

## Right hemisphere dominance in perceiving coherence of visual events

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### Abstract

The visual world consists of static pictures as well as of coherent visual events. The present study investigated neural substrates underlying the perception of coherence of visual events that evolves over time. We measured brain activity using functional magnetic resonance imaging (fMRI) while adults watched briefly presented static images that were extracted from movie clips depicting coherent visual events. The images were presented either in the coherent order as they were displayed in the movie clips or in a random order. Relative to the random order presentation condition, static images presented in the coherent order generated stronger activation in the right middle temporal cortex, the right posterior superior temporal cortex, and the right inferior postcentral gyrus. The results provide neuroimaging evidence for the dominance of the right hemisphere in perceiving coherent visual events.

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We live in a world consisting of coherent events which contain visual and auditory information that evolves over time and has a coherent structure. When watching movie clips showing a student knocking at a door, walking into a classroom, and sitting behind a desk, the images projected onto the retina may change drastically. However, we are able to perceive these different images as a coherent event. If the movies clips are shown in a random order, we may feel difficult to understand the coherent structure of the agent's actions. Similarly, when listening to spoken languages or music, we can understand easily the meaning of languages or music structure when pieces of languages or music are presented with temporal coherence. We may feel difficult to understand languages or music if their coherent structures are destroyed. The neural substrates that underpin the processing of coherence of auditory information have been investigated in neuroimaging studies by contrasting auditory stimuli with coherent structure with the corresponding scrambled counterparts [1,2]. It was found that comprehension of two sentences with coherent meaning increased activities of the medial frontal cortex relative to sentences that lack coherence of meaning. Music induces

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depicting human activities were used in this study. One movie clip showed two persons meeting and walking at a subway station. Another movie clip showed a student entering a classroom, sitting behind a desk, raising a hand, and asking questions. Sixty images were extracted at every second from each movie clip. At a viewing distance of 70 cm, each image subtended a visual angle of  $28^\circ \times 16^\circ$  (width  $\times$  height). One scan of 280 s was obtained from each subject, which consisted of four one-minute epochs, alternating pseudo-randomly between the coherent and random order conditions. There were 60 images in each epoch. Each image was presented for 1000 ms. A blank screen was presented for 10 s before each epoch to set up a baseline for each epoch of stimuli. Subjects were asked to view freely the images while keeping their heads still.

Scanning was performed on a 3T Siemens Trio system using a standard head coil at Beijing MRI Center for Brain Research. Thirty-two transversal slices of functional images that covered the whole brain were acquired using a gradient-echo echo-planar pulse sequence ( $64 \times 64 \times 32$  matrix with  $3.4 \times 3.4 \times 4.4$ -mm spatial resolution, TR = 2000 ms, TE = 30 ms, FOV = 220 mm, flip angle =  $90^\circ$ ). Anatomical images were obtained using a standard 3D T1-weighted sequence ( $256 \times 256 \times 176$  matrix with  $0.938 \times 0.938 \times 1.3$ -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. The functional images were realigned to the first scan to correct for the head movement between scans. The anatomical image was co-registered with the mean functional image produced during the process of realignment. All images were normalized to a  $2 \text{ mm} \times 2 \text{ mm} \times 2 \text{ mm}$  Montreal Neurological Institute (MNI) template in Talairach space [16] using bilinear interpolation. Functional images were spatially smoothed using a Gaussian filter with a full-width at half maximum (FWHM) parameter set to 8 mm. The image data were modeled using a box-car function. Contrasts were defined to compare the difference between stimuli in the coherent and random order conditions. 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 at the cluster level for values exceeding a  $p$ -value of 0.05 (corrected for multiple comparisons). The SPM coordinates for standard brain from MNI template were converted to Talairach coordinates [16] using a non-linear transform method (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>).

After scanning, subjects were asked to report which epochs contained coherent visual events. All subjects reported perceiving coherent visual events in the coherent order condition but not in the random order condition. fMRI signals in the coherent order condition were contrasted with those in the random order condition. This contrast revealed activations in the right middle temporal cortex (centered at 51,  $-54$ , 6,  $Z = 4.71$ ,  $p < 0.05$ , corrected, voxel number = 147; and 57,  $-30$ ,  $-4$ ,  $Z = 4.45$ ,  $p < 0.001$ , corrected, voxel number = 352, corresponding to Brodmann's Area 21), the right posterior superior temporal cortex (centered at 61,  $-33$ , 15,  $Z = 4.33$ ,  $p < 0.05$ , corrected, voxel number = 151,

corresponding to Brodmann's Area 42), and the right inferior postcentral gyrus (centered at 46,  $-16$ , 37,  $Z = 3.93$ ,  $p < 0.05$ , corrected, voxel number = 145, corresponding to Brodmann's Area 1, 2, 3). The activated brain areas are illustrated in Fig. 1. We also calculated the reverse contrast, i.e., the contrast between stimuli in the random order condition and those in the coherent order condition. This contrast did not show any activation in any brain areas at the threshold of 0.05 corrected by multiple comparisons.

Because the same images were used in the coherent and random order conditions, the low-level visual features of the stimuli such as contrast, shape, and color were identical in the two conditions. Thus, any differences in the neural activities between the two conditions could not be attributed to the difference in low-level visual features. As moving objects in the movie clips usually appeared at neighboring locations in two successive static images in the coherent order condition, the images in the coherent order condition might generate apparent motion and thus induce the brain activations observed in the current study. However, this is unlikely because each image was presented for 1 s in the current study and thus the apparent motion implied by the two successive images was weak and comparable (if any) in the coherent and random order condition. This analysis is supported by the fact that MT and MST that are sensitive to short-range apparent motion [4] and biological motion [17] did not show any stronger activation in the coherent order than the random order conditions.

Alternatively, because moving objects or human bodies in two consecutive images usually appeared in continual locations in the coherent order condition, it is possible that images in the coherent order condition might generate stronger coding of order information or stronger coding of time information in working memory than the images in the random order condition and thus induced brain activations in the current study. Nevertheless, a prefrontal-parietal neural loop (including left dorsolateral and anterior prefrontal cortex and bilateral posterior parietal cortex) is involved in coding order information in working memory [11] and bilateral premotor cortices are the critical brain structures engaged in time perception [15]. The brain areas involved in perceiving static images in the coherent order condition observed in the current study are different from those involved in coding order information or time perception. Thus, the activated brain areas observed here may not simply reflect coding of order or time information in memory.

Finally, it is possible that subjects might automatically evaluate intention or desires of human characters when perceiving them in the coherent visual events. There has been abundant neuroimaging evidence showing that mental state reasoning when reading stories or viewing cartoon pictures activates the medial prefrontal cortex (MPFC) [3]. The MPFC is also strongly activated when adults view movie clips relative to static image extracted from the movie clips but presented in a random order [5]. Moreover, the MPFC activation was evident when viewing movie clips of human activities but not when viewing movie clips of animal activities, suggesting that the MPFC is automatically involved in mental attribution of human behaviors. Bilateral temporo-parietal junctions are also involved in mental attribu-

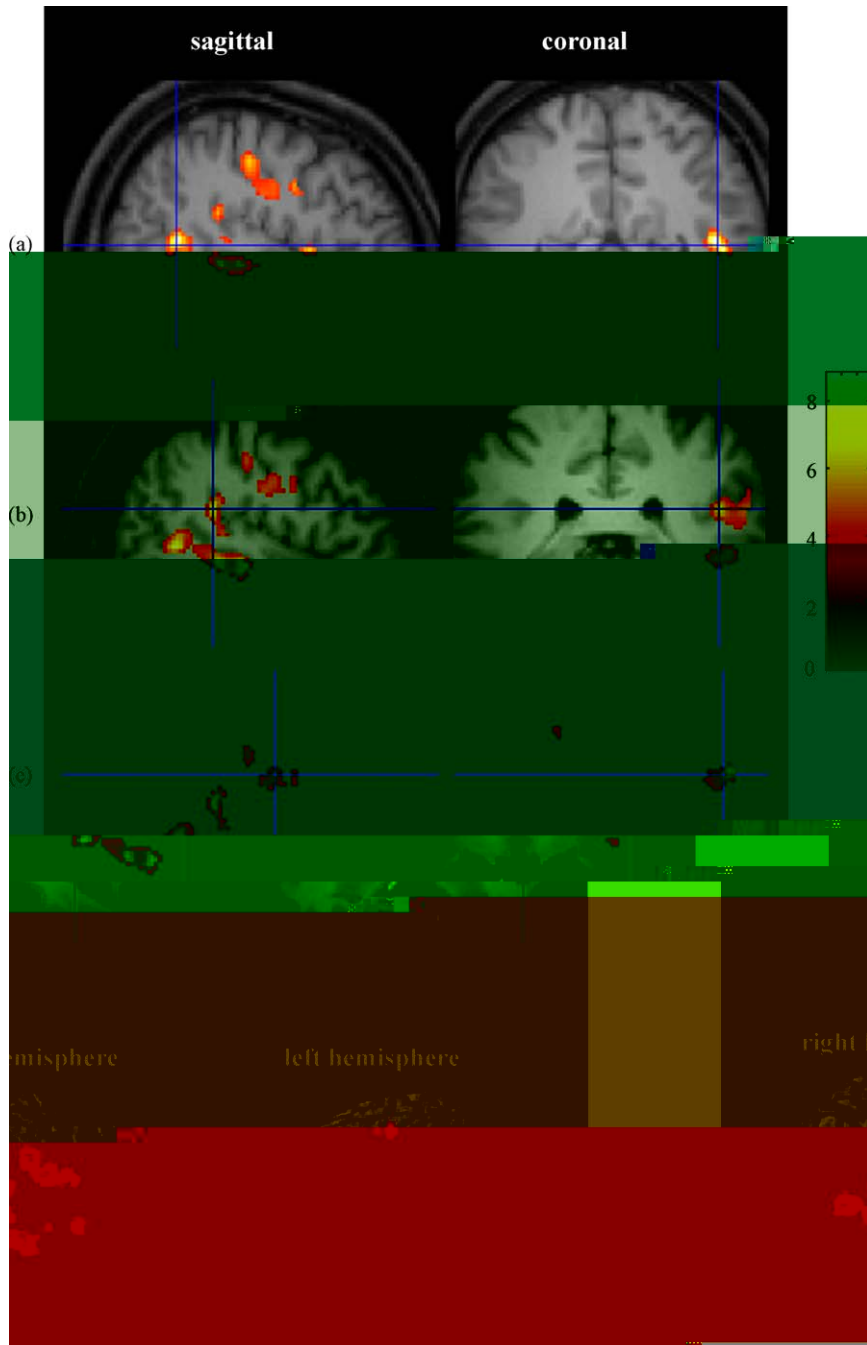


Fig. 1. Brain areas showing stronger activations in the coherent order condition relative to the random order condition. (a) Activation of the right middle temporal cortex illustrated in a representative subject's anatomical image; (b) activation of the right posterior superior temporal cortex illustrated in a representative subject's anatomical image; (c) activation of the right inferior postcentral gyrus illustrated in a representative subject's anatomical image; (d) the results of the group analysis from 12 subjects were rendered on a 3D anatomical image of the MNI template provided by SPM99. Threshold for activation of all clusters was  $p < 0.05$  corrected for multiple comparisons.

tion [13]. Activated brain areas observed in the present study, however, do not overlap with those involved in mental state reasoning, indicating that neural activities in the coherent order condition may not simply reflect the process of mentalization.

Note that the contrast between stimuli in the random order condition and those in the coherent order condition did not show activations in any brain areas. This further supports that the perceived coherence of visual events in the coherent order condition

was critical for the activated brain regions in the right hemisphere. We suggest that the right middle temporal cortex, the right posterior superior temporal cortex, and the right inferior postcentral gyrus are involved in the processing of coherence nature of visual events that were perceived in the coherent order condition but not in the random order condition. In other words, these areas are engaged in the processing of coherent relation between visual stimuli in successive static images, which is

critical for the understanding of the visual events. Unlike the processing of temporal coherence of language or music that is mediated mainly by the frontal cortex [1,2,9,12], the processing of coherence of visual events is mediated by the posterior part of the right hemisphere. Why does the right hemisphere dominate the perception of the coherence of visual events? A possible account is that, as locations of human bodies or objects evolve coherently in time, perception of the spatial relation between objects or humans is critical for understanding the coherence of visual events. Because the right hemisphere is supposed to dominate spatial cognition [7], the perception of coherence of visual events is thus mainly mediated by the right hemisphere.

Recent brain imaging studies have identified a few brain areas involved in the perception of actions. For instance, perception of hand actions enhances the activity of the postcentral gyrus [6]. Perception of intentional body actions increases the activity of the right posterior superior temporal cortex [14]. Accessing knowledge of actions through pictures also activates human MT/MST and nearby regions of the lateral temporal cortex bilaterally [8]. Our results extend the previous work by showing that the right middle temporal cortex, the right posterior superior temporal cortex, and the right inferior post-central gyrus are engaged in the perception of the coherence nature of visual events. The perception of the coherence nature of visual events is accomplished on the basis of action perception and thus was localized in the posterior brain areas closed to those underlying perception of actions. It appears that the perception of the coherence nature of visual events (based on action perception) is distinct from the perception of the coherence of auditory-linguistic stimuli (based on language processing), and thus the neural substrates for the perception of the coherence of visual and auditory-linguistic stimuli are dissociated between the anterior and posterior parts of the brain.

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