

Information routing by visual attention in striate and extrastriate cortex

— for *Neural Basis of Consciousness*, a class by C. Koch —

Daniel A. Wagenaar, March 2001

I propose to measure mutual information between spike trains recorded with tetrodes from cell ensembles in macaque MT and moving bar stimuli. These measurements will be taken for three situations: (1) with the monkey attending the stimulus; (2) with the monkey attending a stimulus elsewhere in the RF of the cell ensemble; (3) with the monkey attending a stimulus outside the RF.

I hypothesize that the mutual information will be enhanced for (1) relative to (3), and suppressed for (2). I propose to investigate the correlation between these changes in mutual information in MT and increased spike rates in V1 at the location of an attended stimulus. I hypothesize that enhancement of firing rates in neurons at attended positions in one visual area affects subsequent areas because cells receiving input from those excited neurons shift and contract their RFs to the attended location.

Previous work in this field has mostly characterized response by (average) firing rates. A description in terms of mutual information allows one to link response content to stimuli at specific locations and provides a more natural framework for investigating the competition between various stimuli within a cell's RF.

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1 Background and significance

1.1 Modeling attention

Attention has been studied extensively from a psychological point of view, using models such as Treisman's feature integration theory [1, 2], but these models do not address the question of biological implementation. Experimentally, imaging studies and electrophysiology have established that attention differentially enhances stimulus response as measured by firing rate. Most effort has been spent investigating large scale attentional effects, perhaps because of the limitations of fMRI. Thus they address how cells increase their firing rate when attention lies within their receptive fields. Most do not study differential effects of attention between several simultaneous stimuli within the cell's RF. Such effects are interesting, because they might be the direct result of — and indeed the functional *raison d'être* for — firing rate enhancement by attention in upstream areas.

1.2 Attention in early visual areas

In the old days, V1 was thought to be merely a preprocessor of visual information, specializing in menial tasks such as edge detection. This left the presence of strong feedback connections to V1 embarrassingly unexplained. Indeed, it has recently been discovered that all early visual areas, including V1, are involved in attentional processing, a supposedly high level task [3, 4, 5, 6].

Attention does not affect the earliest response in V1, so it is thought that attentional processing originates elsewhere [4] — perhaps in IT cortex [5] or PP cortex [6] — and affects V1 through feedback [7].

However, macaque monkeys (and hence presumably people) do not seem to be directly consciously aware of what goes on in those areas [8]. Therefore a change in firing rate in such areas is not a behaviorally useful result of attention, unless it affects information processing further downstream. I propose to study how attention affects information flow in macaque MT and how this correlates to enhancement of activity in V1.

One of the earliest papers in this field finds that receptive fields in V4 contract around attended stimuli [9]. I hypothesise that this is a much more general feature of visual processing systems, and propose to study it in more detail using an information theory approach.

1.3 Information flow

For many years researchers have realized that simple minded rate coding is not sufficient to process the kind of fast changing information that organisms are so well adapted to. Therefore, it is appropriate to study neural responses in terms of their mutual information with the stimuli presented, rather than in terms of their integrated firing rate per se. Mutual information describes how much of the information density¹ of one data stream is captured by another. A standard textbook reference for the application of information theory to neural processing is [10].

Although the very early investigations in this field obtained surprisingly low information rates for cortical neurons [11], this was corrected later when it was realized that brains are not at all specialized for representing information about static stimuli. First, it was found that spike trains can exhibit high temporal precision — jitter as low as 2 ms was found in MT [12]. Then, much higher information rates were discovered for dynamic stimuli — about 30 bits/sec in MT [13].

¹or *entropy* in information theory jargon.

Attention related modulation of firing rate is strongest in higher visual areas such as MST and LIP, but their more complex afferent connections make these areas less suitable for this study.

2 Specific aims

I propose the following program of studies, the first two steps being preliminary requirements for the other two:

- a. **Establish procedures for recording from macaque MT using tetrodes;**
- b. **Determine a class of stimuli that result in highest informational representation in MT;**
- c. **Study the modification of the extent and precise location of a cell's receptive field by attention;**
- d. **Relate such modifications to enhanced activity in the corresponding part of V1.**

3 Methods

a. Tetrode recording from macaque MT

Using tetrodes rather than conventional electrodes offers the possibility of recording from several nearby neurons simultaneously. Neighboring neurons tend to have similar classical receptive field but different orientational and directional tuning. As such, they complement each other in describing a stimulus at the location of their RF, and collectively they can be expected to have higher mutual information with complex dynamic stimuli.

Tetrodes have hitherto been employed for cortical recording mainly in rodents and in cats [14], but recent work at Caltech has successfully applied them to macaque cortex [15, 16].

b. A class of stimuli with high informational representation in MT

Finding optimal stimulation sets has at least two aspects: first, for each new electrode position, a search through the visual field has to be made to map out the classical receptive field of the cells near the electrode. This process is mostly mechanical, and has been successfully automated by other groups, e.g. [3]. Second, we need to know what 'kind' of stimulation results in highest informational representation in MT. Moving gratings with changes of direction at a rate of about 5 to 20 Hz are a good starting point, but there are many parameters that should be explored here. To add to the complexity, there is certainly no guarantee that a stimulus set that is optimized for one cell also works well for another. Fortunately, this problem is somewhat alleviated by the tetrode method, since ensembles of cells can be expected to be more alike to each other than individual cells are.

It is important to realize that a single neuron's response to a stimulus may occur over a large timescale. The effective receptive field may vary with latency [17]. Therefore mutual information with stimuli at a particular location must be considered as a function of latency. This can be done using the stimulus reconstruction method of information estimation described at pages 156ff of [10].

Only once these prerequisites have been fulfilled can work begin on the main goals of this project.

c. Modification of the extent and precise location of a cell’s receptive field by attention

We will measure the informational capacity of neuronal channels for the stimuli selected above in three settings: first, when the monkey is attending to the area where they are presented; second, when the monkey is attending elsewhere but within the cells classical RF; third when the monkey’s attention is fixed outside of the cRF. I hypothesize that the mutual information between the response and the stimulus will be largest in the first case, and smallest in the second case (when the cell is mostly processing information from another, attended stimulus). Situation three corresponds more closely to the classical setup where attention is not controlled.

It is important not to confuse the response to an attentional cue with the sought after information. I propose to tackle this issue by using cues in a different, but related modality, specifically color, because the response of MT cells does not depend strongly on color. Green circles will appear at irregular intervals of about 10 s at various positions in the visual field. The monkey’s task is to press a lever quickly when the hue change appears twice at the same location. Performing this task requires focusing attention on the spot where the light was last seen. Color may have some direct influence on information, but this effect can be subtracted out by having the same number of green flashes in the ‘attended’ dataset as in the ‘non-attended’ datasets.

Many authors have suggested that attentive selection only occurs when a system is threatened with information overload. Therefore, we will use stimuli that fill the entire visual field and that vary on an angular scale smaller than the cRF of the cells under study. An impression of a possible stimulus is shown in Figure 1.

The monkey’s performance can be used to verify that it is indeed attending the stimulus. When attention is lost, or the monkey saccades away from fixation, data collected surrounding this disturbance can be discarded.

Perhaps the most interesting research question that can be addressed in this paradigm is how to reconcile the apparent low angular resolution of area MT and the high subjective resolution with which we perceive motion. One exciting hypothesis to resolve this issue is this: although the receptive fields of cells in MT are rather big, attention may enhance processing of stimuli that are in certain subparts of this field. Experimentally, such ‘shrinking’ of RF (Figure 2) has been reported in V4 [9]. I hypothesize that shrinking also occurs in MT, and that the mutual information of a cell’s spike train with an attended stimulus is differentially enhanced (Figure 3).

A related possibility is that the RF of an MT cell might shift as a result of attention to encompass regions of visual field that are not normally responded to. To study this, one would draw the monkey’s attention to a region just bordering on the classical RF of the cells under investigation and compute the mutual information between the response stream and various subregions of the visual field near the attended

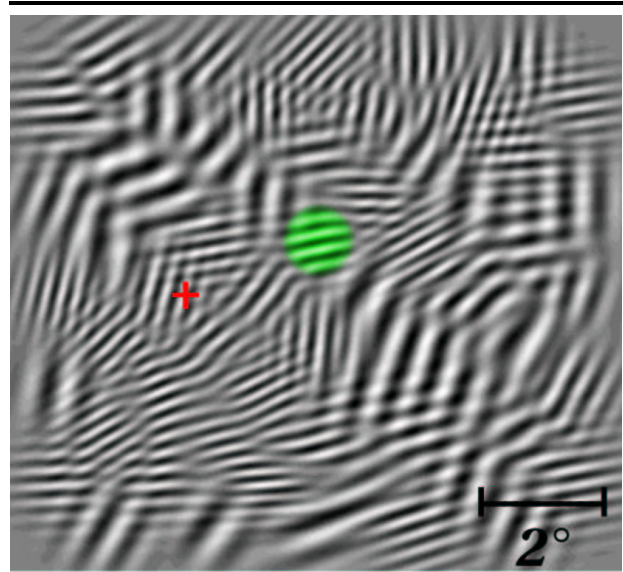


Figure 1: An example stimulus. The area to be attended is marked, as is the fixation point. The image would move rapidly, locally perpendicular to the lines shown. Direction of motion would change asynchronously for each Gabor patch at an average rate of 5 to 20 Hz.

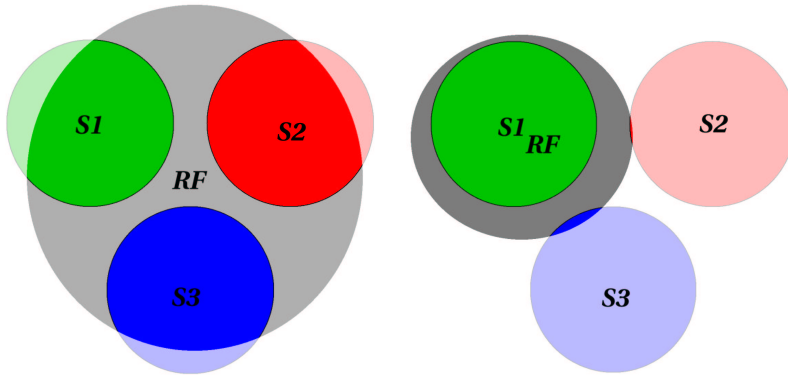


Figure 2: Three stimuli presented simultaneously in the receptive field of an MT cell (*left*). The receptive field shrinks around attended stimulus (*right*).

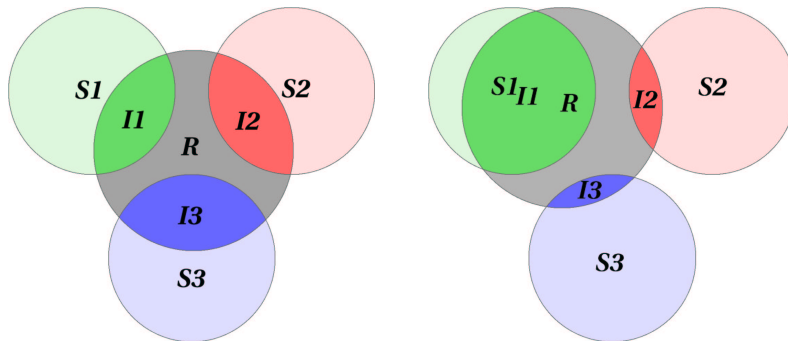


Figure 3: Venn diagrams of entropy in stimuli ($S1..S3$) and response (R). Regions $I1..I3$ represent the mutual information. Without attention, all stimuli are weakly represented by the spike train (*left*). With attention, the response describes the attended stimulus in much more detail, and becomes almost independent of the unattended stimuli (*right*).

position. My hypothesis predicts that the mutual information with the attended region is differentially enhanced.

d. Relating RF modifications to V1 activity

Enhanced mutual information between attended stimuli and spike trains in MT could be attained by increased firing rates in earlier visual areas at the attended location. This is possible because many V1 cells project (indirectly) to each MT cell, and a V1 cell with increased rate will dominate its colleagues. Thus this hypothesis also solves the riddle that enhancement of firing rates also enhances noise [5]: while this remains true, the result now is that the output of neighboring cells is drowned in the noise, whereas the attended cell does not suffer reduction of signal to noise ratio. A graphical representation of this hypothesis is shown in Figure 4.

To test this hypothesis, it will be necessary to record simultaneously from MT and from the corresponding region in V1. This is definitely a challenging assignment, but using tetrodes will make the task less menacing: since a tetrode can pick up signals from many nearby cells, finding the exact location becomes somewhat less critical. The search process is also facilitated. On the downside, tetrodes are bigger, and consequently cause more tissue damage.

Should simultaneous recording turn out to be impractical, the activity in V1 will have to be measured independently of the activity in MT. In that case, the relationship must be tested by statistics rather than directly.

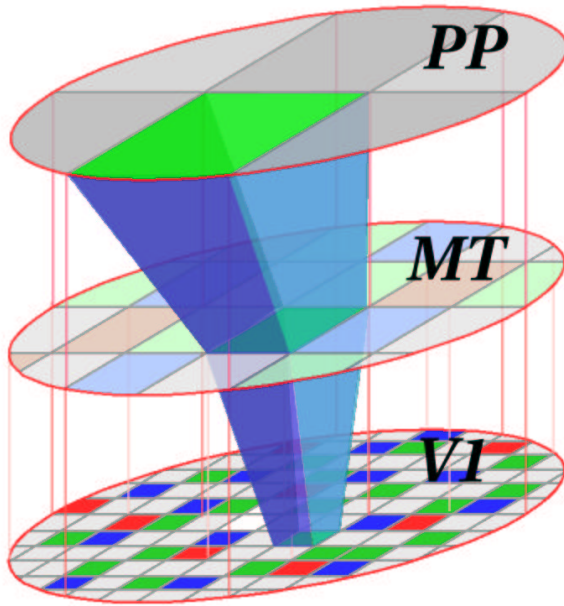


Figure 4: Firing rates in V1 are increased at the location of the attended stimulus. This causes this stimulus to dominate the response of cells in MT with RFs including it. Mutual information and firing rate are increased for this region in MT, while other regions show less organized activity, since they average over many V1 cells. Consequently, the attended region also dominates in PP. Several other visual pathways would represent attention in a similar way.

4 Future directions

Figure 4 shows an attractive hypothesis about small scale visual attention, but the experiments proposed here can certainly not prove it conclusively. First of all, the attention dependent information flow from MT to PP cortex should be investigated. Secondly, other visual pathways should be examined to see if similar contracting of dynamic RFs occur. Finally, this study does not address the question of the *source* of visual attention. Attention might originate in one particular brain area, or it might be the collective product of several interacting areas. The hypothesis described in this proposal would favor the latter, since it describes how attention can propagate up the visual pathways in addition to the top-down mechanisms suggested elsewhere.

On the ‘big picture’-level, the interaction of this small scale attention with models for large scale attention, such as Treisman’s feature integration theory are worthy of study.

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