Perceptual Gain and Perceptual Loss: Distinct Neural Mechanisms of Audiovisual Interactions*

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Abstract. What we see can be influenced by what we hear. However, the neural basis of the audiovisual interactions, and whether common or distinct mechanisms can be involved, remains unclear. Here we showed that auditory beeps can either induce illusory light flashes (perceptual gain) or reduce perceived number of physical flashes (perceptual loss), when beeps mismatched with simultaneous flashes. Moreover, we reported neuroimaging data on the neural substrates of perceptual gains and perceptual losses in visual perception. Illusory gains in perceived flashes produced activations in the left supramarginal gyrus, the left prefrontal cortex, and the right cerebellum, reflecting a neural network associated with integrative processes in working memory. Illusory losses of perceived flashes, however, were associated with activations in the medial occipital cortex and thalamus, linking with brain regions associated with early visual processing. The results suggest that distinct neural systems underlie distinct audiovisual interactions in the human brain.

Keywords: fMRI, perceptual gain, perceptual loss, audiovisual interaction

1. Introduction

Our perception of the world usually requires the integration of information from multiple modalities, such as vision and audition. There is now considerable evidence for interactions between visual and auditory information simultaneously presented to observers. One well-known example of visual information affecting the perception of auditory stimuli is the McGurk effect [1], where a sound is systematically misperceived when paired with a mismatching lip movement. This visual-auditory interaction can take place as early as 150 ms after sensory stimulation [2] and involves the posterior superior temporal sulcus (STS), the right thalamus, and the right cerebellum in visual-auditory binding [3].

Auditory stimuli can also influence visual perception. For example, the perceived intensity of a visual stimulus can be enhanced in the presence of sound [4], whilst the perceived direction of ambiguous visual motion [5] and the perceived duration of a seen stimulus can be altered [6] by sound presented simultaneously. The perceived number of visual stimuli can also be affected by simultaneous auditory events [7]. When a single flashed disk is accompanied by more than one beep, it can be perceived to flash twice or more. These illusory gains in visual perception are particularly salient when stimuli are displayed in the periphery and there is a minimal interval between the visual and auditory events [8]. Moreover, visual evoked potentials (VEPs) associated with visual perceptual gains, recorded at the occipital area, are similar to those produced by physical flashes [9], suggesting a possible common neural mechanism for the perception of illusory and physical flashes. However, the limitation of spatial resolution of VEPs makes it difficult to assess brain structures involved in such auditory-visual interactions. In addition, it is unclear whether the mechanisms mediating these bidirectional cross-modal interactions are the same or different.

In the present paper we first extend our knowledge of audiovisual interactions by demonstrating a new illusion of visual-perceptual loss, supplementing prior evidence on visual-perceptual gains [7]. When brief visual flashes are accompanied by simultaneous auditory beeps, the number of perceived flashes is

influenced by the beeps: there is a perceptual gain, i.e., auditory beeps induce illusory light flashes when there are more beeps than flashes [7], and a perceptual loss, i.e., auditory beeps reduce perceived number of physical flashes when there are fewer beeps than flashes. We then employed functional magnetic resonance imaging (fMRI) to investigate the neural substrates of these effects. We compared brain activations in conditions where the visual and auditory stimuli mismatched with baselines where there were only visual stimuli or the visual and auditory stimuli matched. Our findings indicate that separate neural circuits underlie the two audiovisual illusions: visual perceptual gains are associated with circuits linked to working memory; visual perceptual losses are associated with an inhibitory circuit including regions linked to early visual processing. Different forms of cross-modal interactions contribute to our conscious perception of the visual world.

2. Method

2.1. Subjects

Fifteen volunteers with no neurological or psychiatric history (7 male, 18-41 years of age, mean 24) participated in the current study. There were ten subjects in the behavioral and fMRI experiments, respectively. Five subjects participated in both experiments. All subjects were right-handed, had normal or corrected-to-normal vision, and were free of any history of neurological or psychiatric problems. This study was approved by the Academic Committee of Department of Psychology, Peking University. Informed written consent was obtained from all subjects prior to scanning.

2.2. Stimuli and Procedure

Stimuli and procedure are illustrated in Fig.1. The flashing stimulus was a uniform white disk on a black background. In the behavioral experiment, the flashed disks (204 cd/m^2) were presented on a 15' LCD monitor. A fixation cross was continuously presented at the center of the screen throughout the experiments. At a viewing distance of 50 cm, each disk subtended a visual angle of 1.6° and was displayed along an imaginary horizontal line that was 4.8° below the fixation cross. Each disk flashed for 17 ms. The auditory stimuli were brief beeps (2 kHz frequency at 80 dB sound pressure level (SPL)) lasting for 7ms presented via well fitted stereo headphones. There were six stimulus conditions: (1) 3F: 3 flashes were presented sequentially, (2) 5F: 5 flashes were presented sequentially, (3) 3F3B: 3 sequentially presented flashes were accompanied with 3 beeps, (4) 5F5B: 5 sequentially presented flashes were accompanied with 5 beeps, (5) 3F5B: 3 sequentially presented flashes were accompanied with 3 beeps, (6) 5F3B: 5 sequentially presented flashes were accompanied with 3 beeps. Under all stimulus conditions, the sequentially presented flashes started from the left visual field. 3F3B and 5F5B conditions were used to test if subjects simply made responses according to the auditory stimuli. The onset asynchrony (SOA) between a beep and the following flash was 23 ms (see Fig.1). The SOA between two successive beeps was 60 ms in conditions with 5 beeps. The SOA between two successive beeps was 120 ms in conditions with 3 beeps. The stimulus interval between two successive beeps or flashes was constant through all stimulus conditions.

The stimuli and procedure in the fMRI experiment were the same as those in the behavioral experiment except the following. The visual stimuli were presented through a LCD projector onto a rear-projection screen located at the subject's head. The screen was viewed with an angled mirror positioned on the head-coil. At the viewing distance of 70 cm, the disk subtended a visual angle of 2.4°and displayed along an imaginary horizontal line that was 7.1°either above or below the fixation cross. The auditory stimuli were presented using a loud speaker located inside the scanner in which the subject was tested. We used the loud speaker rather than a headset because the sound quality was better with the speaker than with the air-tube headset provided in the magnet. Because the MRI scanner produced noise (89.2 dB SPL) louder than the auditory beeps (2 kHz frequency at 83.3 dB SPL), the scan sequence was adjusted so that each TR had a 500-ms delay during which the scanner stopped acquiring data and thus produced a silent period for presentation of the both visual and auditory stimuli. Subjects used ear plugs in the scanner which produced an attenuation of 37.1 dB at 2 kHz.
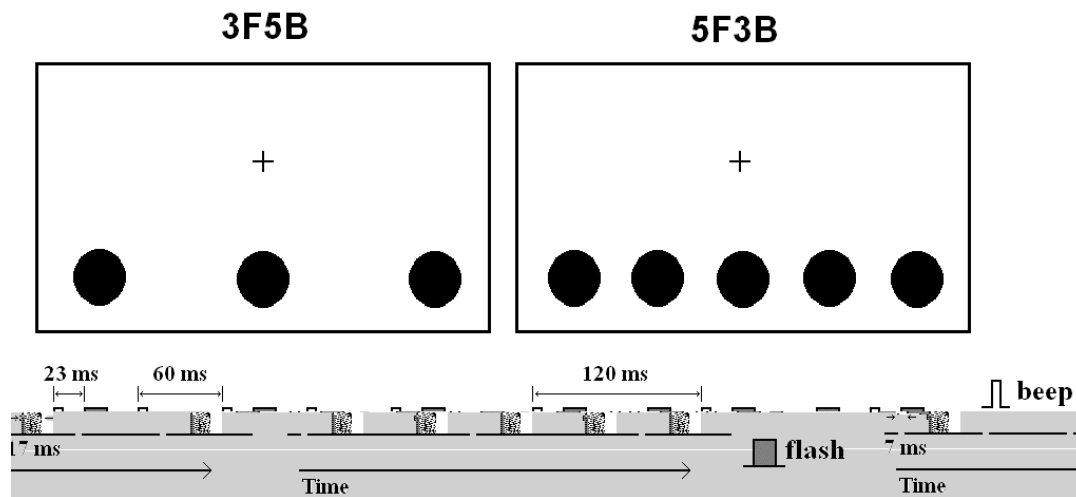
Fig.1: Illustrations of the stimuli and procedure used in the current study. 3F5B: 3 flashes accompanied with 3 beeps, 5F3B: 5 flashes accompanied with 3 beeps.

Subjects were asked to remain fixated on the fixation cross during the experiments. In the behavioral experiment, subjects were required to judge the number of the flashing disks on each trial. They wrote down the perceived number of flashes on an answer sheet and then pressed a key to start the next trial. There were 16 trials in each of the six conditions which were presented in a random order. In the fMRI experiment that employed a box-car design, subjects were not required to make any responses during the scan procedure. Each trial was presented within the 500-ms delay during each TR. Six scans of 164 s were first obtained from each subject. Each scan consisted of eight 20-second epochs of 10 trials, alternating randomly between the 3F, 5F, 3F5B, and 5F3B conditions. The first 4 seconds of each scan were excluded from statistical analysis to obtain a steady baseline. Another three scans of 124 s were obtained with the identical foregoing parameters and three conditions, i.e., 3F5B, 5F3B, and 5F5B. Additional two scans were also obtained, which included only three conditions, i.e., 3 or 5 beeps with fixation and fixation with no beeps. The epoch of beeps (including 10 trials) or baseline also lasted for 20 s.

2.3. fMRI Data Acquisition and Analysis

Scanning was performed on a 3T Siemens Trio system using a standard head coil at Beijing MRI Center for Brain Research. Twenty-four axial slices of functional images that covered the whole brain were acquired using a gradient-echo echo-planar pulse sequence ($64\times64\times24$ matrix with $3.4\times3.4\times6$-mm spatial resolution, TR=2000 ms, TE=30 ms, FOV=220 mm, flip angle=90°). Anatomical images were obtained using a standard 3D T1-weighted sequence (resulting in a $256\times256\times176$ matrix with $0.938\times0.938\times1.3$-mm spatial resolution, TR=1600 ms, TE=3.93 ms). Subjects' heads were immobilized during the scanning sessions using pieces of foam.

SPM99 (the Wellcome Department of Cognitive Neurology, UK) was used for data processing and analysis. Following correction for differences in the timing of slice acquisition within a volume, the functional images were realigned to the first scan to correct for the head movement between scans. The structural image was coregistered with the mean functional image produced during the process of realignment. All images were normalized to a $2\times2\times2$ mm^3 Montreal Neurological Institute (MNI) template in Talairach space [10] using bilinear interpolation. Functional images were spatially smoothed using a Gaussian filter with a full-width at half maximum (FWHM) parameter set to 8 millimeters. The image data were modelled using a box-car function. Contrasts were defined to compare the effect of sound on visual perception. Regions preferentially engaged in visual illusion were defined as areas more activated by 3F5B than by 3F conditions. Regions preferentially engaged in perceptual loss of flashes were defined as areas more activated by 5F3B than by 5F conditions. Contrast between 'beeps lonely' and silent baseline condition

was used to identify neural substrates for the processing of simple auditory stimuli. Random effect analyses were then conducted across the group of subjects based on statistical parameter maps from each individual subject to allow population inference. Areas of significant activation were identified using a voxel-based t-test and a significance threshold of $P < 0.005$ (uncorrected). The SPM coordinates for standard brain from MNI template were converted to Talairach coordinates using a non-linear transform method (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html).

3. Results

3.1. Behavioural Data

The reported numbers of visual flashes in each condition are shown in Fig.2. There were both perceptual gains and perceptual losses in visual perception when the visual and auditory stimuli mismatched. Perceptual gains were demonstrated by the increased number of flashes reported in Condition 3F5B than in Condition 3F (3.58 vs. 3.25, t (9) = 3.86, p<0.005) and the increased number of flashes reported in Condition 3F5B than in Condition 3F3B (3.58 vs. 3.01, t (9) = 3.50, p<0.007). Perceptual losses were also apparent. There were fewer reports of visual flashes in Condition 5F3B compared with the baseline, Condition 5F (3.06 vs. 3.83, t (9) = 4.84, p<0.001), and fewer reports of visual flashes in Condition 5F3B than in Condition 5F5B (3.06 vs. 3.83, t (9) = 4.97, p<0.001). The magnitudes of these two illusions were assessed in a repeated measure analysis of variance with Flash Number (3 or 5 flashes) and Beep (presence or absence of beeps) as independent variables and performed on 3F, 3F5B, 5F, and 5F3B conditions. There was a significant interaction between Flash Number and Beep, due to the face that the effect of perceptual loss was stronger than that of perceptual gain (F (1, 9) = 19.0, p<0.002). These differences were not simply due to subjects reporting the number of beeps, since more flashes were reported in condition 5F5B than in condition 3F5B (3.83 vs. 3.58, t (9) = 2.29, p<0.05) even though there were five beeps in both conditions.
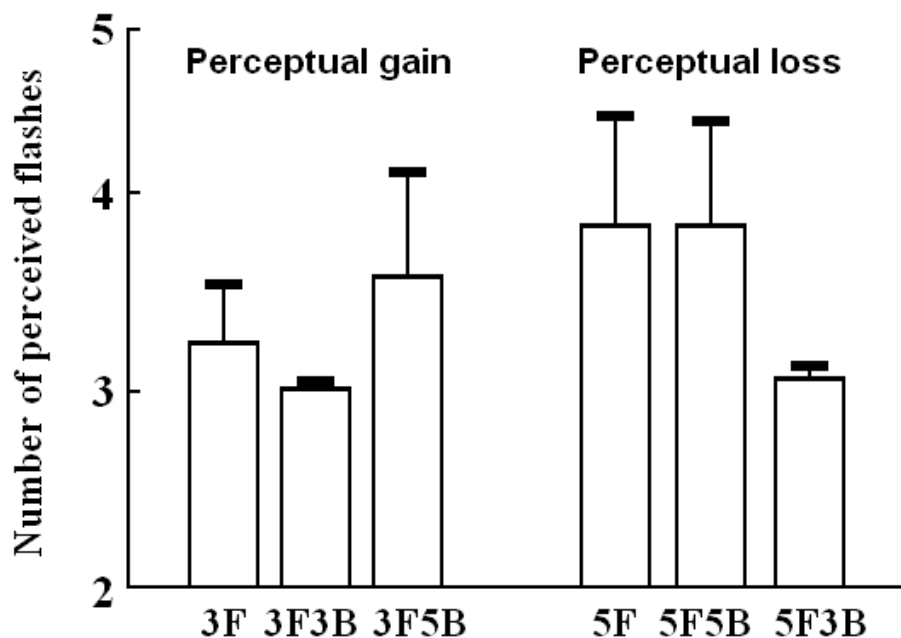

Fig.2: Behavioral results in the current study. Mean perceived numbers of flashes with standard deviations are plotted in different stimulus conditions.

3.2. fMRI Data

Because preliminary analysis showed that there were no differences between the conditions when flashes

were presented above or below the fixation, the data in the two conditions were pooled for further analyses. We assessed the brain regions affected by the visual-auditory interactions, using the contrasts reported in Table 1. Each illusion condition was compared with conditions that were matched for the number of physical flashes but not for the number of perceived flashes. For the perceptual gains, condition 3F5B was compared with its visual physical-match baseline (3F), to test for any regions associated with the additional perceived flashes. This revealed activations in bilateral superior temporal gyri (Brodmann Area (BA) 22/42), the left supramarginal gyrus (BA 40), the left prefrontal cortex (BA 10), and the right cerebellum, as illustrated in the top row of Fig.3. The activation in the left superior temporal gyrus was more posterior than that in the right hemisphere. There was no evidence for increased activation in early visual processing areas in the occipital cortex.

Table 1. Brain activations in each contrast in the fMRI experiment.

| Anatomical region	Side	x	y	z	t-statistic	P-value
3F5B minus 3F						
Superior temporal gyrus (BA 22)	L	-59	-40	13	3.93	0.002
Superior temporal gyrus (BA 22/42)	R	67	-21	7	6.31	0.000
Supramarginal gyrus (BA 40)	L	-61	-51	34	9.32	0.000
Middle prefrontal gyrus (BA 10)	L	-24	63	10	5.41	0.000
Cerebellum	R	42	-69	-23	10.30	0.000
5F3B minus 5F						
Superior temporal gyrus (BA 22)	L	-65	-32	15	4.48	0.001
Superior temporal gyrus (BA 22/42)	R	69	-21	3	6.23	0.000
Medial occipital cortex (BA 17/18)	R	12	-82	-6	5.63	0.000
Thalamus	L	-6	-21	7	4.90	0.000
	R	6	-19	10	4.02	0.002
5F3B minus 3F						
Medial occipital cortex (BA 18/19)	R	2	-95	7	6.53	0.000
5F minus 5F3B						
Lateral occipital cortex (BA 18/19)	L	-28	-72	7	11.01	0.000
	R	34	-71	16	8.94	0.000
5F minus 3F						
Lateral occipital cortex (BA 18/19)	L	-20	-87	6	3.51	0.003
	R	22	-91	5	4.17	0.001
Beeps minus Silent baseline						
Superior temporal gyrus (BA 41/42)	L	-69	-27	11	16.99	0.000
	R	55	-25	12	13.38	0.000
3F5B minus 5F5B						
Inferior prefrontal gyrus (BA 11)	L	-32	32	-15	3.68	0.003
Middle prefrontal gyrus (BA 10)	L	-36	48	21	3.31	0.005
Cerebellum	R	42	-54	-24	5.84	0.000
5F3B minus 5F5B						
Medial occipital cortex (BA 19)	L	-16	-62	-4	7.29	0.000

Note: BA: Brodmann area.
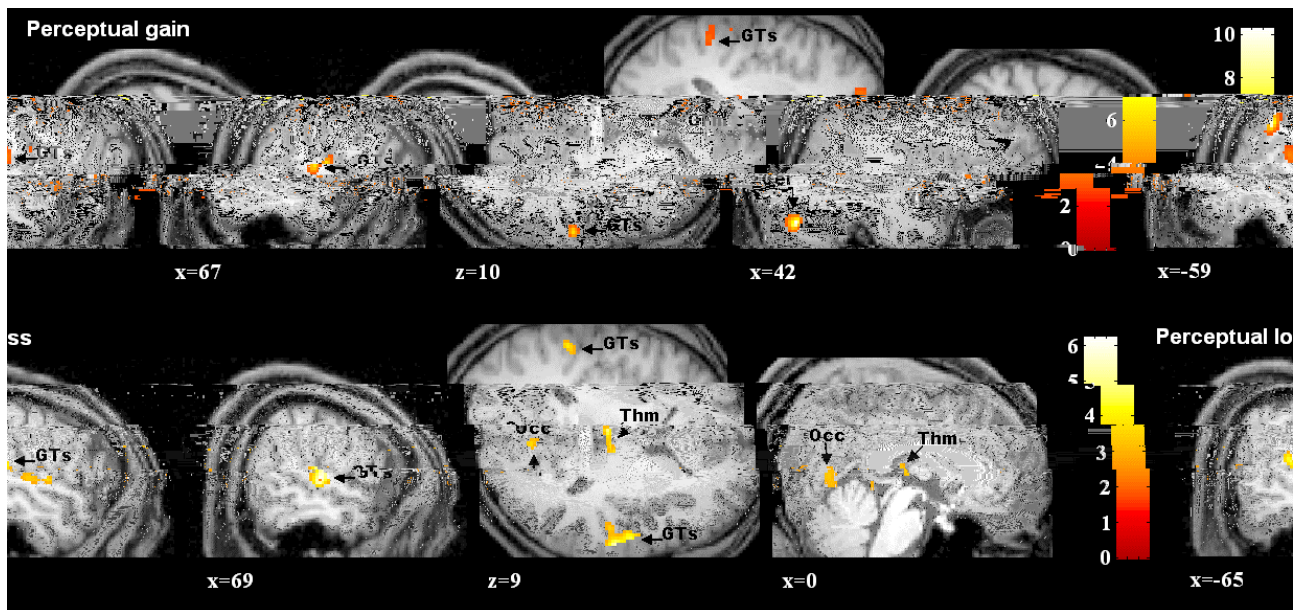
Fig.3: Brain activations associated with sound-induced perceptual gain and perceptual loss. The results of the group analysis from 10 subjects were plotted on MR images of a representative subject. The color bar indicates the scale of z values. Cer = cerebellum; GFm = middle frontal gyrus; Gsm = supramarginal gyrus; GTs = superior temporal gyrus; Occ = occipital cortex; Thm = thalamus.

For the perceptual loss condition (5F3B), we compared activation with its visual physical-match baseline (5F). This revealed activations in bilateral superior temporal gyri (BA 22/42) with the left locus being more posterior that the right one. There were also enhanced activations in the medial occipital cortex (BA 17/18., right hemisphere) and bilateral thalamus (Fig.3, bottom row). That is, these areas were more activated when the visual stimuli were not perceived than when they were actually present. This suggests the involvement of some active inhibitory processes when the auditory beeps led to suppression of the visual stimuli. When the perceptual loss condition (5F3B) was compared with its perceptual-match baseline (3F), there was also activation of the medial occipital cortex (BA 18/19, Fig.4a), particularly in the right hemisphere. This is again consistent with there being suppression of the visual activation associated with perceptual loss.

To identify whether perceptual losses (5F vs. 5F3B) and lack of physical flashes (5F vs. 3F) shared common neural substrates in the visual cortex, contrasts were defined by comparing 5F with 5F3B and 5F with 3F conditions. Both contrasts showed activations in bilateral occipital cortex (BA 18/19, Fig.4b and 4c).

To rule out the possibility that activations outside the primary auditory cortex in conditions 3F5B and 5F3B arose from the processing of pure auditory stimuli, further two scans were obtained in which 20-second epochs of 3 (or 5) beeps with fixation and silence with fixation were presented randomly. Unimodal auditory beeps were contrasted with the silent baseline condition and showed increased activations in bilateral primary auditory cortex (BA 41/42, see Table 1 and Fig.4d). There were no activations in areas critical to the illusion conditions.
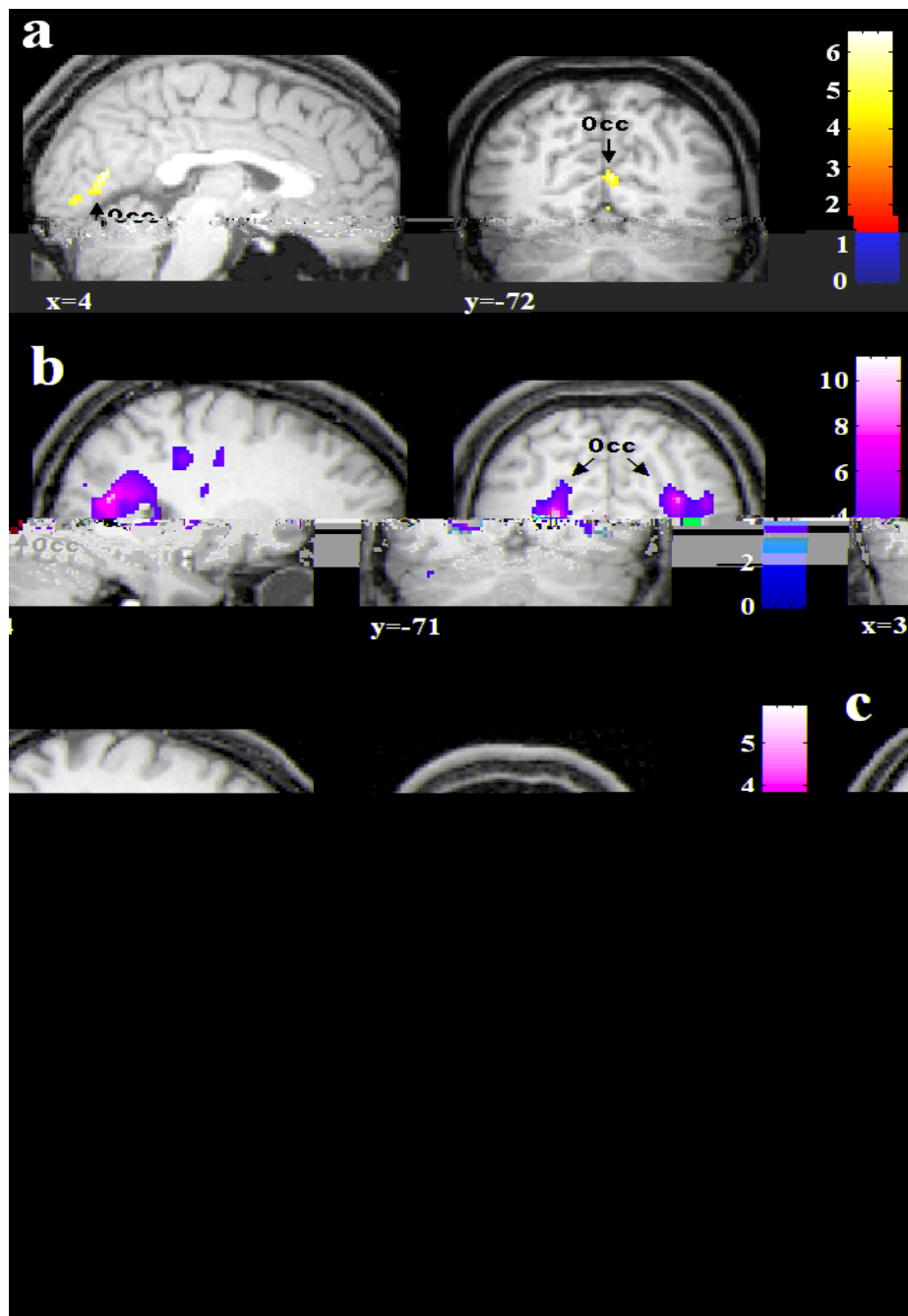
Fig.4: Brain activations associated with lack of perceptual and physical flashes. (a) Brain activation in the medial visual cortex shown in the contrast between 5F3B with 3F conditions; (b) Brain activations in bilateral visual cortices shown in the contrast between 5F with 5F3B conditions; (c) Brain activations in bilateral visual cortices shown in the contrast between 5F with 3F condition; (d) Brain activations in bilateral superior temporal gyri in the contrast between unimodal auditory stimuli and silent baseline conditions. The results of the group analysis from 10 subjects were plotted on MR images of a representative subject. The color bar indicates the scale of z values. GTs = superior temporal gyrus; Occ = occipital cortex.

Finally we examined if the activations observed in bilateral superior temporal cortex associated with perceptual gains and losses reflected early audiovisual interactions that are not specific to the illusions. 20-second epochs of 3F5B, 5F3B, and 5F5B conditions were presented randomly in three scans. Conditions 3F5B and 5F3B were respectively contrasted with Condition 5F5B in which no perceptual gains and perceptual losses occurred. In addition, flashes and beeps were presented simultaneously in the 5F5B condition and thus early audiovisual interactions also occurred, similar to those in the 3F5B/5F3B conditions.

Therefore the contrast between 3F5B/5F3B and 5F5B should eliminate activations underlying early audiovisual interactions but preserve those specific to perceptual gains and perceptual losses. The contrast between 3F5B and 5F5B showed activations in the left prefrontal cortex (BA 10) and the right cerebellum, whereas the contrast between 5F3B and 5F5B showed activations in the medial visual cortex (BA 19) (see Table 1 and Fig.5a and 5b).
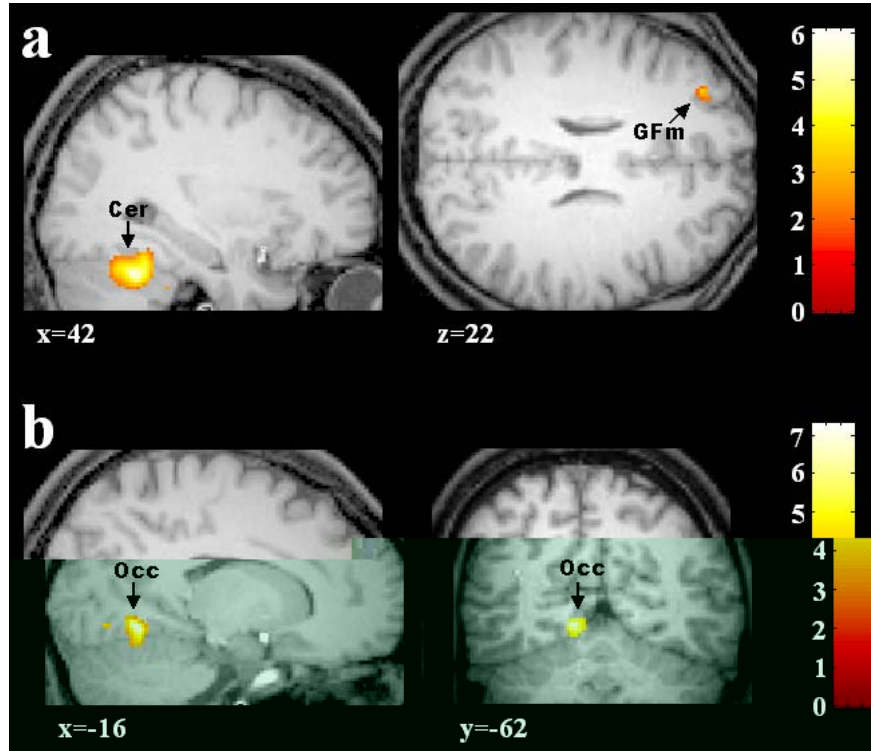

Fig.5: Brain activations associated with perceptual illusion and perceptual loss using 5F5B as a control condition. (a) Contrast between 3F5B with 5F5B conditions showed activation the left prefrontal cortex and cerebellum; (b) Contrast between 5F3B with 5F5B conditions showed activations in the medial occipital cortex; The re

which fewer flashes are reported compared with physically matched baseline. The recruitment of the posterior thalamus in the perceptual loss effect fits with other research showing the involvement of the thalamus when information from multiple modalities is integrated [3, 21]. However, the thalamus activation might not be specific to perceptual losses because the thalamus activation was eliminated when auditory beeps were used in the baselines (5F5B) to contrast the perceptual losses (5F3B). It may be that subcortical interactions help to establish the inhibition of the visual signals when perceptual losses take place.

Although there were clear difference in activation between the perceptual gain and loss conditions, there were also common areas involved. In particular, the superior temporal gyrus (BA 22/42) was activated in both illusion conditions compared with the baselines with only flashes. Interestingly, in the present comparisons, the evidence for superior temporal gyrus activation was eliminated when comparisons were made with baselines where auditory beeps were recruited (3F5B vs. 5F5B; 5F3B vs. 5F5B). However, the activation was not produced by the auditory beeps alone, since the contrast between 'beeps lonely' and silent baseline showed activation in the different part of the superior temporal gyrus (Table 1). This lack of an effect when the beeps occurred as well as the flashes, and the common activation irrespective of the direction of the illusion, suggest that the superior temporal gyrus (BA 22/42) reflect early stage of audiovisual integration. That is, early activation in the superior temporal gyrus register the presence of simultaneous cross-modal events, with integration being achieved either through top-down activation of working memory (perceptual gains) or visual suppression (perceptual loss).

Our findings of two distinct neural mechanisms of audiovisual interactions reveal cognitive and neural mechanisms that may serve other sound-induced changes in visual perception. For instance, two objects that move steadily towards one another, coincide, and then move apart are perceived to continue in their original directions in most cases. However, introduction of sounds at the point of their coincidence changes the motion direction of the objects so that they are perceived to collide and bounce, reversing directions [5]. It may be proposed, on the basis of our findings, that the sound-induced changes in visual motion directions involve both perceptual gains of new motion directions of the objects and perceptual losses of their original motion directions. Indeed, enhanced neural activities have been observed in the left prefrontal cortex, the right cerebellum, and the right thalamus in association with the sound-induced changes in visual motion directions [22]. It is possible that both networks underlying perceptual gain and perceptual loss are engaged in the audiovisual interactions leading to the changes in visual motion directions.

In conclusion, we have shown that sound-induced change in visual perception can be bidirectional. Sounds can either produce perceptual gains or perceptual losses of particular features of visual stimuli (e.g., presence or absence in the current study, or motion direction in the prior work [22]. Our fMRI data further indicate that neural mechanisms underlying perceptual gains and perceptual losses are essentially different. A prefrontal-cerebellum loop is engaged in perceptual gains, possibly reflecting interactions of visual and auditory information coded in working memory. In contrast, the visual cortex is involved in perceptual losses, reflecting modulations of early sensory-perceptual processing.

5. Acknowledgements

6. References

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