Attention and the Parietal Cortex

(Steinmetz, M.A., Connor, C.E., Constantinidis, C., and McLaughlin, J.R., "Covert attention suppresses neuronal responses in area 7a of the posterior parietal cortex", *Journal of Neurophysiology*, Vol. 72, No. 2, pp 1020-1023, 1994)

The study by Steinmetz *et al* suggests that the posterior parietal plays a dual role in the perception of visual-spatial relationships and in the orientation of attention.

The responses of 60% of the visual neurons measured in area 7a were influenced by shifting attention to the location of the stimulus.

55% of the visual neurons had their activity *suppressed* when attention was directed to the stimulus location as compared with the responses evoked at the same location, but with attention directed elsewhere.

A small number of cells responded more vigorously when attention was directed to the stimulus location.

The rest of the visual neurons were not influenced by shifts in attention.

In general, visual neurons in 7a are relatively insensitive to stimuli presented when animals are in a non-attending state.

Two possible functions for the observed effects:

- The enhancement of neurons away from the locus of attention may play a role in the re-directing of attention

- The outputs of the neurons in area 7a are used to inhibit responses in corresponding visuotopic maps in other cortical areas, thereby leading to an apparent "shrinking" of receptive fields in these areas about the attended stimulus.

(Bushnell, M.C., Goldberg, M.E., and Robinson, D.L., "Behavioral enhancement of visual response in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention", *Journal of Neurophysiology*, Vol. 46, No. 4, pp 755-772, 1981)

It has been demonstrated that many cells in area 7 of the parietal cortex respond to visual stimuli independent of behaviour. This response may be enhanced when the animal makes an eye movement to a stimulus.

Enhancements were found in about half the cells when the animal had to attend to a peripheral stimulus without making an eye movement.

Visually responsive parietal neurons also exhibited enhanced responses when the animal had to reach out and touch a stimulus without making an eye movement to it.

Thus, the enhancement of the response in these neurons is independent of the particular type of movement to be made, and suggests that this enhancement is related to spatial attention.

Attention vs. Intention

(Gnadt, J.W. and Andersen, R.A., "Memory related motor planning activity in posterior parietal cortex of macaque", *Experimental Brain Research*, Vol. 70, pp 216-220, 1988)

(Bracewell, R.M., Barash, S., Mazzoni, P., and Andersen, R.A., "Neurons in the macaque lateral intraparietal cortex (LIP) appear to encode the next intended saccade", *Soc. Neurosci. Abstracts*, Vol. 17, p 1282, 1991)

Gnadt and Andersen found cells in LIP (Lateral IntraParietal) that appear to encode the *intention* to make an eye movement to a given location.

Their study used a memory task in which a monkey had to make an eye movement to a target after some delay time after the target stimulus disappears.

These LIP cell were active from the appearance of the target, through the delay time (when the target stimulus was not present) and stopped only when the eye movement was made.

These cell could be active even though the stimulus was not in the cell's receptive field, indicating that the cells were representing the desired eye movement rather than the location of the sensory stimulus.

A modified experiment was done where, in some of the trials, the target would flash on in a new location during the delay, and the animal was required to move to that new target after the delay. The activity of the LIP cells would turn on and off consistent with the motor plan that the animal had to formulate.

Many of the cells exhibited intended movement activity for both visual and auditory stimuli.

Memory activity seemed to be present only for the next intended movement (if a sequence of movements actually had to be executed).

The enhanced response of these movement intention cells can be interpreted as attention being directed to the target of the eye movement. This activity should persist even if there is no actual movement, until a new movement is planned.

(Colby, C.L., "A neurophysiological distinction between attention and intention", **Attention and Performance XVI**, pp 157-177, 1995)

Colby and co-workers have studied the effect on parietal cell responses to attending to a stimulus and to intending to perform a particular motor act.

To study the effects of attention, they compared the neural response to a behaviourally irrelevant stimulus with the response to the same stimulus when it is made behaviourally relevant.

They found that the amplitude of the response to stimulus onset increases when the stimulus becomes a target for action. This enhancement does not depend on the kind of action.

In contrast to the change in amplitude of response produced by attention, the intention to perform a particular kind of action can shift the spatial receptive field of a neuron.

For example, when a monkey is intending to make an eye movement, the receptive field of a parietal neuron can shift even before the eye movement occurs (note that in a head-centred visual map, it is expected that the receptive fields will shift after an eye movement).

This pre-shifting of the receptive fields may allow the animal to anticipate the consequences of the impending eye movement.

Colby and colleagues performed an experiment which looked at the effect of eye movements on the LIP "memory" neurons. In this experiment the monkey first fixates on a point and a stimulus is flashed in the receptive field of the cell. The response to the stimulus is significant. Then, in a second condition, the stimulus is flashed outside the receptive field. The cell does not respond. But then, a saccade is made to a location such that the receptive field of the cell now falls over the location where the stimulus occured. The cell now responds, indicating that the memory trace of the stimulus has itself somehow been shifted.

Thus, memory signals carried by LIP cells appear to be re-mapped in conjunction with saccades.

This re-mapping serves to maintain an alignment between the external world and internal representation of it.

By remapping memory traces the parietal cortex constructs a spatial representation that encodes stimulus location in terms of distance and direction from the current center of gaze (fovea). Hence these neurons encode the memory of a stimulus in terms of retinotopic coordinates rather that head-centred coordinates.

This may be due to the fact that this representation is to be used in generating eye movements, rather than, say, arm movements. Similar remappings in terms of head or body centered coordinates may also be performed somewhere in the brain.

It was found that the intention to make a saccade was sufficient to shift the receptive field of an LIP neuron.

The neurons respond, *in advance*, to a stimulus that will be in their receptive field *after* the saccade.

This activity requires two conditions: intention to move to a location, and a visual stimulus at some point in time. If there is no visual stimulus, a saccade can be made, but these neurons will not respond. Similarly, if there is a visual stimulus, but no intended saccade, the neurons will not respond.

A shift of attention alone is not sufficient for one of these LIP neurons to exhibit this type of response.

This suggests that the function of these neurons is to provide a (predicted) remapping of the internal spatial representation, since in an attentional shift nothing moves on the retina.