

Seminar: Cognitive and Behavioral Neuroscience Seminar (603)
Meeting Date: September 13, 2001

Chairs: Herbert S. Terrace, Peter Balsam, Jon Horvitz, and Yaakov Stern

Speaker: Michael Goldberg, Columbia University

Topic: Tracking the Spotlight of Attention: physiological and psychophysical mechanisms in the monkey.

Seminar Participants:

John Hilton, Columbia University
Brain Rakitin, Neurology, Sergievsky Center
Josh Wallman, Biology, City College
Colin Beer, Rutgers University-Newark
Christian Habeck, Neurology, Sergievsky Center
Jon Horvitz, Psychology, Columbia University
Peter Balsam, Psychology, Barnard
Jen Manly, Neurology, Sergievsky Center
Tammy Moscrip, Psychology, Columbia University
Anya Soldan, Psychology, Columbia University
Chara Malpani, Columbia University
Tao Sheng Liu, Psychology, Columbia University,
Desiree Bird, Sergievsky Center
Christopher Summerfield, Psychology, Columbia University
Herbert S. Terrace, Psychology, Columbia University
Peter Balsam, Psychology, Barnard College
Jon Horvitz, Psychology, Columbia University
Yaakov Stern, Sergievsky Center, Columbia University

Rapporteur: Kate Lynch

Dr Goldberg's topic was the visual and attentional properties of parietal neurons and the relationship of parietal neurons to the generation of eye movements. He began with a brief overview of attention in general and then discussed several new experiments on the quantification of attention in the monkey. He showed that the spatial location and the timing of an individual monkey's attention can be predicted by the activity of a monkey's parietal neurons.

Dr. Goldberg began his discussion of attention with a quote from William James:
"Everybody knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought... It implies withdrawal from some things in order to deal effectively with others."

James says that attention is either passive, effortless and involuntary or active and voluntary. In passive immediate sensorial attention, the stimulus is a sense-impression, either very intense, voluminous, or sudden and grabs your attention without any effort. The immediate effects of attention are to make us: perceive, conceive, distinguish, remember and have a shorter reaction time.

Dr. Goldberg then described the phenomenon of change blindness in which observers fail to notice even large changes in a visual scene if attention is not focused on the portion of the scene where the change takes place. This phenomenon shows us that perceptual attention is not uniform throughout the visual field, that attention changes perceptual thresholds and that it can be driven by both top down and bottom up processes. Nineteenth century clinical neurologists, like Dejerine, Hughlings, Jackson, and Head implicated the parietal lobe in the attentional processes described by James and exemplified by the phenomenon of change blindness.

The neuronal substrate for attention should have a representation of salient or attention-worthy objects in the visual field rather than the entire visual field. Attention filters incoming information and selects particular objects or events for further analysis. Neurons subserving attentional processes should respond to objects made salient through top down and bottom up processing. The neuronal processes related to attention should parallel psychophysical aspects of attention. Dr. Goldberg concentrates on one particular area of the parietal cortex in the monkey in his discussion of attention, the parietal LIP (lateral intraparietal area). The LIP is of particular interest because it separates the inferior from the superior lobule of the parietal lobe. The LIP is connected to the oculomotor system and has reciprocal projections from the frontal eye field, which is the cortical area that drives eye movements. It also has reciprocal connections to the superior colliculus, another area important in driving eye movements. However, the LIP is not just related to the ocular motor system. It has powerful projections to the visual system and specifically to the ventral stream of the visual system, which is important for pattern recognition. It has direct connections to V4, the inferior temporal cortex, TEO and TE, and also the parahippocampal gyrus, which is important in spatial working memory. Since we are dealing with visual attention in our discussion, the LIP is in the perfect place to look at attentional processing.

The research presented in this talk involves analysis at the level of single neurons in LIP. The monkey is trained to look at a fixation point. While the monkey is looking at the fixation point another stimulus is flashed on the screen. A response in the neuron is evident 100ms after the stimulus is flashed. Responses (numerical measure of the frequency) are averaged and then probability densities are created to look at the time of neuronal firing. The cell responds to the appearance of the visual stimulus in the receptive field. Horizontal and vertical eye movements are measured while the monkey looks at stimuli. Dr. Goldberg posed the question of whether the response of the parietal neurons reflects visual processing (photons on the retina) or visual attention. Is using an eye movement to bring a stable stimulus onto the receptive field (photons) equivalent to flashing the stimulus onto the receptive field (attention)? These questions are investigated in the experiments described below.

Summary of Experiments:

The Stable array task was used to look at these issues. The monkey looks at a stable array of 8 stimuli on the screen for the duration of the trial. The monkey first fixates on a point such that the receptive field of the neuron is outside of the array. The monkey then makes saccades across the screen and different stimuli in the array are brought into the receptive field. When the saccade brings a stable stimulus into the visual field, the LIP neuron responds weakly (much weaker than when a stimulus is flashed). The visual information is the same in both instances (visual stimulus flashed in the visual field vs. saccade bringing the visual stimulus into the visual field). The only difference between these two examples is the sudden flashing of information, which draws attention. Thus it can be concluded that the greater response of the neuron in the case in which the stimulus is flashed results from an attentional response rather than a visual response.

However, there are problems with this task. The assumption that these two events are identical except for the attentional component is weak. The Recent stimulus task was used to produce a result that is not reliant on this assumption. In the Recent stimulus task, as in the Stable array task, objects don't change at all in the event. Again the monkey first fixates so that the objects in the array are outside of the receptive field. At this point there is no stimulus in the place that the monkey is about to fixate. Then, the stimulus to which the monkey is about to fixate flashes on the screen immediately before the saccade occurs. Then there are eye movements to the recent stimulus. The cell fires just as enthusiastically as in the flashed stimulus case described above. The response of neurons in LIP to the sudden appearance of a visual stimulus in their receptive field reflects the attention evoked by the recent flash, and not merely the appearance of a set of photons on the retina. Sudden motion of a stable object also evokes attention, and evokes a response in LIP neurons.

Dr. Goldberg next addressed the question of how a stable object can be made more salient. He claims that one can make a stable object salient using the Sparse Array task in which the monkey is trained to fixate on a spatial location, such that the receptive fields of the LIP neurons that are being recorded lie outside the array. In this task there is only one stimulus in the array. A saccade brings the stable stimulus into the receptive field. The neuron fires more when there is only one stimulus in the array than when there are eight. Similarly, the Recent Stimulus task was repeated with only one stimulus in the array. Here again, the neuron fired more when there was only 1 stimulus in the array.

In another task, a cue was flashed outside the receptive field (identical to the one in the array). When a saccade is made to the center of the array, the monkey must make a second saccade to the stimulus. The difference between these two conditions is the importance of stimulus to the animal. The LIP responds to the salient visual world, depending on the importance of the stimulus in the visual field. Stable objects can be relevant to behavior.

So far, in summary, the LIP has a representation of the salient visual world, not the entire visual world. It responds to intrinsically salient stimuli (James' involuntary attention),

such as stimuli that are flashed or moving, and to stimuli that are salient because of context (James' voluntary attention), such as stable objects that are relevant to behavior and stable objects in a very sparse environment. It is hypothesized that the neuronal activity in LIP represents the objects of attention. However, the neurons in LIP also respond during saccadic eye movements. Is LIP driving saccades? Or attention? Dr. Goldberg provided evidence that addressed the relationship between neuronal activity in LIP and saccade generation. A memory guided saccade task was used to study the physiology of eye movements. The monkey looks at fixation and then a stimulus is presented outside of the receptive field. The stimulus vanishes before a saccade is made. LIP neurons have a classic response to the visual stimulus in the interval between the disappearance of the stimulus and eye movement to the place where the stimulus was presented (delay period activity). A burst of neuronal activity occurs when the saccade is actually made. Does the generation of a delayed saccade then suppress the visual response of neurons in LIP? A distractor task was used to answer this question. When planning a rapid eye movement, attention is pinned at the target of the saccade. If these neurons are driving saccades, then once the brain is committed to a saccade the neural response should be relatively unresponsive to a distractor. In this task, the monkey fixates and then a target appears outside of the receptive field. The target turns off, and then a distractor turns on. Once the distractor turns off, the fixation point also turns off, indicating to the monkey that it is time to make a saccade toward or away from the receptive field, depending on whether the distractor was in or out of the receptive field. The saccade should be away from the distractor. Visual response in the receptive field is enhanced when the monkey is planning to saccade away from the receptive field across the population. The pre-saccadic response cannot distinguish between saccade into the Receptive field (distractor outside) and saccade out of the receptive field (distractor inside). Although the distractor evokes a huge presaccadic response, it has no effect on saccade velocity, latency, accuracy, or early trajectory. These neurons are doing something other than simply planning saccades. The distractor isn't affecting eye movement.

The LIP is important in specifying the locus of attention. Neuronal activity in the distractor task enables two predictions about a monkey's attention:

- The default locus of attention, i.e. the locus of the lowest perceptual threshold will be at the target for a memory guided saccade task.
- A distractor will draw attention away from the saccade target, even though it does not interfere with the saccade plan.

Dr. Goldberg next turned to the question, how we can quantify attention in the monkey? In the task devised to answer this question, the monkey is trained to fixate for 500ms. A saccade target then appears for 100ms. A delay of 700, 1200 or 1700ms was imposed followed by a Go-Nogo cue appearing for one video frame (approx 17ms). Finally a 500ms delay occurred before the fixation point disappears. Once the fixation disappears the monkey should either go, or not go, to the previously shown target, depending on which cue was presented. Luminance of the cue above the background was used as an index of perception. Goldberg was interested in determining whether or not there is an advantage at the saccade target. Threshold is the contrast at which the monkey gets 70% right. It was found that the saccade target location had a lower perceptual threshold.

There was an attentional advantage when the go cue was presented at the same point as the point at which the target was originally presented and no advantage was found at other places. The saccade goal has a privileged perceptual threshold for target-cue intervals as long as 1800ms.

Two hypotheses were made about the activity of neurons during the delayed saccade distractor task. The first hypothesis was that the default locus of attention, for example, the locus of the lowest perceptual threshold, will be pinned at the goal in a memory-guided saccade task. This prediction was confirmed. The second hypothesis was that a distractor will draw attention away from saccade goal, but will not alter the saccade plan. This prediction was confirmed as well. The distractor draws attention away from saccade goal. The spotlight of attention swings to the distractor at approximately 550ms after it is presented, but then swings back to the target. The monkey has an attentional spotlight that rests at the goal of the memory-guided saccade by default. It is manifest as the area of the visual field with the lowest contrast threshold. A flashed, task-relevant distractor pulls the spotlight of attention away from the saccade goal. The activity of neurons in LIP tracks the attentional spotlight.

To summarize, attention is the process that enables the brain to select objects in the visual field for further analysis. The monkey has a spotlight of attention, a locus in space associated with lower perceptual threshold. The default locus of attention lies at the target of a planned saccade, but is easily dissociated from it. Neuronal activity in LIP always specifies the locus of attention, both bottom up (James' involuntary attention) and top down (James' voluntary attention). The locus of attention is determined in a winner-take-all manner at the spatial location associated with greatest LIP activity. Higher spike frequency is associated with a higher probability of winning the attentional spotlight, but not with more attention. The ensemble of neuronal activity in LIP predicts the locus of attention reliably.

Dr. Goldberg next discussed these experiments in the context of the broader attention literature. He first addressed the issue of orienting. It is clear that under most circumstances you look at what you attend to. This type of attention, which involves eye movements or head movements, is referred to as overt attention. However, attention can be shifted to something in the visual field without eye movements. This is referred to as covert attention. Dr. Goldberg gave the example that the baby monkey learns very quickly never to look at the alpha male (overt attention), but certainly attends to the alpha male using covert attention. There is an attentional mechanism that selects something from the visual field that ordinarily is not there. The oculomotor system is informed about the presence of the object in the visual field through privileged connections from the parietal cortex to the oculomotor system. Dr. Goldberg used the anti-saccade test, which is used to test for frontal deficits in humans, to show this connection in the monkey. In the anti saccade test the monkey is instructed to look away from a target. Gottlieb and Goldberg recorded in the LIP while the monkey performed the anti saccade test, and discovered that the target stimulus always evoked a response, even though the monkey was looking away from the target. A normal human subject is able to look away from the visual stimulus. However, a patient with frontal deficit can't look away from the target stimulus. This shows that although attention and eye movements are closely linked, in the normal brain they are segregated.

Wallman asks for clarification on whether the monkey is actually attending to different shapes in the display or simply shifting attention to different spatial locations? Goldberg responds that there is clearly some kind of attention that is independent of where the eyes are fixating. When you are attending to an object, you keep your attention on that object, regardless of where your eyes are fixating. However, there is also a type of attending that is more retinotopic, as in the experiments discussed in this lecture. LIP doesn't respond to object information. There is a quantitative difference for some patterns for some neurons. But basically LIP has much more information about spatial location than it does about pattern. Dr. Goldberg says that the function of LIP neurons is the guiding of attention to the portion of the visual field that is important. Neurons in LIP do not respond differentially depending on how this importance is determined. The LIP spotlight moves attention to a spatial location and anything that is presented at that location will be perceived better because attention is focused there. However, there are also object effects in attention subserved by neurons in the ventral stream.

Terrace questioned whether it is reasonable to ask the monkey to wait a longer period of time. Goldberg responded that the largest delay found by Goldman and Raiche is about 6 seconds and that the delay activity would probably last throughout the 6 seconds. Terrace followed up by pointing out that the monkey must resurrect or re-present the object to himself by some other cue during this delay period, that is the monkey must be attending to a stimulus that is not visually present. Goldberg responded that he has looked at this issue with both the anti-saccade task and the Black Hole test, in collaboration with Gottlieb. In the Black Hole task the monkey fixates the center of the array and then a stimulus appears. Then a cue appears and the task is to saccade to the cue rather than the target. They looked at pre-saccadic activity in LIP when the target disappeared and found that when the monkey makes a saccade to the black hole there is not much activity in LIP. During the pre-saccadic response, LIP neurons give their maximal response when there is a stimulus present.

Malpani asked about the specificity of representations in LIP. Goldberg responded that the frontal eye field tells us to where the monkey will make the movement. There are projections between LIP and the frontal eye field, and the frontal eye field influences activity in LIP. However, there are no neurons in LIP that indicate when an eye movement will occur or if there will be an eye movement at all.

Hilton described the experiment in which the distractor, was not the relevant stimulus. The monkey was supposed to focus on the target. Hilton asked if the effect is a frontal effect that serves as attention management, suggesting that monkeys with frontal lesions wouldn't be able to do this task. Goldberg agreed that monkeys would be unable to make a saccade to the distractor in this case. The LIP tracks and hopefully drives the spotlight of attention. Goldberg's research team plans to lesion LIP in an upcoming experiment, to determine whether there is still an attentional advantage.

Liu asked whether the spotlight has a measurable physical speed.

Goldberg responded that the spotlight of attention probably moves so quickly, that it does not resemble scanning.