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Attentional modulation of neural activity in the macaque inferior temporal cortex during global and local processing

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Abstract

To examine whether visual attention to global and local features of visual stimuli modulates neural activity in the monkey visual cortex, we applied positron emission tomography techniques to monkeys while they were discriminating either global or local features of visual stimuli. The posterior inferior temporal cortex was more activated in discriminating global features than in discriminating local ones, whereas the anterior inferior temporal cortex was more activated in discriminating local features than in discriminating global ones. The results suggest that a functional difference exists in terms of processing of global and local features within the inferior temporal cortex.

Keywords: Macaque monkeys; Inferior temporal cortex; Global and local features; PET; Visual attention; Hierarchical visual stimuli

1. Text

Objects in our visual world have hierarchically organized structures. For example, a house consists of a roof and walls, which are then composed of slates, pillars, doors, windows, and other parts. We can direct and confine visual attention to either the entire house (the whole or the 'global' feature) or its components (the parts or the 'local' features). Some patients with damage in the visual cortex of the right cerebral hemisphere suffer selective impairment in processing global features, whereas those with damage in the visual cortex of the left cerebral hemisphere exhibit difficulty in processing local features (Delis et al., 1986; Robertson et al., 1988). Consistent with these clinical observation, brain imaging studies in normal subjects have shown that selective attention to global and local features enhances neural activity in the right and left cerebral hemispheres, respectively (Fink et al., 1996; Martinez et al., 1997; Weber et al., 2000). However, the cortical areas activated during each condition were not consistent among the studies. In addition to this uncertainty in the cortical areas activated during these processes, it is also difficult to interpret the results of brain imaging studies in terms of information processing due to the paucity of knowledge of physiology and anatomy of the human visual cortex. In this study, we applied positron emission tomography (PET) techniques to macaque monkeys whose visual system has been the most intensively studied both physiologically and anatomically among all primates (Ungerleider and Mishkin, 1982; Felleman and Van Essen, 1991), and searched for brain regions preferentially involved in processing global and local features of visual objects.

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We conducted PET scans in two monkeys (*Macaca fuscata*) while they were performing a visual discrimination task. They were trained to direct their visual attention to either global or local features of hierarchically organized visual stimuli (Fig. 1), and discriminate target letters (N, Z) from non-target letters (reversed N, reversed Z) at an attended level. The visual stimuli, 'N', 'reversed N', 'Z', or 'reversed Z' were presented in a pseudorandom order within the same blocks of trials. PET scans were performed for 60 s under global and local task conditions separately, and the PET data with above 90% of the correct performance rate were used for statistical analysis (15 scans in monkey MKT and 21 scans in monkey SNAT for each task condition). The monkeys responded with a shorter latency to global targets than to local targets (response time to global and local targets: mean $\pm$ S.D., 333 ± 33 and 345 ± 40 ms in monkey MKT, 347 ± 30 and 362 ± 37 ms in monkey SNAT, $P < 0.001$, t-test; see also Tanaka and Fujita, 2000), which is a classically known phenomenon termed 'global advantage' in humans (Navon, 1977). We identified brain areas whose regional cerebral blood flow (rCBF) changed differentially between global and local task conditions.

Two areas in the temporal lobe were differentially activated under the two task conditions. Regions in the posterior inferior temporal cortex (area TEO) were more activated under global task conditions than under local ones (sites 1 and 2 in Fig. 2, site 2 may include area V4 partially), whereas regions in the anterior inferior temporal cortex (area TE) were more activated under local task conditions than under global ones (sites 3–6 in Fig. 2). No other activated regions were observed in a consistent manner between the two monkeys. There was a slight difference of the exact location between sites 1 and 2 within area TEO, and the two sites were found in the different hemispheres of the monkeys. All the activated regions except for site 1 were located in the right hemisphere. This asymmetric activation was not due to a difference in the stimulus position on the retina, because their gaze during stimulus presentation was maintained at the center of the visual stimulus and did not differ between the two task conditions (Fig. 3). Visual stimuli were presented only for 100 ms to prevent the monkeys from making saccades during the stimulus presentation. We did not analyze the eye movements during inter-stimulus intervals, as the monkeys directed their gaze outside the computer display ($20 \times 20°$) beyond the area where the gaze direction was measurable. However, the differential activation of areas TEO and TE was not likely due to a difference in eye position during inter-stimulus intervals between global and local task conditions, because PET scans were performed in a dark room to minimize neural activation by surrounding scenes during inter-stimulus intervals.

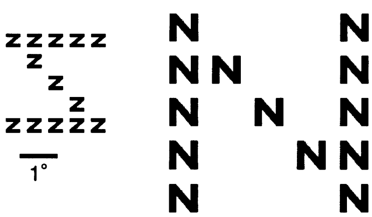

Fig. 1. Examples of visual stimuli. All visual stimuli consisted of 13 small identical letters. The global and local letters were 'N', 'Z', 'reversed N' or 'reversed Z'. The visual stimulus was presented for 100 ms at the center of a display. To instruct the monkeys in the timing of visual presentation and response, a small point ($0.2 \times 0.2°$ square) was presented for 500 ms before the stimulus presentation and for 600 ms after the stimulus disappearance. In global (or local) trials, the monkeys had to discriminate the global (or local) forms. When 'N' or 'Z' appeared at the attended level, they were required to push a lever down with their right hand within 500 ms after the disappearance of the visual stimulus. When 'reversed N' or 'reversed Z' appeared at the attended level, they had to wait until the small point was turned off and then push the lever down. Small (global/local = 2.7°/0.4°, left) and large (5.3°/0.8°, right) stimuli were intermingled in the same block of trials during PET scans with the attended level kept constant to exclude possible effects of the stimulus size within the range where the response time to global targets was shorter than that to local ones (Tanaka and Fujita, 2000). All experiments were performed in accordance with the Guide for the Care and Use of Laboratory Animals (1996) from the National Institutes of Health.

Selective attention to global and local features differentially enhanced the neural activity in areas TEO and TE, respectively. Areas TEO and TE are two successive visual areas in the later stage of the 'ventral visual pathway' which is crucial for object vision in non-human primates (Ungerleider and Mishkin, 1982; Felleman and Van Essen, 1991). According to topographical comparison between surface-based maps of macaque and human cerebral cortices (Van Essen et al., 1998), areas TEO and TE seem to correspond to areas in the human occipital–temporal cortical junction. Neuropsychological and brain imaging studies have shown a functional asymmetry between the two hemispheres of the human cerebral cortex, i.e. the right hemisphere for global processing and the left hemisphere for local processing (Delis et al., 1986; Robertson et al., 1988; Fink et al., 1996; Martinez et al., 1997; Weber et al., 2000). In the two monkeys tested in the present study, area TE of the right, not left, hemisphere was more activated under local task conditions than under global ones. This at least indicates that the left hemispheric dominance for local processing reported in human subjects does not strictly apply to macaque monkeys. Obviously, it requires further experiments involving a larger number of monkeys to determine whether the hemispheric dominance in processing global and local features exists in macaque monkeys.

The enhanced activation in area TE during local tasks complements the results of local cooling experiments, which showed selective impairment in the pro-

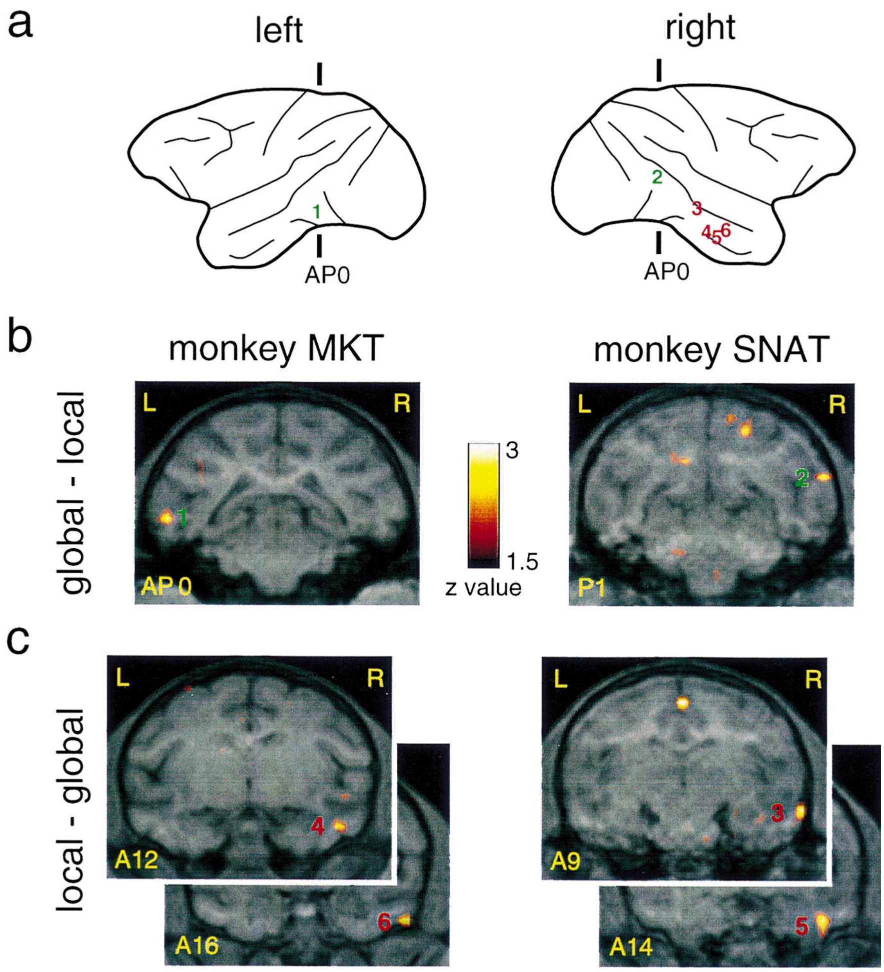

Fig. 2

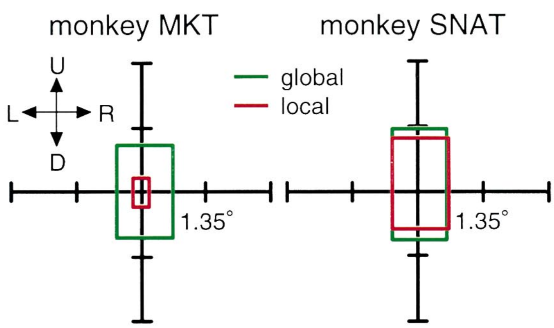

Fig. 3

Fig. 2. Brain regions activated differentially between global and local task conditions. PET scans were carried out using an SHR-7700 PET camera (Hamamatsu Photonics K.K., Japan). The spatial resolution was 2.6 × 2.6 × 3.2 mm full width at half maximum. PET scans were performed for 60 s by a bolus injection of $H_2^{15}O$ ($\cong$ 1.2 GBq) under global and local task conditions, separately. Accumulated PET data for 60 s were reconstructed (pixel size, 1.2 × 1.2 mm) and then smoothed with a 3.0 mm isotropic Gaussian filter. Subtraction analysis between the global and local task conditions was performed in each monkey using SPM95 software (Wellcome Department of Cognitive Neurology, UK). Brain regions with a differential rCBF change between the two conditions were identified at a statistical threshold of $Z = 2.58$ ($P < 0.01$, uncorrected). In PET experiments in monkeys, most activated regions are small, ~3 × 3 × 3 mm, and the maximum Z-values are typically < 3. We used a more liberal statistical threshold than that frequently used in human studies. More details on monkey PET experiments have been described elsewhere (Onoe et al., 2001). (a) The differentially activated regions are shown on a surface view of monkey brain (sites 1–6). Green numbers (sites 1 and 2) indicate the regions that were more activated under global task conditions than under local ones and red numbers (sites 3–6) indicate the regions that were more activated under local task conditions than under global ones. (b) SPM{Z} maps are overlaid on sections of magnetic resonance images of each monkey. The numbers in each coronal section correspond to those in (a). An activation spot in the parietal lobe of monkey SNAT is found only in this monkey and, not consistent in the two monkeys. Maximum Z-values at sites 1–6 are 2.94, 2.88, 3.25, 2.75, 3.00, and 3.06, respectively.

Fig. 3. Mean eye position during a stimulus presentation. Eye movements during PET scans were measured using an infrared charge-coupled device (CCD) camera system (Hamamatsu Photonics K.K., Japan) with 0.5° of the spatial resolution within a 20 × 20° measurable area of the monkey's visual field. The center of rectangle represents the mean eye position during 100 ms epoch of stimulus presentation under global (green) and local (red) task conditions, and the rectangle represents the area of the mean eye position ± S.D. during the period.

cessing of local features of visual stimuli during reversible inactivation of area TE (Horel, 1994). Some TE neurons exhibit extremely high sensitivity to subtle changes in local features of visual stimuli (Tanaka et al., 1991; Fujita et al., 1992; Kobatake and Tanaka, 1994). The activity of these neurons may be enhanced under local task conditions when monkeys direct their attention to local features. These results suggest that area TE is critically involved in processing local features of a visual object. On the other hand, the present study shows that area TEO is more activated during global processing than during local processing. Previous lesion studies suggest that area TEO plays an important role in visual pattern discrimination, whereas area TE is more involved in visual object recognition (Iwai and Mishkin, 1968; Kikuchi and Iwai, 1980). The present results suggest a new aspect of functional differentiation along the posterior–anterior axis of the macaque inferior temporal cortex.

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