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Multisensory Integration: How Visual Experience Shapes Spatial Perception

Dispatch

Martin Eimer

The localisation of auditory and tactile events is strongly affected by visual information, reflecting the dominant role of vision in spatial perception. New research suggests that early visual experience is critical for the establishment of such multisensory links.

It is commonly believed that vision, hearing and touch are entirely separate 'perceptual modules', each operating independently to provide us with unique information about the external world. Recent studies, however, have revealed that our perceptual experience is in fact shaped by a multitude of complex interactions between sensory modalities. A number of powerful multisensory illusions demonstrate that the senses are inextricably linked, and that our perception of visual, auditory or tactile events can be altered dramatically by information from other senses. When a sound is accompanied by a visual stimulus at another location, people tend to perceive this sound incorrectly at the same position as the visual stimulus — the ventriloquism effect [1]. When two objects are lifted that differ visibly in size, but are equal in weight, the larger object is felt to be heavier — the size–weight illusion [2]. When people see a life-sized rubber model of their hand being touched at the same time as their own hand, which is hidden from view, they experience the touch on the rubber hand, and often report that the rubber hand feels as if it was their own [3].

In these cases, auditory and tactile perception are substantially altered by simultaneously available visual information. As a general rule, our sensations tend to be dominated by the modality that provides the most detailed and reliable information about the external world. Because vision provides highly accurate and detailed spatial information about three-dimensional properties of external objects, it is used to guide spatial judgements in other modalities as well, and can therefore influence (and sometimes distort) our spatial perception of auditory and tactile events.

Recent research has begun to uncover the neural basis of such interactions between sensory modalities in spatial perception. Neurons responding to multimodal stimuli have been found in numerous brain areas, including the superior colliculus and parietal areas [4]. These multisensory neurons typically have spatially overlapping receptive fields, which means that they are activated maximally in response to simultaneous visual, auditory and tactile events at the same external location.

If vision provides the major source of spatial information, and therefore dominates spatial perception in other sensory modalities, the important question arises of how auditory and tactile perception develop and function when visual information is completely absent from birth. As a result of their lack of any visual experience, congenitally blind people have to rely exclusively on spatial information delivered by the remaining intact senses, such as hearing and touch. Thus, it seems likely that spatial perception in congenitally blind and in sighted people will develop along different trajectories, and will operate in a qualitatively different fashion in adulthood. Results from a study published recently in *Current Biology* [5] suggest that this is in fact the case, and that early visual experience is essential for the normal development of tactile spatial perception.

Until recently, there has been little direct evidence for the existence of qualitative differences in perceptual processing between sighted and blind people. Numerous studies (see [6] for review) have investigated whether and how the sighted and the congenitally blind differ with respect to their perceptual spatial skills. If the spatial information provided by touch and hearing is inferior to the information that can be derived from visual experience, one might expect that auditory and tactile spatial perception is generally impaired in congenital blindness. Interestingly, this does not seem to be the case.

Sighted and blind people actually have very similar absolute sensory thresholds for detecting tactile stimuli, and tactile 'two-point thresholds' — the minimal distance between two tactile stimuli required to discriminate them — are even slightly reduced for congenitally blind Braille readers [6]. There is also no clear evidence that auditory localisation skills are impaired in the congenitally blind. For example, Röder *et al.* [7] asked congenitally blind and sighted participants to localise tones presented either centrally or on the right side. Localisation performance did not differ between the blind and sighted group for central sounds, but blind people were in fact better able to locate peripheral sounds.

How can the observation that congenitally blind people perform equally well or even better than sighted people in tactile and auditory spatial-perceptual tasks be reconciled with the hypothesis that visual information is essential to guide spatial judgements in hearing and touch? One explanation is that the loss of one sensory modality results in an increased use of the remaining intact sensory systems. This will improve their efficiency, and can also trigger large-scale cortical reorganisation processes. For example, Braille reading provides a large amount of tactile practice, and such practice can result in an expansion of representations of the reading finger in primary somatosensory cortex [8]. In addition, neurons that would normally respond to visual stimulation can be recruited by other sensory modalities when visual input is entirely absent. In fact, predominantly visual brain areas appear to be activated when blind participants read Braille [9]. Finally, the input of auditory and tactile signals to multimodal brain

School of Psychology, Birkbeck College, University of London, Malet Street, London WC1E 7HX, UK.
E-mail: m.eimer@bbk.ac.uk

regions involved in spatial perception and attention [4] will increase when there is no competing visual input. A recent functional imaging study [10] has shown that multimodal parietal brain regions are activated more strongly in congenitally blind as compared to sighted participants during an auditory localisation task.

The overall picture emerging from these recent studies is that, when visual input is permanently absent, complex cortical reorganisation processes take place, which increase the cortical space available for the remaining intact modalities, such as hearing and touch. As a result, spatial perception within these modalities improves, apparently neutralising possible deficits in auditory and tactile spatial processing caused by the lack of visual information. While this implies that there may be quantitative differences between sighted and blind people in their perceptual skills, the question whether there are also qualitative differences has so far remained unanswered. The new results of Röder *et al.* [5] show for the first time that the absence of visual input during early development not only produces quantitative changes, but can also result in important qualitative changes of tactile perception.

Röder *et al.* [5] asked a group of congenitally blind participants, a group of participants who had lost vision later in life, and a sighted control group to judge the temporal order in which two tactile stimuli were delivered to their left and right hands. In different parts of this experiment, hands were either crossed over the body midline or rested in their normal uncrossed position. For sighted people, where vision dominates spatial perception, the localisation of tactile events in external space involves a visually defined spatial reference frame. Crossing the hands induces a conflict between external spatial codes, which define tactile events as left *versus* right in visual space, and somatotopic codes, which specify the anatomical identity of the left versus right hand. This conflict can impair tactile judgements [11] and the attentional selection of tactile events [12,13].

As expected, Röder *et al.* [5] found that temporal order judgements of sighted participants were less accurate with crossed than with uncrossed hands, as a result of the conflict between external and somatotopic spatial codes. In marked contrast, congenitally blind participants were completely unaffected by this hand posture manipulation. This group performed well — and in fact better than their sighted counterparts — regardless of whether their hands were uncrossed or crossed. This result provides new evidence for the existence of qualitative differences in tactile perception between the sighted and the congenitally blind. Whereas sighted people always use a visually defined reference frame to localise tactile events in external space, and thus are impaired in the presence of conflicting external and somatotopic spatial information, congenitally blind people do not use external spatial coordinates by default when localising tactile stimuli, and therefore remain unaffected by this conflict.

Remarkably, Röder *et al.* [5] also found that the performance of participants who had lost their sight later in life differed dramatically from that of the congenitally blind group. As for the sighted group, temporal order judgements of late blind participants were substantially impaired with crossed hands. In fact, the performance of late blind and sighted participants was virtually indistinguishable. This unexpected finding suggests that early visual experience plays a crucial role in the development of tactile perception. Participants in the late blind group had lost vision between the age of 12 and 23, and therefore have had sufficient visual experience to acquire a visually determined external spatial reference frame. But all of them had been blind for at least five years (one participant for over 40 years). The fact that temporal order judgements of late blind and sighted participants were equally affected by crossing the hands indicates that, once a visually defined external frame of reference is acquired, it will continue to be used in the localisation of tactile events, even though visual information may no longer be available.

Converging evidence for this new hypothesis that the development of multisensory interactions between vision and other sensory modalities depends on early perceptual experience comes from animal studies. Juvenile barn owls exposed to horizontal displacements of visual space induced by prismatic spectacles adapt to these changes with adjustments of auditory spatial maps [14], suggesting that representations of auditory space are dominated by visual experience. In adult owls, similar recalibrations of auditory spatial representations were only observed for individuals which had been exposed to prismatic visual displacements as juveniles, but not for individuals without this early experience.

Along similar lines, it has been shown that multisensory neurons, although already present in newborn monkeys, acquire their spatially specific multimodal properties in an experience-dependent fashion during the first few months of life [15]. Together with the results of Röder *et al*. [5], these findings suggest that early visual experience is necessary to establish functional connections between vision and other sensory modalities. Once in place, these connections will remain and continue to affect spatial perception in audition and touch, even when vision is subsequently lost.

While these recent studies have demonstrated that early visual experience plays an important role in the development of multisensory interactions, many questions remain to be answered. In the future, it will be important to find out whether there are specific critical periods in the course of perceptual development, during which visual experience is instrumental in establishing stable multisensory links between vision and other modalities, and where the absence of visual input will result in qualitatively different ways of processing auditory and tactile information.

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