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Involuntary orienting to sound improves visual perception

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To perceive real-world objects and events, we need to integrate several stimulus features belonging to different sensory modalities. Although the neural mechanisms and behavioural consequences of intersensory integration have been extensively studied[1–4], the processes that enable us to pay attention to multimodal objects are still poorly understood. An important question is whether a stimulus in one sensory modality automatically attracts attention to spatially coincident stimuli that appear subsequently in other modalities, thereby enhancing their perceptual salience. The occurrence of an irrelevant sound does facilitate motor responses to a subsequent light appearing nearby[5–7]. However, because participants in previous studies made speeded responses rather than psychophysical judgements, it remains unclear whether involuntary auditory attention actually affects the perceptibility of visual stimuli as opposed to postperceptual decision and response processes. Here we provide psychophysical evidence that a sudden sound improves the detectability of a subsequent flash appearing at the same location. These data show that the involuntary orienting of attention to sound enhances early perceptual processing of visual stimuli.

The influence of involuntary auditory attention on speeded motor responses to visual stimuli has been examined in experiments wherein an auditory cue, such as a sudden burst of noise, was presented to the left or right side of a participant who looked at a central spot[5–11]. A visual target was then presented unpredictably either on the same side as the cue or on the opposite side, and participants had to respond as quickly as possible to the target. Studies involving location-based go/no-go judgements[5] or elevation discriminations[6,7] have shown that motor responses were typically faster for targets appearing on the same side as the cue than for targets appearing on the opposite side when the delay between the cue and target was brief ($<$ 300 ms between cue and target onsets). On the basis of these findings, some investigators have proposed that involuntary orienting of attention to a sudden sound enhances perceptual processing of subsequent visual stimuli, as if the sensory responses to those stimuli in the brain were being amplified[12,13]. However, speeded motor responses cannot be taken as definitive evidence for improvements in perceptual processing because response times are also influenced by a number of postperceptual factors. In particular, the appearance of a spatial cue can modify an observer's willingness to respond[14] and can reduce the uncertainty of an observer's decision[15]. The spatial relationship between cue and target can also give rise to stimulus–response compatibility effects and surprise-related disruptions that can affect motor reaction times[16].

Here we used signal detection measures to investigate whether involuntary orienting of attention to a sudden sound influences the perceptual or postperceptual processing of a subsequent visual stimulus appearing nearby. Unlike reaction times, signal detection measures allow for the separation of perceptual and decision-level effects of attention. In the framework of signal detection theory, the d' parameter reflects an observer's ability to discern a sensory event from its background[17]. Thus, if the involuntary orienting of attention to a sound's location facilitated visual perceptual processes, d' should be larger for flashes appearing in proximity to a previous sound than for flashes appearing farther away. Conversely, if the involuntary orienting of attention to a sound's location affected only postperceptual decision processes, then observers might simply require less visual information to decide whether a target is present when it appears closer to the sound source. Such a change in decision would be reflected by a reduction of the decision criterion parameter, β.

We tested these predictions in two cross-modal spatial cueing experiments. The methods were adapted from those recently used to study the effects of visuo-spatial attention on visual detection performance[18,19]. As shown in Fig. 1, a spatially nonpredictive auditory cue appeared to the left or right side of fixation. This was followed after a brief interval by a visual mask either at the same location (valid trials) or at the opposite location (invalid trials). On half of the trials, a faint visual target was presented at the masked location immediately before the onset of the masking stimulus. On the other half of the trials, the target was absent from the display. Target-present and target-absent trials were randomly intermixed. Participants were informed that the auditory stimulus provided no information about the location of the visual stimuli or whether the target would be present or absent. The task was to press a button to indicate that the target was present, and to refrain from pressing the

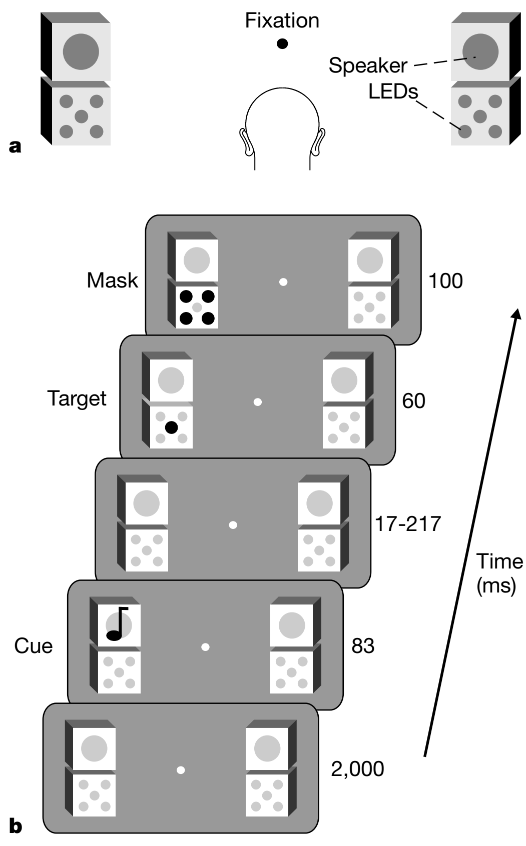

Figure 1 Experimental set-up. **a**, Schematic illustration of the audiovisual apparatus (not drawn to scale). **b**, Illustration of the events occurring on a valid, target-present trial. The cue–target stimulus onset asynchrony is obtained by adding the cue duration and the variable time interval that follows.

same button to indicate that the target was absent. Because only a single mask was presented on any given trial, participants were completely certain about the location at which the target may have occurred. Under such conditions, the observer's report must be based on sensory information arising from that single location, thus eliminating decision-level effects related to reduction of spatial uncertainty[15,18,19].

To assess the auditory cue effects on visual detection performance, the mean response times, hit rates, d' values, and β values were subjected to separate analyses of variances with probe location (left versus right) and cue validity (valid versus invalid) treated as within-subject factors. Trials were excluded from the analyses if the participant's eye position deviated from the central fixation spot or if a blink was made. The results from experiment 1 are shown in Fig. 2. On average, participants detected the visual target 20 ms more quickly on valid trials than on invalid trials, $F_{1,14} = 16.4$, $P < 0.001$ (Fig. 2a). Similarly, the mean hit rate (that is, per cent correct responses on target-present trials) was 9% higher on valid trials than on invalid trials, $F_{1,14} = 56.4$, $P < 0.00001$ (Fig. 2b). These data are consistent with recent response time findings[5–7]. Of primary interest, however, were the results from the signal detection analyses. Perceptual sensitivity (d') averaged 9% higher on valid trials than on invalid trials, $F_{1,14} = 15.6$, $P < 0.001$ (Fig. 2c). This confirms the hypothesis that involuntary orienting of attention to the location of a nonpredictive sound can improve the perceptual quality of a subsequent visual stimulus.

Analysis of the response criterion (β) data showed that involuntary orienting of attention to the location of the auditory cue also influenced the participants' willingness to respond, $F_{1,14} = 10.1$, $P < 0.008$. The decision criterion was on average 29% lower on valid trials than on invalid trials (Fig. 2d). Neither the main effect of probe location nor the probe location × cue validity interaction approached significance in any of the analyses.

Participants in experiment 1 were instructed to respond as quickly and as accurately as possible. One potential problem with this approach is that the speeded response requirement might reduce the validity of d' as a measure of perceptual sensitivity[20]. Thus, the effect of cue validity on d' that was observed in experiment 1 might have been partially attributable to the need for rapid responding rather than a genuine effect on perceptual sensitivity. Experiment 2 evaluated this possibility. Experiment 2 was similar to experiment 1, except that response accuracy was emphasized over response speed. Participants were instructed to respond as accurately as possible before the onset of the next warning sound (that is, the cue), which occurred 2–2.5 seconds after the onset of the probe. Upon debriefing, all participants said that they had no difficulties making detection responses within this interval. The intensity of the target was reduced overall to maintain a 70–80% hit rate.

Figure 3 displays the results of experiment 2. Overall, mean response times were longer (552 ms versus 457 ms) and d's were lower (1.65 versus 1.92) in experiment 2 than in experiment 1. Despite these changes, subjects still detected visual targets more quickly, $F_{1,17} = 21.0$, $P < 0.0002$, and more accurately, $F_{1,17} = 11.3$, $P < 0.0004$, on valid trials than on invalid trials (Fig. 3a and b). In accord with these findings, d' was 8% higher on valid trials than on invalid trials, $F_{1,17} = 6.5$, $P < 0.02$ (Fig. 3c). Thus, experiment 2 confirms that involuntary orienting of attention to a sound improves the perceptual quality of neighbouring visual stimuli. Additionally, the auditory cue had a significant effect on decision processes. As in experiment 1, β was lower on valid trials than on invalid trials, $F_{1,17} = 7.2$, $P < 0.02$ (Fig. 3d). This effect was larger for right visual field stimuli (36%) than for left visual field stimuli (8%), $F_{1,17} = 6.0$, $P < 0.03$. On the basis of these results, we conclude that, under the conditions used here, involuntary attention orienting to a sound influences vision at early perceptual levels as well as at later, decision-related levels.

An irrelevant sound can influence the perception of both concurrent and subsequent visual events. For example, a brief burst of noise can augment the perceived intensity of a concurrent flash of light[2]. In contrast with the present results, however, this intersensory effect did not depend on the relative locations of the auditory and visual stimuli and occurred only when the participants were looking at the flashes. These differences indicate that the effects of a sound on the processing of concurrent and subsequent visual stimuli arise from different neural mechanisms. Neurophysiological studies in animals suggest that the influence of a concurrent sound on

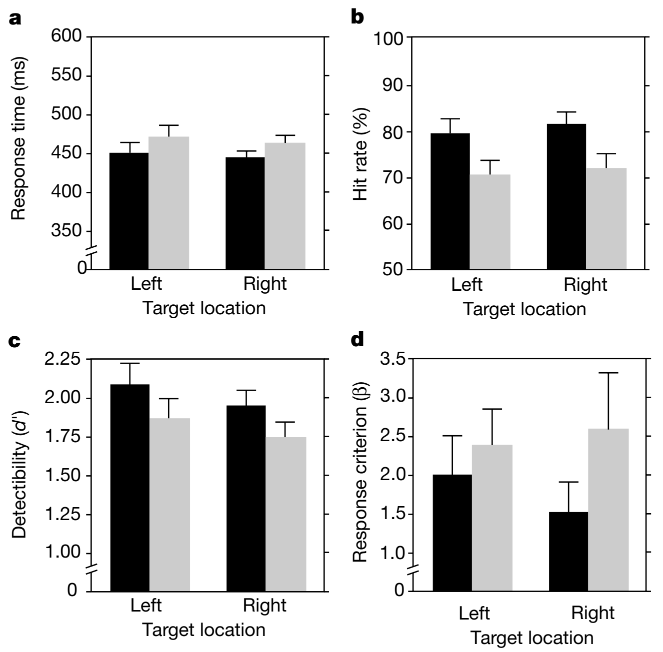

Figure 2 Mean data over all participants from experiment 1. **a**, Response times. **b**, Hit rates. **c**, Perceptual sensitivities (d'). **d**, Response criteria (β). Black bars represent valid conditions and grey bars represent invalid conditions.

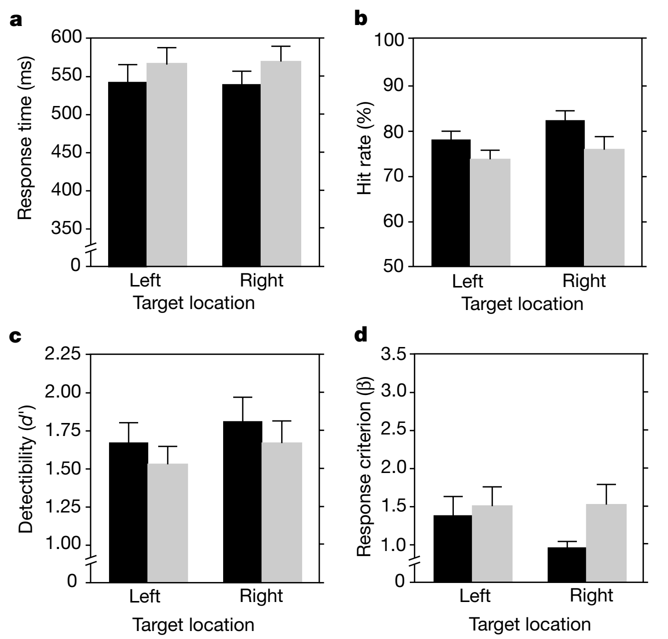

Figure 3 Mean data over all participants from experiment 2. **a**, Response times. **b**, Hit rates. **c**, Perceptual sensitivities (d'). **d**, Response criteria (β). Black bars represent valid conditions and grey bars represent invalid conditions.

visual-evoked brain activity results from the passive integration of auditory and visual inputs by multisensory neurons in the brain[3,21]. Such integrative effects are minimal when stimuli are separated by 100 ms or more. Because the present design used intervals of 100–300 ms between the auditory cue and visual target, the spatially specific facilitation of visual processing that we observed cannot be explained by passive multisensory integration alone. Instead, the improvement in d' for detection of the visual target can be ascribed to an involuntary orienting of attention to the location of the preceding auditory cue.

It has also been found that a spatially congruent, temporally overlapping sound improved response accuracy (per cent correct) for discriminating the orientation of a 'T' that was surrounded by distractor 'T's but not for discriminating the orientation of a line that was surrounded by distractor lines[22]. This latter, null effect indicated that visual processing at early, feature-extraction levels may not be altered by concomitant sounds. We found, however, that a preceding sound increased perceptual sensitivity (d') for simple luminance detection under conditions of brief, masked target presentations. This pattern of results is diagnostic of an attention effect upon the early perceptual processing of the spatially congruent visual target[15,18–20]. This cross-modal facilitation brought about by involuntary spatial attention may be a fundamental operation for enhancing the perceptual salience of natural stimuli in a multisensory world. □

Methods

Participants

Fifteen paid volunteers (8 women) between the ages of 19 and 30 years participated in experiment 1, and eighteen paid volunteers (9 women) between the ages of 19 and 37 participated in experiment 2. Informed, written consent was obtained from each participant.

Stimuli and apparatus

The experiment was conducted in a dimly lit, sound-attenuated chamber. The background sound level within the chamber was 32 dB(A). Participants sat in the chamber and faced a fixation point that was mounted at the centre of a 2.4-m horizontal arc. Loudspeakers mounted on the arc were positioned 38° to the left and right of the central fixation point (see Fig. 1a). A visual display was situated directly below each loudspeaker. Each light display contained four red light-emitting diodes (LEDs) arranged in a 1° square and one green LED positioned at the centre of the square. The distance between the centre of the loudspeaker cone and the centre of the light display was 2°, which is smaller than the minimum audible angle in the far periphery[23]. The auditory cue was a 76-dB (A) burst of broadband (500–5,000 Hz) 'pink' noise delivered from one of the two loudspeakers. The visual target was a flash of the green LED on either side of the fixation point. The visual mask was a simultaneous flash of all four red LEDs on either side of the fixation point. The luminance of the mask was 150 cd m^{-2}, and the luminance of the target varied between 20 and 100 cd m^{-2}. The luminance of the background was 2 cd m^{-2}.

Procedure

Each trial began with a 2,000-ms fixation period, during which time the fixation point, loudspeakers and light displays were all visible. Following the fixation period, an 83-ms cue period occurred during which a noise appeared with equal probability from either the left or right speaker. Then, after a random 100 to 300 ms (rectangular distribution), a 60-ms target period occurred. On half of the trials, the target appeared with equal probability on either the left or right side during the target period (target-present trials). On the other half of the trials, no target appeared during the target period (target-absent trials). Immediately following the target period, a mask was presented for 100 ms to either the left or right of fixation. In addition to masking the visual target, the mask indicated the location at which the target may have occurred. Participants were informed that the target and mask never appeared at different locations, and hence their present/absent judgement should be based solely on the masked location. The cue and mask appeared at the same location on 50% of the trials ('valid' trials) and at opposite locations on the other 50% of the trials ('invalid' trials). Thus, the noise cue provided no information about either the location of the mask or whether the target would be present or absent.

Each subject participated in a practice session followed by 15 experimental blocks. The intensity of the target was adjusted during the practice session so that each subject's hit rate was between 70% and 80%. Further adjustments were made between blocks if the subject's hit rate fell outside the 70–80% interval. Each block consisted of 28 valid trials and 28 invalid trials. In experiment 2, there were 14 additional trials per block on which no target or mask occurred. These catch trials were added to reduce anticipatory responses. Participants responded by pressing a button with their left or right thumb on alternating blocks.

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Ghrelin induces adiposity in rodents

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The discovery of the peptide hormone ghrelin, an endogenous ligand for the growth hormone secretagogue (GHS) receptor[1,2], yielded the surprising result[3] that the principal site of ghrelin synthesis is the stomach and not the hypothalamus. Although ghrelin is likely to regulate pituitary growth hormone (GH) secretion[3,4] along with GH-releasing hormone and somatostatin, GHS receptors have also been identified on hypothalamic neurons[5] and in the brainstem[6]. Apart from potential paracrine effects, ghrelin may thus offer an endocrine link between stomach, hypothalamus and pituitary, suggesting an involvement in regulation of energy balance. Here we show that peripheral daily administration of ghrelin caused weight gain by reducing fat utilization in mice and rats. Intracerebroventricular administration of ghrelin