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TILE II. LATENCY DIFFERENCES AND EFFECTS OF SELECTIVE ATTENTION TO GRATINGS IN THE CENTRAL AND RIGHT VISUAL FIELDS

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II. LATENCY DIFFERENCES AND EFFECTS OF SELECTIVE ATTENTION TO GRATINGS IN THE CENTRAL AND RIGHT VISUAL FIELDS

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INTRODUCTION

This study extends our previous work utilizing sinusoidal grating stimuli (see George et al., this volume) by focusing on effects associated with selective attention to features of grating stimuli. Attention was manipulated by having subjects respond, with a reaction-time task, to one of four stimulus types while physiological measures were obtained to all four stimuli concurrently. This design allows for the comparison of neural responses as a function of 1) type of stimulation (stimulus differences) and 2) selective attention to different features of a stimulus (effects of attention). For example, it is possible to compare responses to a stimulus when it is attended, not attended, or shares features in common with the attended stimulus (e.g., spatial frequency or visual field). Amplitude, latency and field distributions associated with these effects car: then be compared.

Immediate goals of the present study are to examine the temporal sequence in which certain types of visual information (such as visual field, spatial frequency, or the conjunction of these features) are processed and to determine whether different neural sources are activated when such features are attended versus not attended. These issues are basic to current models of visual selective attention (see reviews 1, 2, 3). However, in order to address the issue of selective attention it is essential to examine the sensory processing of these stimuli by the visual system. For example, how does the size of a pattern (i.e., spatial frequency) interact with its location in space? If a particular stimulus is processed by the visual system more quickly than another, is there an earlier effect associated with attending that stimulus? Since data analysis is still in progress, the focus will be on two general levels of processing: attention to visual field and spatial frequency. Interactions within these levels will not be considered at present.

Because we observe considerable inter-subject variability in the data, also noted by Brenner et al. (4), we feel compelled to deal with this issue outright. Evidence available on human anatomy attests to the uniqueness of individual brains. Not only are there differences in cortical geometry between subjects (5) but differences can also be seen at the most peripheral neural levels such as the retina (6). It is difficult to dispute that there are functional correlates to these anatomical and physiological differences between individuals which argues in favor of single-subject analyses rather than across-subject analyses.

METHOD

The method is essentially the same as in the previous experiment with the addition of a selective attention task. Subjects were instructed to respond, by pressing a fiberoptic-coupled mechanical switch with the left index finger, to one of four equiprobable and randomly presented stimulus types: 1) 1 cycle per degree (cpd) grating presented in the right visual field (LO RVF); 2) 5 cpd grating presented in the right visual field (HI RVF); 3) 1, cpd grating presented in the central visual field (LO CVF) and 4) 5 cpd grating presented in the central visual field (HI CVF). Subjects were informed before each trial block as to which of the four stimuli required a reaction-time response. Each trial block consisted of 100 trials (25 passes of each stimulus type) and was replicated four times. The order of replications and trial blocks were counterbalanced. Individual reaction-time responses were within .6 seconds of target stimulus onset, otherwise the trial was repeated.

Magnetic (MEG) and electrical recordings (ERPs) were obtained simultaneously to each of the tour stimuli during each attention condition. Reaction-time (RT) data were also obtained from the task-relevant (attended) stimulus. MEG responses were monitored at a minimum of 14 sensor locations (areas around the maxima), primarily from the left occipital and parietal regions. Electrical recordings were obtained from sites O1 (left occipital), C3 (left central), and F3 (left frontal) and were referenced to the right earlobe. Statistical analyses (MANOVA, ANOVA and Scheffes) were performed on the amplitudes of the MEG maxima and ERP recordings at specified points in time for each subject. In two subjects, a more extensive mapping was undertaken including 42 magnetic sensor locations and 12 electrode placements which spanned both left and right hemispheres. A minimum of two replications was obtained at each of these locations.

RESULTS

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Latency Differences.--Figure 1 shows abstracted MEG waveforms of two adult males (2.5 cm left of midline and 5.5 cm above the inion) demonstrating the kind of individual variability typically seen in these studies. Responses obtained from subject GM (right portion) show major differences associated with visual field (VF) rather than spatial frequency (SF) in a positive component peaking around 125 msec. This component is of greater amplitude and has a longer latency to peak during central field stimulation. Subject LD, on the other hand, shows an interaction between SF and VF. The peak of the tirst positive component is seen to peak earlier in time for LO SFs when compared with HI SFs and for RVF when compared with CVF. The LO RVF condition, however, has the earliest peak latency. Figure 2 shows reaction-time data for all subjects. Across subjects, LO CVF is responded to most quickly.



Figure 1. Abstracted MEG waveforms for two subjects showing differences in response latency between different stimuli. Subject L.D. shows different peak latencies of the early positive component (100-125 msec) as a function of both SF and VF while subject G.M. shows significant differences in latency between the RVF and CVF conditions only.



Figure 2. Reaction-times for four subjects Individual analyses were statistically significant and showed that three of four subjects responded to the LO CVF stimulus most quickly.

Attention or Effects of Task Relevance.--Figure 3 shows the temporal sequence in which different features of the stimulus were processed for both MEG (2.5 cm to the latt of midline and 5.5 cm above the inion) and ERPs at locations O1 and F3. The waveforms depicted in this figure are responses averaged across the four stimuli. The waveform representing 'VF' reflects an average of responses to each of the four stimuli when visual field was in common with the attended condition. Similarly, 'SF' reflects an average across each stimulus when spatial frequency was in common with the attended condition and 'NEITHER' reflects an average across responses when they had

nothing in common with the attended condition. For example, if a subject responded behaviorally to the LO RVF condition then 'NEITHER' reflects neural responses to the HI CVF stimulus; 'VF' reflects responses to the HI RVF stimulus and 'SF' reflects responses to the LO CVF stimulus. These three relevance levels (VF, SF and Neither) were obtained from each of the four attention conditions and within a relevance level, responses to the four stimuli were averaged together. Each tracing reflects the average of 400 individual neural responses.



Figure 3. Above--MEG and ERP waveforms for one subject (LP) demonstrating effects associated with attention to different visual features. Earliest effects are noted in the MEG waveform (150 msec) associated with attending to VF (solid lines versus closed boxes--cross-hatched area).

Figure 4. Right--Contour plots for one subject (CA) when HI CVF was attended versus nonattended. The dots reflect actual data points. The MEG waveforms (top portion of Figure 3) demonstrate an early (150 msec), significant effect associated with attending VF (compare solid line with closed boxes--cross-hatched area). The ERP data do not show significant differences at this same point in time. In comparison, early effects associated with attending SF are not noted in the MEG data but are of statistical significance in the ERP recorded at F3 (statistically significant at 240 msec-- compare open boxes with solid lines). Finally, note that effects of attending VF in the MEG data occur earlier in time than effects associated with SF in the F3 data (150 versus 240 msec).

Figure 4 shows contour plots for the first positive component peaking at 115 msec for subject CA for attend and not-attend conditions. The left side reflects the amplitude distribution when both features of the HI CVF stimulus were attended (SF & VF). The right portion shows the distribution to the same stimulus when LO RVF was attended (i.e., NEITHER condition). There is evidence of several dipoles in these plots, which is to be expected with central field stimulation since both upper and lower and left and right fields are stimulated simultaneously. But, more importantly, differences noted between the contour plots are primarily differences in amplitude and not in the location or orientation of the primary dipoles. The amplitude of the positive component increases with the attention task.



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DISCUSSION

Latency Differences.--Several investigators have reported shifts in latency of the neural response associated with increasing spatial frequency in central vision (4, 7). These differences have been interpreted as reflecting the preferential activation of X-cell or Y-cell types in the retina depending upon the SF of the stimulus (see George, Aine and Flynn this volume for a brief review). An alternative explanation for the psychophysical and MEG data is based on average receptive-field size (8). Receptive-field size increases as one progresses from the fovea to the periphery and larger receptive fields are correlated with faster conduction times. Subject GM's

responses (Figure 1--right portion), show an increase in latency with VF (longer latencies to CVF compared with RVF) and little effect of SF within a given field which is consistent with an explanation based on the average receptive-field size of the retinal ganglion cells stimulated. However, the responses of subject LD (left portion of Figure 1) cannot be explained in terms of average receptive-field size alone since there is an interaction between VF and SF. Not only is there a notable latency difference between the 1 and 5 cpd stimulus in CVF but this difference also exists in the RVF data.

Some latency differences observed between the spatial frequencies may be accounted for by differences in the *perceptual* contrast between stimuli (7). However, this explanation cannot account for the fact that in several subjects the HI RVF condition showed faster latencies than the HI CVF condition. A decrease in perceptual contrast should be more evident for HI SFs in the periphery (implying longer latency responses) compared to central vision if contrast alone accounted for these differences. It is possible however, that perceptual contrast is correlated with (or a function of) other aspects of the neurophysiological response.

When taking the reaction-time data into consideration, we see that all four subjects respond most quickly to the LO CVF condition (one subject responded equally fast to the LO RVF and LO CVF). These results do not correlate with the first positive deflection in the MEG waveforms (corresponding to the P1 component in the ERP data) for any of the subjects. Studies on humans and monkeys suggest that the P1 component reflects the first thalamocortical projection to layer IVC (9). Since this component reflects early sensory activity, we question the validity of using RTs for inferring differences between *early* sensory events at the cortical level (7).

Selective attention.--In all four subjects effects associated with attending VF preceeded effects associated with attending SF. Generally speaking, the MEG data and data obtained from O1 showed an earlier onset of the VF effect compared with other electrode locations. This is consistent with the results of extensive mapping of two subjects which showed an occipital source for the P1 component. The enhanced amplitude of the positive component in Figure 3 (top portion) also suggests that an effect of attending VF is to enhance the sensory processing or information transmission associated with this stimulus feature. Figure 4 confirms this interpretation, again showing a general enhancement of amplitude associated with attention rather than a change in the orientation or location of the source. This result and interpretation is consistent with data and ronclusions of Kaufman and Williamson (10).

Effects associated with attending the spatial frequency of the stimulus, however, were generally small, occurred later in time (after 200 msec poststimulus), and in some cases, were nonexistent. When these effects were evident, they were seen in different sensor and electrode locations between subjects. A careful examination of these data is still underway.

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