# *Why is attention limited? Implications from neural coding*

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## Abstract

Neurophysiological recordings from visual system suggest that the evidence for a role for precisely timed spikes relative to other spike times (~1-10ms resolution) is inconclusive. This suggests that the visual system does not carry a signal that identifies whether the responses were elicited when the stimulus was attended or not. Simulations show that the absence of such a signal reduces but does not eliminate the increased discrimination between stimuli that are attended compared to when the stimuli are unattended. The increased accuracy asymptotes with increased gain-control, however, suggesting limited benefit from increasing attention. Paradoxically, the absence of a signal identifying the attentional state under which stimuli were viewed can produce the greatest discrimination between attended and unattended stimuli. Furthermore, the greatest reduction in discrimination errors occurs for a limited range of gain-control. These coding issues suggest attention maximises the discrimination of attended from unattended stimuli that is "target detection" and that as such, the effects of attention should be limited.

## Introduction

- The number of precisely timed spikes of TE neuronal responses during a DMS task indicates are predictable from the changes in the coarse temporal response measures (Figure 1).

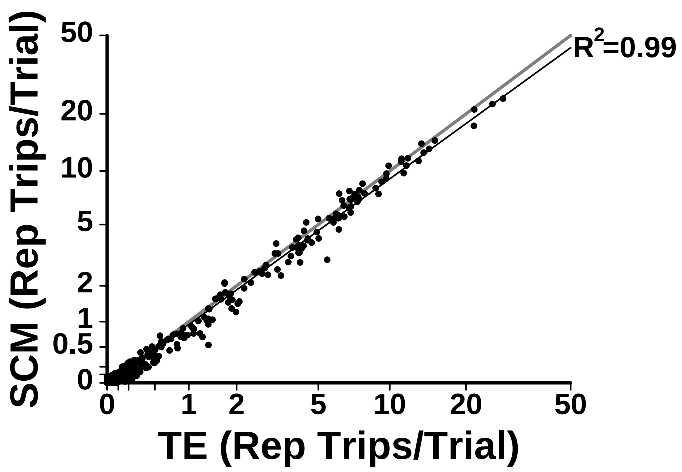


**Figure 1. The Spike count matched model predicts the precisely timed spike patterns in TE data from a DMS task.** The number of precisely timed spike patterns (repeating triplets) found in responses of single TE neurones during the different phases of a delayed match to sample task are predicted using the spike count, spike count variability and temporal variations in the PSTH, even though the number of precisely timed spike patterns varies with attention (Oram et al. 1999, 2002)

- The information available from the precisely timed spike patterns is redundant with the information available from the spike count (Figure 2).

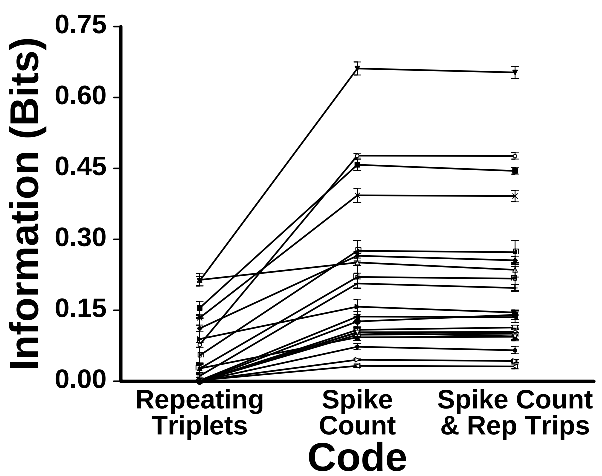


**Figure 2. The information carried by precisely timed spike patterns is redundant with the information carried by spike count.** The information about the stimulus-identity/DMS-phase combination was calculated from the number of repeating triplets, the spike counts and from the dual code of the spike count and the number of repeating triplets. Each line represents the results from a different neuron. The redundancy of information from repeating triplets with the information from spike count was observed for all individual cells (p > 0.05 each comparison).

- The influence of behavioural significance on stimulus elicited neural responses in the non-human primate suggests that attention acts as a "gain-control", scaling the responses to each stimulus by a constant (Desimone and Duncan, 1995; Motter, 1994; Treue and Maunsell, 1996) but otherwise leaving the neural code unchanged (Oram et al., 1999; Wiener et al., 2001).
- Imagine the responses to two stimuli A & B. Under passive viewing conditions the mean spike count elicited by stimulus A could be higher than that elicited by stimulus B. With no signal to indicate the behavioural condition, a high spike count could be due to stimulus A being viewed under passive conditions or stimulus B viewed when attended.
- This ambiguity could be addressed by the presence of a signal from a second source indicating whether the responses should be decoded using the mean responses associated with the attended or unattended state.
- Different population codes are examined to see if the absence of a signal of attention state "makes sense".

## Methods

The mean spike counts of 10 simulated neurones to 100 stimuli were taken as having Gaussian tuning curve (SD=15, see upper panels of Figure 3 & 4). The variance of the responses to each instance was set as twice the mean spike count. Spike counts were either simulated as being in an unattended (gain-control=1.0, thin lines) or attended state (gain-control=1.0 - 2.5). Assuming an equal probability of each stimulus instance, $p(s_1)=p(s_2)\ldots=p(s_n)$, the probability of each of the possible 100 instances of the stimulus was assessed for each simulated trial for each neurone using $p(s|r) = p(r|s)/\Sigma_{i=1..100}p(r|s_i)$ where p(s|r) is the probability of stimulus s being present given the trial response of r spikes, p(r|s) is the probability of observing r spikes given that stimulus s was present and $\Sigma_{i=1..100}p(r|s_i)$ is the sum of the p(r|s) over all n stimulus instances (see Oram et al., 1998 for review). The p(r|s) were obtained from the truncated Gaussian distributions given by the mean and variance. Assuming independence, the probability of stimulus instance s being present is given by the product of the p(s|r) from all neurones. The error in estimating the most likely input stimulus from the responses of a simulated population of neurones was calculated from 10000 simulated trials using four decoding strategies:

(1) The ideal observer who "knows" the response distributions to each stimulus/attention condition (circles).
(2) Constant decoding assuming spike-count distributions derive from unattended stimuli (triangles).
(3) Constant decoding assuming the spike-count distributions derive from attended stimuli (triangles).
(4) Decoding assuming the spike-count distributions come from 50% attended and 50% unattended state (diamonds).

## Results

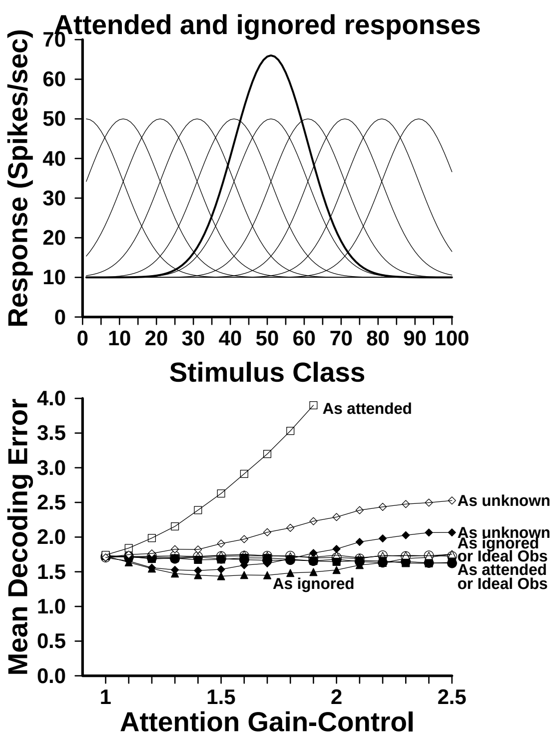


**Figure 3. Limitations of attention: discriminating attended from unattended stimuli. Upper**: The mean spike counts of 10 simulated neurones are plotted to 100 different classes of stimuli (e.g. fruit, vegetable, furniture). The variance of the responses to each instance was set as twice the mean spike count. Spike counts were either simulated as being in an unattended state (gain-control=1.0, thin lines) or in an attended state (gain-control=1.4, thick lines) when attention was selective towards only one stimulus class (class 50). **Lower**: Plot of the error as a function of the multiplicative gain-control due to attention. Solid symbols show the error when the stimuli are presented whilst attended. Hollow symbols show the error when the stimuli are presented but unattended. The error using four decoding strategies are plotted. (1) The ideal observer (circles). (2) Assuming spike-count distributions associated with unattended stimuli (triangles). (3) Assuming the spike-count distributions associated with attended stimuli (triangles). (4) Decoding assuming the response distribution for each stimulus could have come 50% from the attended and 50% from the unattended state (diamonds).

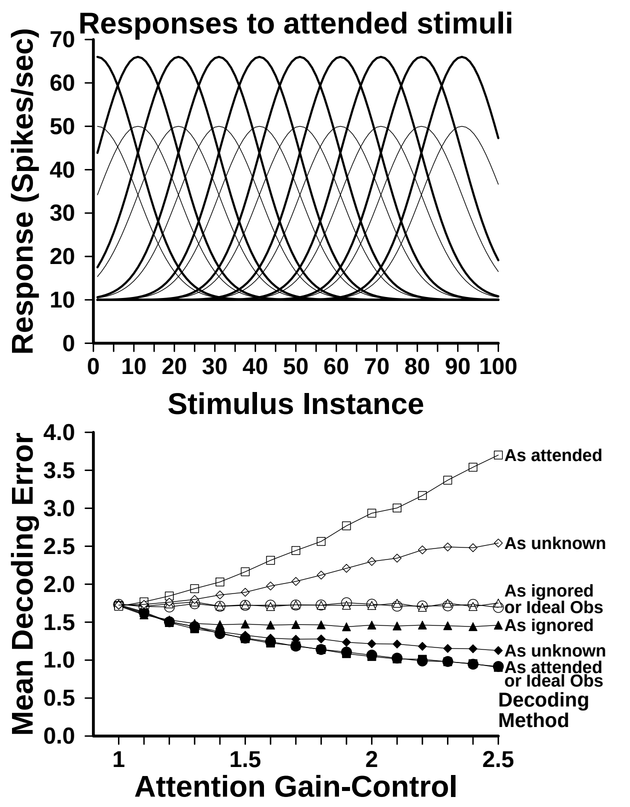


**Figure 4. Limitations of attention: discriminating amongst attended stimuli.** Modelling attention as a spike-count gain control reveals possible limitations of attention. **Upper**: The mean spike counts of 10 simulated neurones are plotted to 100 different instances of stimuli (e.g. apple, pear and orange are all instances of fruit). Gain-control=1.4, for attention) or in an attended state (gain-control=1.4, thick lines). **Lower**: Plot of the error as a function of the multiplicative gain-control due to attention. Solid symbols show the error when the stimuli are presented whilst attended. Hollow symbols show the error when the stimuli are presented but unattended. The error using four decoding strategies are plotted. (1) The ideal observer (circles). (2) Assuming spike-count distributions associated with unattended stimuli (triangles). (3) Assuming the spike-count distributions associated with attended stimuli (triangles). (4) Decoding assuming the response distribution for each stimulus could have come 50% from the attended and 50% from the unattended state (diamonds).

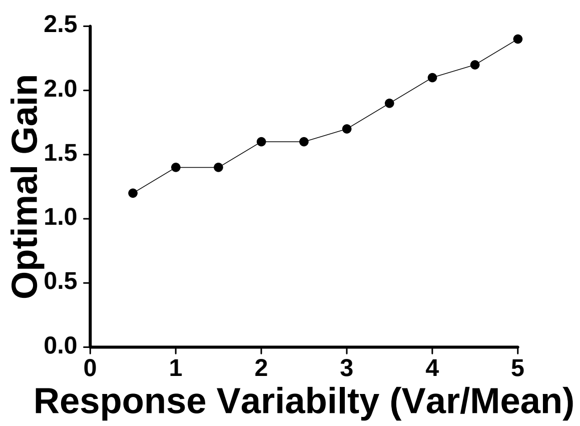


**Figure 5. Optimal gain co-varies with response variability.** The gain control that produces the minimum decoding error from any of the four methods is plotted as a function of the fano factor used in the simulated neural population (fano factor = variance / mean).

## Conclusion

- A context-specific signal indicating the state of attention is not evident in the neural codes of inferotemporal cortical neurones.
- Discriminating attended from unattended stimuli should not involve a context-specific signal (Figure 3)
- Maximising the discrimination between attended stimuli involves the presence of a context-specific signal (Figure 4).
- Thus, the neural codes suggest that attention maximises the discrimination of attended from unattended stimulus classes.
- It is predicted that taking the response variability of individual neurones into account will explain some of the variability in the attention gain control observed for different neurones, both within and between different brain areas.