

Hearing visual motion in depth

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Auditory spatial perception is strongly affected by visual cues. For example, if auditory and visual stimuli are presented synchronously but from different positions, the auditory event is mislocated towards the locus of the visual stimulus—the ventriloquism effect^{1,2}. This ‘visual capture’ also occurs in motion perception in which a static auditory stimulus appears to move with the visual moving object^{3,4}. We investigated how the human perceptual system coordinates complementary inputs from auditory and visual senses. Here we show that an auditory aftereffect occurs from adaptation to visual motion in depth. After a few minutes of viewing a square moving in depth, a steady sound was perceived as changing loudness in the opposite direction. Adaptation to a combination of auditory and visual stimuli changing in a compatible direction increased the aftereffect and the effect of visual adaptation almost disappeared when the directions were opposite. On the other hand, listening to a sound changing in intensity did not affect the visual changing-size aftereffect. The results provide psychophysical evidence that, for processing of motion in depth, the auditory system responds to both auditory changing intensity and visual motion in depth.

The visual-motion aftereffect is a well documented phenomenon in which, after a prolonged viewing of a moving visual pattern in a particular direction, a stationary pattern appears to move in the opposite direction^{5,6}. Similar auditory aftereffects have been reported for such stimuli as horizontal motion^{7,8}, spectral motion⁹, intensity change^{10,11} and frequency change¹². It has been implicitly

assumed that motion aftereffects reflect fairly low-level neural processing and that they do not occur across sensory modalities, that is, adaptation in one modality produces aftereffects in the same modality only. Here we combine two aftereffects in different sensory modalities: an auditory changing-loudness aftereffect^{10,11} and a visual changing-size aftereffect¹³.

In our first experiment, we investigated whether adaptation to visual size-changing affects the auditory aftereffect. The image of an object changing in size produces a strong sensation that the object is moving in depth¹⁴. The visual adapting stimulus of 2 s duration was a white square either expanding or contracting between 0 and 2 deg at $\pm 1 \text{ deg s}^{-1}$. It appeared to move towards the observers from far away or vice versa. Sinusoids of 1,000 Hz were used as auditory stimuli for adaptation and test. The auditory adapting stimulus was either increased or decreased in level between 20 and 60 dB sound pressure level at $\pm 20 \text{ dB s}^{-1}$. The duration was also 2 s. Thus, the auditory and visual adapting stimuli were perfectly synchronized. The duration of the test tone was 1.5 s and the sound pressure level of the onset was set at 40 dB. We measured the magnitude of the auditory aftereffect after adaptation to each of the eight conditions, two adapting directions (increasing or decreasing) $\times$ four combinations of auditory and visual adapting stimuli: (1) auditory stimulus only (A+, A-); (2) auditory and visual stimuli changing in a compatible direction (A+V+, A-V-); (3) auditory and visual stimuli changing in an opposite direction (A+V-, A-V+); and (4) visual stimulus only (V+, V-). In the adapting conditions, one of the combinations of adapting stimuli was presented 60 times, after which only the auditory test stimulus was presented and the observers judged the direction of loudness change, not the direction of motion in depth.

The results (Fig. 1) showed that adaptation to visual size-changing influenced the auditory changing-loudness aftereffect. Ehrenstein and Reinhardt-Rutland¹⁵ found slight shifts in auditory localization after adaptation to visual horizontal motion. However, we found a strong auditory aftereffect after adaptation to visual stimulus alone (V+, V-). After viewing the square changing in size, the subjects perceived a steady test tone as though it changed in loudness in the direction opposite to that of the square's change in

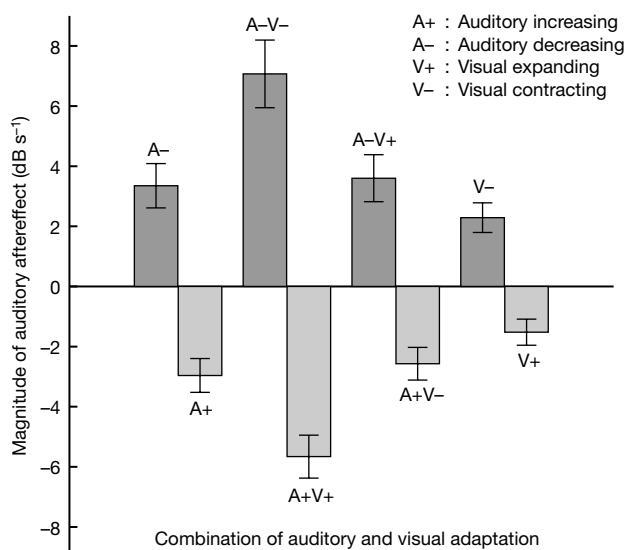


Figure 1 Magnitude of the auditory changing-loudness aftereffect after adaptation to combinations of auditory changing-intensity and visual changing-size stimuli. Averages of the ten subjects are shown. Error bars indicate the standard error of the mean. All of the four combination conditions produced the significant aftereffect ($P < 0.01$). Two-way analysis of variance (ANOVA) (adapting direction $\times$ adapting combination) for absolute value of the magnitude showed a significant main effect of the adapting combination ($F_{3,27} = 15.204$, $P < 0.01$), whereas the main effect of direction is not significant. A posterior pairwise comparison (Tukey's Honestly Significant Difference, HSD) of the adapting combination showed that the aftereffect of the same-direction combination (A+V+, A-V-) was stronger than the other combination conditions ($P < 0.01$).

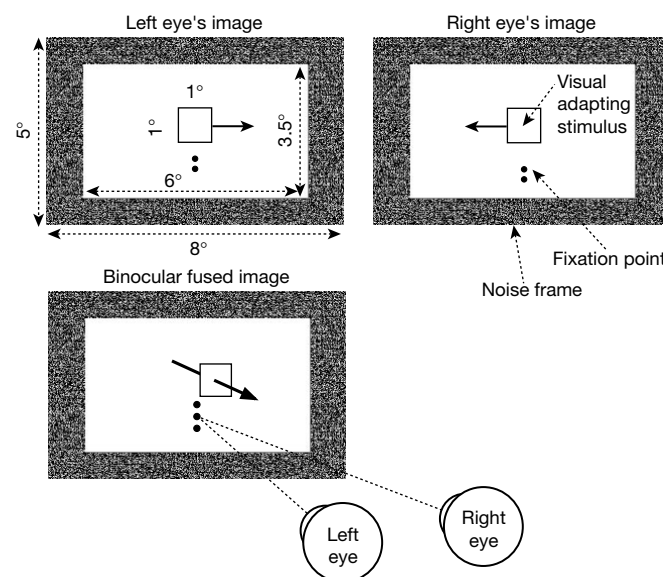


Figure 2 Schematic illustration of approaching visual stimulus. Each pattern for left and right eyes consisted of a white square and a frame of noise pattern surrounding the square. The patterns viewed by the left and right eyes were stationary and identical except for the square moving independently to the centre. When presented stereoscopically, the square appeared to move towards the observers, as shown in the binocular fused image.

size. The aftereffects produced by adaptation to the visual stimulus alone are smaller than those produced by auditory adaptation (A+, A-), although there is no significant difference between these two combinations. When auditory and visual adapting stimuli were combined in a compatible direction (A+V+, A-V-), the magnitude of the aftereffect increased significantly. This exceeds the sum of the two aftereffects in auditory-alone and visual-alone conditions. Almost the same magnitude was obtained in the auditory-alone condition and the opposite-direction condition (A+V-, A-V+), indicating that, when the directions were opposite, the aftereffect resulted from auditory adaptation, with little or no effect from visual adaptation. These properties—cross-modal enhancement for congruent inputs and no effect for incongruent inputs—are consistent with previously reported results in which aftereffects were not used¹⁶.

In our second experiment, we attempted to confirm that just the visual motion-in-depth cue influences the auditory aftereffect. The left and right eyes each viewed a square moving in opposite directions on the flat screen. In the binocular fused image, the square appeared to move in stereoscopic depth either towards or away from the observers (Fig. 2). A fixed-size square changing in retinal disparity between -20 and +20 min at $\pm 10 \text{ min s}^{-1}$ was used as the visual adapting stimulus. This disparity range corresponds to a distance of about 40 cm in the three-dimensional world. The auditory adapting and test stimuli were identical to those in experiment (1). The changing-loudness aftereffect was measured after adaptation to each of the eight adapting conditions. In these results, we still see the same pattern of the visual effect as in experiment (1) (Fig. 3), although the effects of visual adaptation are relatively small. The auditory aftereffect observed after adaptation to visual stimulus only (V+, V-) was statistically significant, and the magnitude of the aftereffect tended to increase when the directions were the same (A+V+, A-V-); moreover, the magnitude obtained in the opposite-direction condition (A+V-, A-V+) was almost the same as that in auditory-alone condition (A+, A-). The visual effect that is smaller than seen with experiment (1) can be attributed to the weak sensation of motion in depth. The disparity

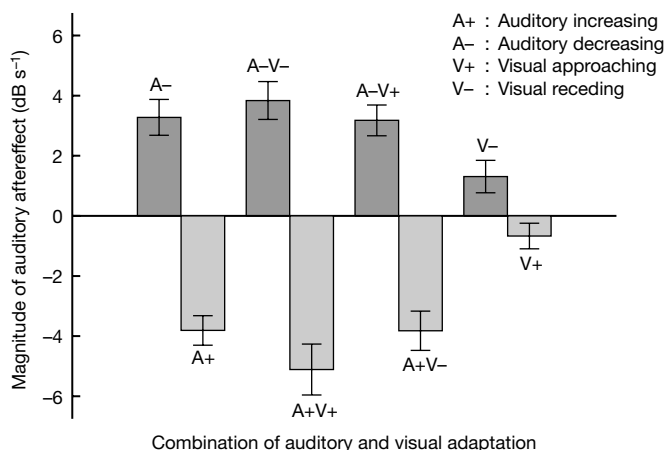


Figure 3 Effect of visual adaptation to changing-disparity on the auditory changing-loudness aftereffect. Averages of the ten subjects are shown. Error bars indicate the standard error of the mean. The aftereffect following adaptation to visual changing disparity alone (V+, V-) was still statistically significant ($P < 0.05$) and the other three combination conditions also produced the significant aftereffect ($P < 0.01$). The absolute value of the magnitude were subjected to two-way ANOVA (adapting direction $\times$ adapting combination). There was a significant main effect of the adapting combination ($F_{3,27} = 17.925$, $P < 0.01$). The aftereffect in the visual alone condition (V+, V-) was weaker than the other combination conditions (Tukey's HSD, $P < 0.01$). The same-direction condition (A+V+, A-V-) increased the aftereffect slightly, although it is not statistically significant.

cue is available only for a relatively short distance and the range of change is limited because the stimulus of a too large disparity is perceived as a double image. Thus, the changing-disparity stimulus should produce a relatively weak impression of motion in depth.

Both visual size- and disparity-changing provide cues for motion in depth and both affected the auditory aftereffect in the same way. Our conclusion is that the visual motion-in-depth cue causes the auditory aftereffect. The auditory system 'senses' sound-source movement in depth from the visual cue of motion in depth, even if there is no sound. It would seem ecologically advantageous for the auditory system to utilize the visual cue. Spatial resolution of the visual system is superior to that of the auditory system. Moreover, it is thought that auditory depth or distance localization, which relies on intensity, reverberation and spectral information¹⁷, is poor compared with horizontal localization in which interaural time and intensity differences can be used. It has been reported that auditory motion perception is more strongly influenced by visual cues in depth than in the horizontal plane⁴.

For spatial events, it is known that visual perception dominates auditory perception¹⁶. In our third experiment, we examined whether the visual changing-size aftereffect¹³ is affected by adaptation to auditory intensity-changing. The changing-size aftereffect is an experience in which, after adaptation to changing size, a subsequently viewed square appears to move in depth in the opposite direction. The test stimulus was a square changed in size from 1 deg $\times$ 1 deg. The auditory and visual adapting stimuli were identical to those in experiment (1). We measured the visual aftereffect after adaptation to each of the eight adapting conditions. There were no aftereffects in auditory-alone conditions (A+, A-) but similar magnitudes of the visual aftereffects were obtained in the other conditions (Fig. 4), suggesting that the auditory adaptation has no effect on the visual changing-size aftereffect. We reconfirm the visual superiority for spatial perception by using the aftereffects.

Most previous auditory-visual interaction studies have examined the visual effect on auditory perception by simultaneous presentation of visual and auditory stimuli. However, by measuring the aftereffect, we found that the presentation of visual stimulus only affects the successive auditory perception. The result suggests that the auditory system, which has been considered to be auditory-

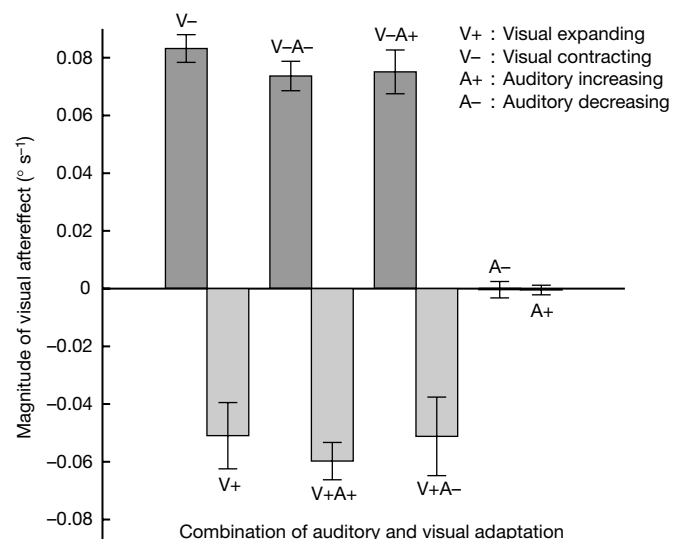


Figure 4 The visual changing-size aftereffect for four combinations in expanding and shrinking directions. Averages of the seven subjects are shown. Error bars indicate the standard error of the mean. Adaptation to auditory changing intensity alone (A+, A-) produced little or no visual aftereffect and the other three combination conditions produced a similar magnitude of the aftereffect.

specific, responds also to visual motion in depth. There are no known direct pathways between auditory and visual cortices, so we suggest that the auditory aftereffect produced by visual adaptation is due to a multimodal process which combines auditory and visual inputs and which subsequently projects back to the auditory motion-in-depth process. Recent evidence from brain-imaging indicates that brain areas which have been considered to be 'unimodal' are activated or modulated by inputs from other sensory modalities^{18–20}. It is suggested that such activation in unimodal areas rely on feedback projections from multimodal areas^{21,22}. In the ventriloquism effect, we actually hear the sound as though it comes from the location of the visual stimulus. To change conscious hearing, a change of neural activities in the auditory area may be necessary.

These results also show properties consistent with previous auditory–visual interaction studies: enhancement for congruent inputs, no effect for incongruent inputs, and visual superiority for spatial perception. The cross-modal aftereffect we have observed may therefore provide a new way to investigate the interaction of the auditory and visual systems for spatial perception and, more generally, interactions between sensory modalities. □

Methods

Ten students participated in experiments (1) and (2). Seven of them also participated in experiment (3). All subjects were naive except for one in experiment (2). All had normal or corrected-to-normal visual acuity, and had no hearing problems. The auditory and visual stimuli were generated by MATLAB with psychophysics toolbox extension^{23,24} on Apple PowerMacintosh. The sampling rate of the sound signal was 44.1 kHz and quantization was 16 bit. The auditory stimuli were converted to analog signals using the computer internal audio interface and presented to both ears through headphones (Sennheiser HDA200). The visual stimuli were presented on a display (SONY GDM-17SE2T, 75-Hz refresh). The experiment was conducted in a darkroom. The subject's head was fixed on a chin rest. The viewing distance was 140 cm. In experiments (1) and (3), viewing was binocular and, in experiment (2), the subjects observed the stimuli through liquid-crystal shutter goggles (Stereographics CrystalEyes).

Procedure

In the adapting conditions, the adapting stimulus was presented 60 times at 200-ms intervals. After the last adapting stimulus offset for 200 ms, a test stimulus was presented, and the subject was instructed to indicate whether this test stimulus appeared to grow louder or lower (experiments (1) and (2)) or grow bigger or smaller (experiment (3)). After the subject's response was given, the adapting stimulus was presented an additional five times to maintain the adaptation, followed by another test stimulus and response interval, and so on. Because a steady test tone after adaptation to a decreasing sound will be perceived as having increasing loudness, a test tone decreasing at a certain rate should be perceived as steady. The double-staircase method²⁵ was used to measure such points of subjective steadiness of the test stimulus, that is, the velocity of the physical change in level (experiments (1) and (2)) or in size (experiment (3)) necessary for the test stimulus to be perceived as steady. After the subjects' response, the velocity of the test stimulus was varied by 1 dB s⁻¹ step in experiments (1) and (2) and by 1 min s⁻¹ step in experiment (3). The point of subjective steadiness was calculated by averaging the last five (out of ten) reversal points of each staircase series. Before each adapting session, the point of subjective steadiness was measured without adaptation. The difference between the point of subjective steadiness in adaptation and no-adaptation conditions (no-adaptation minus adaptation) was taken as the magnitude of the aftereffect.

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Embryonic assembly of a central pattern generator without sensory input

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Locomotion depends on the integration of sensory information with the activity of central circuitry, which generates patterned discharges in motor nerves to appropriate muscles^{1,2}. Isolated central networks generate fictive locomotor rhythms (recorded in the absence of movement), indicating that the fundamental pattern of motor output depends on the intrinsic connectivity and electrical properties of these central circuits^{3,4}. Sensory inputs are required to modify the pattern of motor activity in response to the actual circumstances of real movement. A central issue for our understanding of how locomotor circuits are specified and assembled is the extent to which sensory inputs are required as such systems develop⁵. Here we describe the effects of eliminating sensory function and structure on the development of the peristaltic motor pattern of *Drosophila* embryos and larvae. We infer that the circuitry for peristaltic

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