitive psychology, brain imaging and psychophysiology. Motivated by current knowledge, which is mainly of a phenomenological nature, they put forth a hypothesis about the brain circuitry that may underlie synesthesia. The hypothesis is inevitably speculative, however, it provides a framework for further inquiry and investigation of the underlying brain mechanisms that are currently poorly understood.

15. McGurk H, MacDonald JW: Hearing lips and seeing voices. *Nature* 1976, 264:746-748.

16. Howard IP, Templeton WB: *Human Spatial Orientation*. London: Wiley; 1966.

17. Rock I, Victor J: Vision and touch: an experimentally created conflict between the two senses. *Science* 1964, 143:594-596.

18. Walker JT, Scott KJ: Auditory-visual conflicts in the perceived duration of lights, tones, and gaps. *J Exp Psychol Hum Percept Perform* 1981, 7:1327-1339.

19. Gebhard JW, Mowbray GH: On discriminating the rate of visual flicker and auditory flutter. *Am J Psychol* 1959, 72:521-528.

20. Shipley T: Auditory flutter-driving of visual flicker. *Science* 1964, 145:1328-1330.

21. Welch RB, Duttenhurt LD, Warren DH: Contributions of audition and vision to temporal rate perception. *Percept Psychophys* 1986, 39:294-300.

22. Scheier CR, Nijwahan R, Shimojo S: Sound alters visual temporal resolution. *Invest Ophthalmol Vis Sci* 1999, 40:4169.

23. Welch RB, Warren DH: Immediate perceptual response to intersensory discrepancy. *Psychol Bull* 1980, 88:638-667.

24. Stein BE, London N, Wilkinson LK, Price DD: Enhancement of perceived visual intensity by auditory stimuli: A psychophysical analysis. *J Cogn Neurosci* 1996, 8:497-506.

25. Sekuler R, Sekuler AB, Lau R: Sound alters visual motion perception. *Nature* 1997, 385:308.

26. Watanabe K, Shimojo S: Attentional modulation in perception of visual motion events. *Perception* 1998, 27:1041-1054.

27. Watanabe K: Crossmodal interaction in humans. [PhD Thesis]. Pasadena: California Institute of Technology; 2001

28. Watanabe, K, and Shimojo S: When sound affects vision: effects of auditory grouping on visual motion perception. *Psychol Sci* 2001, 12:109-116.

29. Scheier C, Lewkowicz D, Shimojo, S: Perceptual reorganization of an ambiguous motion display by auditory stimulation in human infants: evidence from eye and head movements. *Invest Ophthalmol Vis Sci* 2000, 41:S327.

30. Shimojo S, Watanabe K, Scheier C: The resolution of ambiguous motion: Attentional modulation and development. In *Visual Attention and Cortical Circuits*. Edited by Braun J, Koch C, Davis J. Cambridge, Massachusetts: MIT Press; 2001:243-264.

31. Shams L, Kamitani Y, Shimojo S: What you see is what you hear.
• *Nature* 2000, 408:788.

This paper presents a visual illusion that is induced by sound. This constitutes the first report of a change in the phenomenological quality of the visual perception caused by another modality even when the visual stimulus is not ambiguous. One of the implications of this finding is that, like other modalities, vision is also malleable by other modalities.

32. Meredith MA, Nemitz JW, Stein BE: Determinants of multisensory integration in superior colliculus neurons. I. Temporal factors. *J Neurosci* 1987, 10:3215-3229.

33. Wallace MT, Stein BE: Cross-modal synthesis in the mid-brain depends on input from association cortex. *J Neurophysiol* 1994, 71:429-432.

34. Saldaña HM, Rosenblum LD: Visual influences on auditory pluck and bow judgments. *Percept Psychophys* 1993, 54:406-416.

35. Calvert GA, Bullmore ET, Brammer MJ, Campbell R, Williams SC, McGuire PK, Woodruff OW, Iversen SD, David AS: Activation of auditory cortex during silent lipreading. *Science* 1997, 276:593-596.

36. Calvert GA, Brammer MJ, Bullmore ET, Campbell R, Iversen SD,
• David AS: Response amplification in sensory-specific cortices during crossmodal binding. *NeuroReport* 1999, 10:2619-2623.

Using fMRI, the authors find that the activity of auditory and visual cortices arising from exposure to audio-visual speech is enhanced relative to that arising from unimodal speech. Because the enhancement is specific to semantically congruent bimodal stimuli, the authors attribute the enhancement to backprojections to modality-specific areas from areas that are involved in cross-modal binding.

37. Macaluso E, Frith CD, Driver J: Modulation of human visual cortex
•• by crossmodal spatial attention. *Science* 2000, 289:1206-1208.

The authors report an enhancement, measured by fMRI, in the activity of visual cortex owing to simultaneous tactile stimulation. On the basis of the connectivity of brain areas, they argue that this enhancement is mediated through backprojections from multimodal cortical areas.

38. Shams L, Kamitani Y, Shimojo S: Sound modulates visual evoked potentials in humans. *J Vis* 2001, in press.