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Attention Modulates the Blood Oxygen Level Dependent Response in the Primary Visual Cortex measured with Functional Magnetic Resonance Imaging

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Introduction

Attention is a basic mechanism which enables the processing of incoming stimuli to be enhanced or attenuated. In the auditory modality, for example, a person can attend selectively to a particular speaker's voice while turning off other, simultaneous, conversations ("cocktail party phenomenon"). Although this process has been the target of extensive research, even a few years ago it would not have been possible even in preliminary form to outline a functional anatomy of the human attentional system. New developments and techniques in neuroscience (positron emission tomography, magneto-encephalography, and functional magnetic resonance imaging) have opened the possibility of studying the anatomical basis of higher cognitive functions, including attentional processes. These new techniques have made possible the delineation of attentional systems that control alertness [1, 2], consciousness [3], spatial visual attention [4], and higher cognitive functions [5]. However, controversy continues as to whether attentional processes modulate neuronal activity within primary sensory areas [6]. Most researchers believe that attentional modulation is related to activity in secondary sensory areas [7]. We report here data supporting the notion that there is indeed modulation of neuronal activity within the primary visual cortex due to attentional processes.

Methods and Materials

Functional Magnetic Resonance Imaging

The system that we used for functional magnetic resonance imaging was the Siemens Magnetom Vision 1.5-T scanner (16 quasicontiguous slices oriented according to the AC-PC line; repeat time, 3 s; two-dimensional echo planar imaging; voxel size: $3.1 \times 3.1 \times 3.3$ mm; echo time: 66 ms; a: 90°, field of view: 200×200 mm). We measured the blood oxygen level dependent response while subjects (six men; mean age, 26.2 ± 5.2 years) were presented with flicker light (average frequency, 3 Hz) via goggles. All subjects gave prior informed consent according to a protocol approved by the Ethics Committee of the Heinrich-Heine University Düsseldorf. A series of 85 images were acquired During each experimental condition ("attention" and "nonattention"). Each series consisted of multiple periods of "baseline" (OFF, rest), during which subjects heard only the ambient machine noise, alternating with periods of "activation" (ON), during which the flicker light was turned on. Each series began with five baseline images (15-s interval), followed by 80 images during which "rest" alternated with "activation" every 30 s (60 s/cycle, 20 images/cycle, 4 cycles). The total duration of each image series was about 4 min. The visual stimulation covered the whole visual field, thus resulting in a "Ganzfeld stimulation" making eye movements unlikely. The frequency of the flicker light changed occasionally for about 2 s from 3 to 2 Hz or from 3 to 4 Hz. These frequency changes were introduced twice per ON period and were separated by an interval of at least 10 s. The order of these frequency changes were counterbalanced across the various ON periods. Subjects were instructed to fixate centrally while the visual stimulation started. In the "attention" condition the instruction was "detect changes in frequency" and during the "nonattention" condition to "ignore" the flicker light and the changing of frequency although watching them. The detection of changing frequency was indicated by lifting the index finger of the right dominant hand. The order of the two conditions was counterbalanced across all subjects.

Image Analysis

Image analysis was performed on SPARC II workstations (Sun Microsystems) using MATLAB (Version 4.2c, Mathworks, Natick, MA, USA) and SPM96 [8]. First, the first five images of each time-series, during which the magnetic resonance signal reaches a steady state, were discarded. The 80 remaining volume images of each condition were automatically realigned to the first image to correct for head movement between scans. Then the images of the two sessions were coregistered and transformed into a standard stereotactic space (depending on the MNI template [8, 9]) approximately corre-

sponding to the atlas of Talairach and Tournoux [10], using the intercommissural line as the reference plane for the transformation. The spatial normalization involves both linear and nonlinear transformations to match each scan to a reference image that already conforms to the standard brain. Within this normalization pixels were smoothed slightly to achieve isotropic voxels representing 4×4 mm in the x and y dimensions, with an interplanar distance of 4 mm. Voxels having values greater than 0.8 of the volume mean in all the images were selected to restrict that analysis to intracranial regions.

The effects of global (whole volume) activity and time were removed as confounds using linear regression and sine/cosine functions (up to a maximum of 2.5 cycles per 80 scans). Removing the latter confounds corresponds to high-pass filtering of the time series to remove low-frequency artifacts which can arise due to aliased cardiorespiratory and other cyclical components. Images were then smoothed with an isotropic gaussian kernel (8 mm full-width half-maximum), in accordance with the statistical requirements for using the general linear model and to account for interindividual differences in sulcal and gyral landmarks. To detect significantly activated voxels both individual and group analyses were performed. Here we report results of only the group analysis because there were no substantial differences between the group and individual analysis.

Results

We first tested for significant activations comparing functional magnetic resonance imaging datasets acquired during OFF periods vs. periods of visual stimulation (ON periods) and found, as expected, strong activity in the primary (V1) and secondary visual cortex (V2). There was no further activation outside the visual cortex. This was not surprising because motor responses during the "attention condition" occurred too seldom (only twice per ON period) to evoke reliable hemodynamic responses within the motor cortex. Calculating the interaction between the two experimental conditions ("attention"/rest vs. "nonattention"/rest) revealed stronger signal changes during the "attention" condition than during the "nonattention" condition in two relatively small clusters within V2 (size of activated volume; 2 ml; maximum activity, Z score 4.9) and, most astonishing, also in V1 (size of activated volume, 1.7 ml; maximum activity, Z score 4.9; Fig. 1).

These anatomical localizations were verified by referring to prominent gyral and sulcal landmarks (lingual gyrus, calcarine sulcus and gyrus, cuneus) and typical Talairach coordinates indicating V1 and V2 both in the individual brains and the mean group brain. There was no further activation outside these areas. To rule out whether the subjects were simply less aroused in the "nonattention" condition we compared the rest periods of the "nonattention" and "attention" conditions, but found no significant differences. Thus it is unlikely that a general arousal effect affected our results.

Discussion

Taken together, our findings show that the visual stimulation applied here evokes a strong hemodynamic response in the primary (V1) and secondary (V2) visual cortex. Most importantly, however, we found stronger hemodynamic responses in V1 and V2 when the subjects were required to attend to the stimuli. This enhancement effect is important for several reasons: First, there is greater activity in V1 and V2 during the "attention" condition than in the "nonattention" condition *although* the physical properties of the stimulation remains the same across the two conditions. Thus attention should be responsible for this enhancement effect. Second, this enhancement effect is found also within V1, a brain area for which a direct modulation of activity by attention has not previously been reported. Previous brain imaging studies on visual attention have found enhancement effects only in extrastriate cortices [4, 11] and in widespread cortical neural pathways where the exact location of the involved cortical regions depended on the nature of the attention task [1–3, 5, 12]. The reason for the enhancement effect in V1 may depend on the nature of the stimulus used in our experiment, which evoked hemodynamic responses only in a relatively small cortical area comprising V1 and V2. Thus only these cortical areas are relevant for the processing of these stimuli. Because attention appears to be expressed as

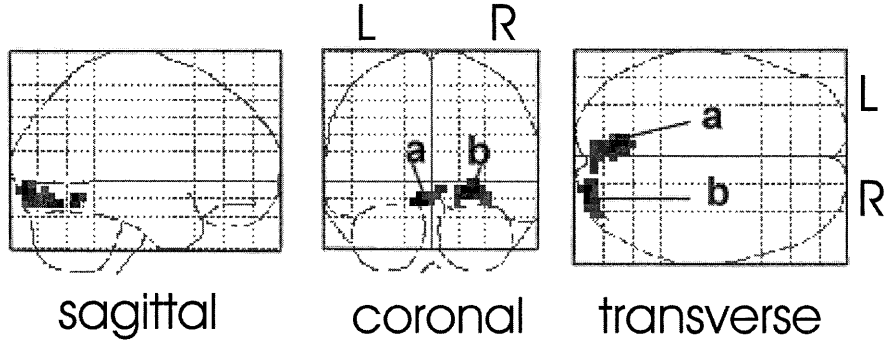

Fig. 1. Significant mean hemodynamic responses (indicated as cluster of gray values) for the interaction effects, comparing hemodynamic responses obtained during the "attention" condition with those obtained during the "nonattention" condition. Areas of significant signal increases (height threshold $Z = 3.09$, spatial extent $P < 0.05$, corrected for multiple nonindependent comparisons) are shown superimposed upon a "SPM glass brain" (views from right-sagittal, back-coronal, and above-transverse). There was no further hemodynamic response outside these visual cortical areas. *a*, Significant activation where visual stimulation during the "attention" condition evoked stronger hemodynamic responses in the primary visual cortex (V1, lingual and calcarine gyrus) than during the "nonattention" condition; *b*, significant activation where visual stimulation during the "attention" condition evoked stronger hemodynamic responses in the conjunction between V1 and V2 (inf. occipital cortex) than during the "nonattention" condition. *R*, Right hemisphere; *L*, right hemisphere

an enhancement of activity in the neural pathways relevant to task performance [12], our finding is consistent with that view.

However, the precise mechanism by which early visual processing is modulated by attention remains unknown. A tonic increase in activity in the visual cortex may occur in anticipation of a stimulus. Alternatively, there could be a phasic modulation such that each stimulus or only each target stimulus elicited a larger response in a visual target area. Future studies will have to disentangle these two alternatives. A further important question which should be investigated in future experiments is whether cortical and subcortical structures are differentially involved in attentional processing. For instance, the research of Wurtz and Mohler [13] on monkeys demonstrates a neuronal enhancement effect within striate cortex occurring during a visual target detection task (and not during passive viewing) for visual targets *and* nontargets, thus supporting the notion that cortical neurons react nonspecifically to visual stimuli. In contrast to this nonspecific cortical enhancement during detection tasks, they found enhanced neuronal activity in the superior colliculus only to targets and not to nontargets, thus suggesting a selective enhancement of neuronal activity before cortical analysis [14]. In addition, it would also be worthwhile to examine the effective connectivity between V1 and V2 and the possible effects of attention on this connectivity. However, we hope that the present results will help to understand the cortical control of attention and also motivate more research on the attentional processes within primary sensory and motor areas.

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Green leaf volatiles inhibit response of red pine cone beetle *Conophthorus resinosae* (Coleoptera: Scolytidae) to a sex pheromone

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Green leaf volatiles were tested to determine whether they inhibit responses of male red pine cone beetles (*Conophthorus resinosae* Hopkins) to a sex pheromone. Hexanal and (*E*)-2-hexenal did not significantly inhibit the response of male beetles to the sex pheromone (±)-*trans*-pityol. However, trap catch was significantly reduced when the four alcohols [hexan-1-ol, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, (*Z*)-3-hexen-1-ol] were presented with the pheromone. Experiments with single presentations of alcohols with the pheromone indicated (*E*)-2-hexen-1-ol was the most disruptive. The addition of the two aldehydes to the quaternary alcohol combination did not enhance the effect of the alcohols. The green leaf alcohol (*E*)-2-hexen-1-ol was detected in trembling aspen, *Populus tremuloides* Michx., but not in red pine, *Pinus resinosae* Ait, the primary host of the red pine cone beetle. This is the first report showing that male cone beetles are deterred by nonhost odors. Green leaf alcohols may be promising pest management tools to protect high value seed orchards from cone beetle damage.

How the red pine cone beetle finds a suitable host remains a mystery. Henson (1962, 1967) hypothesized that cone beetles leave the forest floor in early spring, where they overwinter, and fly towards the most intense illumination above the tree crown. Once there, they orient towards dark silhouettes and land on exposed branches. Mattson et al. (1984) developed a conceptual model of cone finding and concluded that beetles al-

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