Seminar: Cognitive and Behavioral Neuroscience Seminar (603)

Meeting Date: March 21, 2002

Chairs: Herbert S. Terrace
Speaker: Dr. Leslie Ungerleider (NIMH)

Topic: "Neural mechanisms of visual attention in the human brain"

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At any given moment in time there are a number of objects present in the visual scene, and a problem is that the visual system has limited attentional resources. All of the objects in a visual scene are therefore competing for neural representation. How does the visual system solve this problem? One method of doing so is through directed attention. When attention is directed to a specific portion of a visual scene, the attended portion of the scene is processed preferentially relative to the other objects in the scene.

For the remainder of the talk, Dr. Ungerleider was focused on evidence obtained from neuro-imaging studies examining two phenomena: 1) Competition for neural representation, and 2) The way directed attention works to overcome the competition for neural representation. As one proceeds forward through the ventral stream, receptive fields become increasingly larger. For example, the receptive field for V1 has a very small receptive field, but the receptive field for area TE is very large. Activity in these areas is enhanced when a monkey directs its attention toward a visual stimulus. When a stimulus is within the visual field, neural activity is greater than when the stimulus is outside of the receptive field. In scenes with multiple stimuli present, there appears to be neural competition. For example, when monkeys are presented with a yellow bar outside of the receptive field, followed by a diagonal red bar within the receptive field, the neural response in the receptive field decreases. However, when the monkey directs its attention toward the yellow bar, competition for neural representation is essentially eliminated, and the neural response to the yellow bar increases.

In the first fMRI study, there were two hypotheses: 1) Multiple stimuli should result in sensory suppression, and 2) that directed attention should eliminate the suppression. The stimuli used were a series of colorful complex images that were presented in two different ways. In both conditions, the subjects were required to fixate at the lower portion of the screen by counting the occurrences of the letter "L" or "T". In the sequential condition, the subjects were presented with four different stimuli each for 20-50ms. The stimuli were presented sequentially and in different locations on the screen. In the simultaneous condition, all four stimuli are presented for 20-50ms at the same time. It was hypothesized that simultaneous presentation should produce more suppression than the sequential condition. The conditions were presented in 18 second blocks in the order of sequential → simultaneous → simultaneous → sequential. The prediction was that both conditions should show some activation, but that the activation should be reduced in the simultaneous condition relative to the sequential condition. The areas measured were V1, V2, V4, TEO. It was found that there were no differences in activation across the two conditions for V1 or V2, but there were differences in the predicted direction for both V4 and TEO. The reason for this difference is that the entire display can fit within the receptive fields of V1 and TEO which makes sensory interactions possible here, yet not in the receptive fields of V1 or V2. In support of this view, increasing spatial separation distance of the stimuli produces no suppression in V4, but does produce suppression in the much larger receptive field in TEO.

In the second experiment, an additional condition was included in which the subject covertly directed attention toward the nearest stimulus location. The hypothesis was that the effect of directed attention should increase activation in both the simultaneous and sequential conditions, and additionally, that the differences observed in the unattended condition should disappear in the attended condition. The reason is that in the attended condition, directed attention should essentially eliminate competition for neural representation and thereby eliminate the source of differences across attended and unattended conditions. The hypothesis was shown to be true for both V4 and TEO. This suggests that these two areas are important sites where top-down attentional input can modulate competition among stimuli. Therefore, it was further hypothesized that damage to these two areas in monkeys would affect the monkey's ability to use attention to filter out distracting stimuli. So, in order to examine this possibility, the dorsal part of area V4 was removed in both hemispheres, thereby affecting both quadrants of the lower visual field. All of TEO was removed in one hemisphere, which affected the upper and lower quadrants of the contra-lateral visual field. This left one quadrant intact, which therefore allowed examination of performance when fixating in the lesioned V4 field, the lesioned TEO field, the combined TEO and V4 lesioned fields, and the intact field.

The monkeys were presented with a contrast grating while fixating. They were required to release a lever if they saw a vertical grating, and to hold the lever if they saw anything other than vertical. This was done both in the presence and in the absence of distractors. The distractors consisted of round discs that surrounded the target. In the normal quadrant, the distractors had no effect on the monkey's performance. The reason is that the monkeys can use directed attention to filter out the distractors. In all three lesioned conditions however, the monkeys showed marked degradation of performance when the distractors were presented. The effect was largest for the combined lesion. During the next phase of the experiment, the saliency of the target was manipulated. Without distractors, the monkeys performed well. With distractors however, monkeys tested with intact areas did well, but monkeys with lesioned areas performed poorly for targets with low contrast, yet performed well on targets of high contrast relative to the distractors. This suggests that the lesioned monkeys performance was governed by bottom-up sensory-driven input. The conclusion was that the top-down attentional influences of areas V4 and TEO counteract bottom-up sensory input.

The first question posed at the beginning of the talk (How are objects selected for attention?) is composed of two parts: 1) What is the source of the attentional signal, and 2) What are its effects on the visual cortex? The source must be outside of the visual ventral stream pathway itself. That is, it is possible to direct one's attention to objects that are not in the visual field. But, even though the attentional signal is generated outside of the visual system, the attentional signal must cause a change in the visual cortex in order to modulate the activity in the ventral stream areas. Previous research in other labs suggests that the effect of attention is to increase base-rate neural firing for receptive fields at the expected location for the to be attended object. This functionally sensitizes these neurons such that when a stimulus is presented, there is an enhanced response.

There is also evidence for increases in baseline firing rates in the human visual cortex as well. In the next experiment, many of the conditions were the same as in the previous monkey experiments. There were both attended and unattended conditions across the sequential → simultaneous → simultaneous → sequential blocks. However, prior to the attended blocks, subjects were cued to shift attention in anticipation of a stimulus that would occur in a given location. When stimuli were presented without attention, there was little activity in the ventral extra-striate cortex. However, in attended conditions both with and without a physical stimulus, there was enhanced activity in the ventral extra-striate cortex. More precisely, there appeared to be enhanced base-rate firing during the expectation of stimulus presentation period, and a subsequent enhanced response once the stimulus was actually presented. In the frontal and parietal cortices, the patterns were slightly different. Without directed attention, these areas showed no activity. With directed attention however, there was activation, and the activation was equal in both attended-with-stimulus conditions and attended-without-stimulus conditions. This suggests that the frontal and parietal cortices may function in directing attention generally, but do not react to the presence of the stimulus per se.

Dr. Ungerleider reports that some of the more recent work conducted in her lab has been focused on examining the allocation of attentional resources. One view is that attentional resources are limited, which explains why subjects do very poorly detecting changes in a visual scene unless attention is shifted directly to the area of change. Unattended items do not reach awareness. An opposing viewpoint is that attentional resources are not necessarily taxed for some types of stimuli -- particularly for stimuli containing emotional content information. The experimental question was: Does activity evoked by emotional content require attentional resources? The stimuli used in the experiment were angry, happy, and neutral faces. The faces were presented in one of two conditions: 1) an attended condition in which subjects attended to the faces, and 2) an unattended condition in which subjects were given a distractor task (to deplete attentional resources). Areas of the brain that respond to faces were identified by means of a face network localizer task in which areas of the brain were mapped while subjects were looking at scrambled and unscrambled faces. Once these areas were identified, the purpose of the experiment was to determine whether valence of the face (happy, neutral, angry) or attention was the most important factor in modulating neural response. It was found while these areas responded strongly to the valences of the faces, they did so only during the attended condition. So, the conclusion is that valence of the faces can bias the competition for neural representation, but it can only function this way if there are some attentional resources available. If attentional resources are completely exhausted, then stimulus valence cannot bias competition for neural representation.

QUESTIONS:

Goldberg: If there is no effect of valence when the subject is not attending, how do you explain the galvanic skin response experiments?

Ungerleider: I think there are attentional resources available during those experiments. I am interested in the relationship between awareness and the presence or absence of attentional resources. That is, just because one is not aware of a visual stimulus does not mean that attentional resources are not being allocated to it.

Terrace: Can you explain the timing of these processes and perhaps elaborate on the temporal order in which these processes occur neurally?

Ungerleider: Well the process initially travels to V1 and then V2, but at each level in the system, there are recurrences back to these earlier areas. With fMRI however, precise timing information is not possible.

Chris Summerfield: It seems that the differences you find between your simultaneous and sequential conditions could be because sequential presentation of the stimuli is inherently more interesting to the monkey than a simultaneous presentation.

Ungerleider: This was initially a concern for us, so we ran a lot of controls in order to rule that out as an explanation. For example, in one set of experiments we projected a visual stimulus just above the horizontal meridian in the visual field and we projected three stimuli below the horizontal meridian in the lower visual field. We then looked at the evoked response upper field quandrant of V4 to the single stimulus and compared it to a case in which that single stimulus and three others were presented nearby. In the nearby stimulus, the response is suppressed.