Attention Reduces Spatial Integration In Primate Primary Visual Cortex

M. J. Roberts, L.S.Delicato, A. Thiele

University of Newcastle upon Tyne, UK

Introduction

- We have previously demonstrated that spatial integration from beyond the classical RF is reduced by Acetylcholine (ACh) application
- This is likely to be due to re-balancing of feed-forward and feedback inputs in favour of feed-forward activation
- The natural release of ACh is strongly bound to states of arousal and attention. We therefore reasoned that selective attention would reduce the spatial integration in a manner similar to external ACh application

Methods

- **Length tuning was measured in V1 of 2 alert and behaving macaques**
- **Animals were trained to fixate and perform a task, which required attention to be directed to stimuli either towards or away from the RF**
- **Stimuli were dark or white bars of variable length (0.1° to 2.4°, 0.1° wide) presented within 1.7 ° -2.6 ° from the fovea**

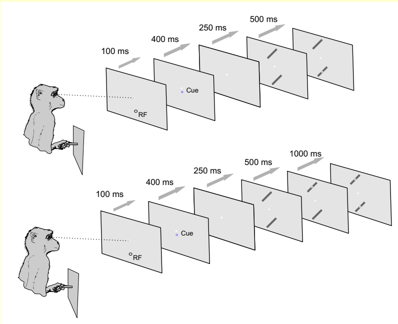


Fig 1 Animals initiated the trial by fixating centrally while holding a touch-bar. After fixation a cue pointed towards the relevant location. The cue was spatially and temporally separated from stimulus onset. Stimuli were two identical bars, one presented at the RF of the neuron under study and one in the opposite hemi-field. 500 ms after bar appearance the central 0.1° of the bar in the cued location could change its brightness (upper task example), or the bar in the un-cued location could change its brightness (lower task example). The monkey had to release the touch-bar within 500 ms after the cued bar changed brightness, and ignore changes at the un-cued bar.

For each cell the preferred length was determined by fitting a Difference of Gaussians (DOG) model to the data. Confidence intervals and significance between the two conditions were determined by a bootstrap method.

Results

Effect of Attention on responses

- **Length tuning was measured in 98 cells. Of these cells 70 were recorded at high contrast (100%) 15 were recorded at low contrast (contrast chosen for each cell to elicit response rates lower than 100% stimuli) and 13 were recorded at both high and low contrast (interleaved)**
- **Response rate was affected by attention in 60% (50/83) of high contrast recordings and 68% (19/28) of low contrast recordings. In almost every case response was facilitated by attention**
- **At high contrast the effect of attention was particularly prominent in responses to short stimuli as evident by ROC analysis. At low contrast ROC values tended to be lowest for medium bar lengths**

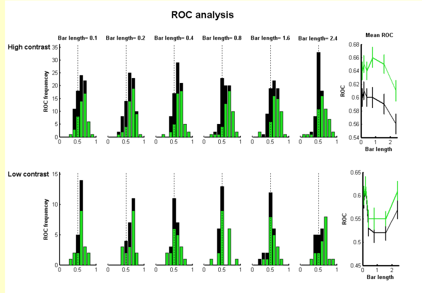


Fig 2 ROC analysis. Upper plots show ROC values from high contrast recordings. Green bars show significant cells black bars show non-significant cells. The plot on the right shows the mean and standard error of population ROCs across bar length. Lower plots show data from low contrast recordings with the same notation.

- **The effect of attention was particularly prominent during the late part of the response. However attentional enhancement was evident from response onset especially in responses to bar lengths 0.1°-0.4° at low contrast. This bar length matches the typical RF size we encountered**

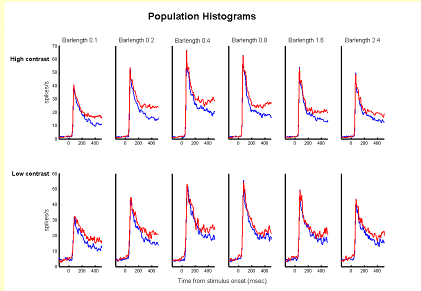


Fig 3 Population response rates for high (upper plots) and low (lower plots) contrast at each bar length. Red curves show data from *Attend towards RF* conditions, blue curves show data from *Attend away* conditions. Data are normalized for each cell.

Effect of Attention on Length tuning

- **Length tuning was assessed by fitting a DOG model to the data. Significance of tuning changes was assessed by a bootstrap method, yielding a distribution of DOG fitting parameters and associated estimates of peak bar length. The median of these estimates was taken to be preferred bar length**
- **Peak responses generally occurred for bar lengths greater than the minimum response field diameter (0.1°-0.4°) demonstrating facilitation from the non-classical receptive field (nCRF)**
- **In the *attend towards RF* condition preferred length tended to shift towards shorter bars**

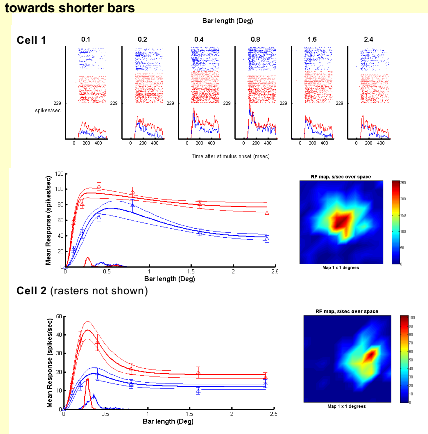


Fig 4 Response across bar length and attention conditions for two example cells. Data from *Attend towards RF* condition are shown in red, *Attend away* in blue. Triangles show mean response over 500msec, error bars are ± 1 standard error. Smooth fitted curves show the median DOG model (plus interquartile range) from the bootstrap procedure. Frequency distribution of peak lengths are shown at the base of the plot. Inset to the right are RF maps generated by flashing 0.1° square dots in pseudo-random locations, while monkeys were passively fixating. Color axes show mean response as a function of stimulus location.

In the *Attend away* condition preferred length is greater than the RF diameter. In the *Attend towards RF* condition preferred length is reduced.

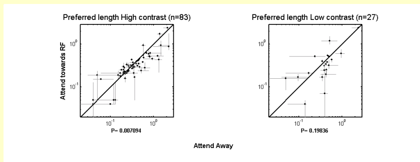
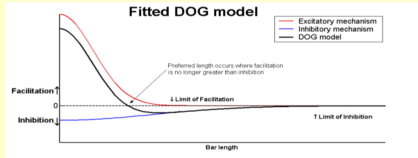


Fig 5 Preferred length as a function of attention condition. Black dots show median peak length from the bootstrap procedure, error bars show upper and lower percentiles. For both high contrast (left plot) and low contrast (right plot) there was a tendency for preferred length to be shorter in the *Attend towards RF* condition (Y axis) than in the *Attend away* condition (X axis). This was significant for high contrast recordings but not for low contrast recordings.

Difference of Gaussians Model

- **The DOG model has two component Gaussians; the narrow excitatory Gaussian represents the RF's summation mechanism while the broad Gaussian represents the RF's inhibitory surround**



- **The model has four fitting parameters and is of the form**

$$R = K_e * (1 - \exp^{-(2y/a)^2}) - K_i * (1 - \exp^{-(2y/b)^2})$$

Where *R* corresponds to the cell response as a function of bar length, K_e corresponds to the *excitatory gain*, *a* corresponds to the *excitatory area*, K_i corresponds to the *inhibitory gain* and *b* corresponds to the *inhibitory area*

- **The medians of the four fitting parameters, taken from the bootstrap procedure, were compared for the *Attend towards RF* and *Attend away* condition**

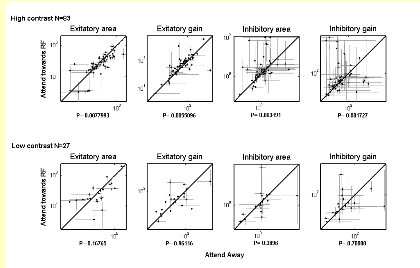


Fig 7 DOG fitting parameters as a function of attention condition. In the high contrast recordings the excitatory area was significantly reduced and the excitatory gain was significantly enhanced. Inhibitory parameters were not consistently affected. At low contrast no parameters were significantly affected, possibly due to small sample size.

Summary and Conclusions

- **Length tuning was assessed in V1 under conditions of attention towards the RF and attention away from the RF**
- **Attention generally enhanced responses, especially to short stimuli, those which matched the typical RF diameter**
- **Response enhancement was most evident in the late part of the response, but was also present from response onset**
- **Attention towards the RF tended to reduce the cell's preferred length especially for high contrast stimuli**
- **Reduction in preferred length seemed to be mediated by a reduction in summation area**
- **The effects of attention are similar to the effects of ACh application and therefore add support for ACh as a key neuropharmacological mechanism of attention**