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Response time course and magnitude are both modulated by attention in monkey V4

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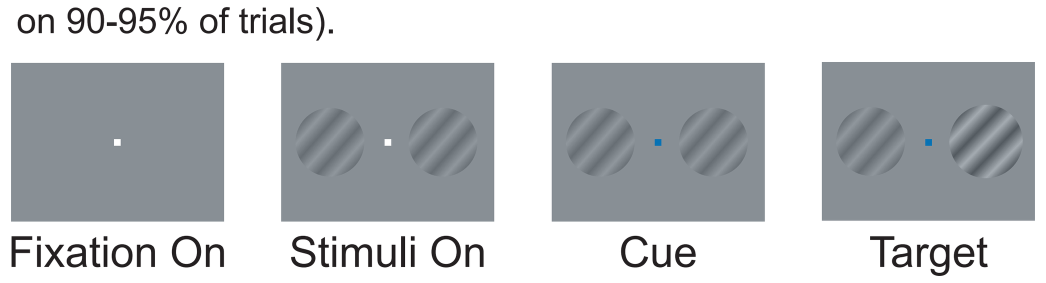
Introduction

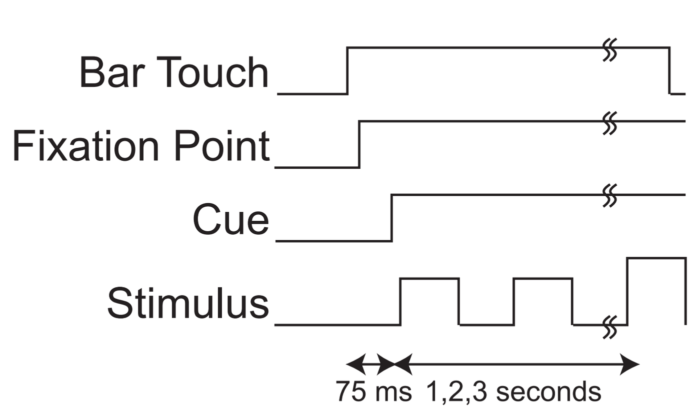
Selective visual attention modulates behavioral performance, increasing sensitivity and shortening reaction times for stimuli in attended regions of visual space. Previous studies in the monkey have shown that the effect of attending to a stimulus in the receptive field of a given neuron is to increase the responsiveness of that neuron in a manner consistent with a change in the receptive fields contrast gain (Reynolds, Pasternak, and Desimone, 2000). However, unlike subcortical and cortical contrast gain controls, which make the visual response more transient, attention has not been observed to produce a change in the time course of neural responses in V4.

The evoked neural activity can be analyzed as a function of contrast, time, and cue in an ANOVA. While significant modulation of the mean firing rate does occur with the cue condition, often the modulation of activity at the stimulus frequency (F1) and its harmonics, both amplitude and phase, is more significant than the modulation of the spike count alone. This supports data that suggests the interaction between the visual afference and the attentional signal is non-additive and further suggests that attention can significantly affect the temporal patterning of spike activity.

Methods

We recorded from single units in V4 while monkeys perform a cued target detection task. Two standing gratings are used as visual stimuli and are flashed in an appearance-disappearance fashion with a square-wave temporal profile. The monkey must maintain central fixation and release a bar to indicate that one of the two gratings has increased in contrast. Trials are blocked according to which grating is most likely to step in contrast, and the fixation point color indicates the cued direction (cue is valid on 90-95% of trials).

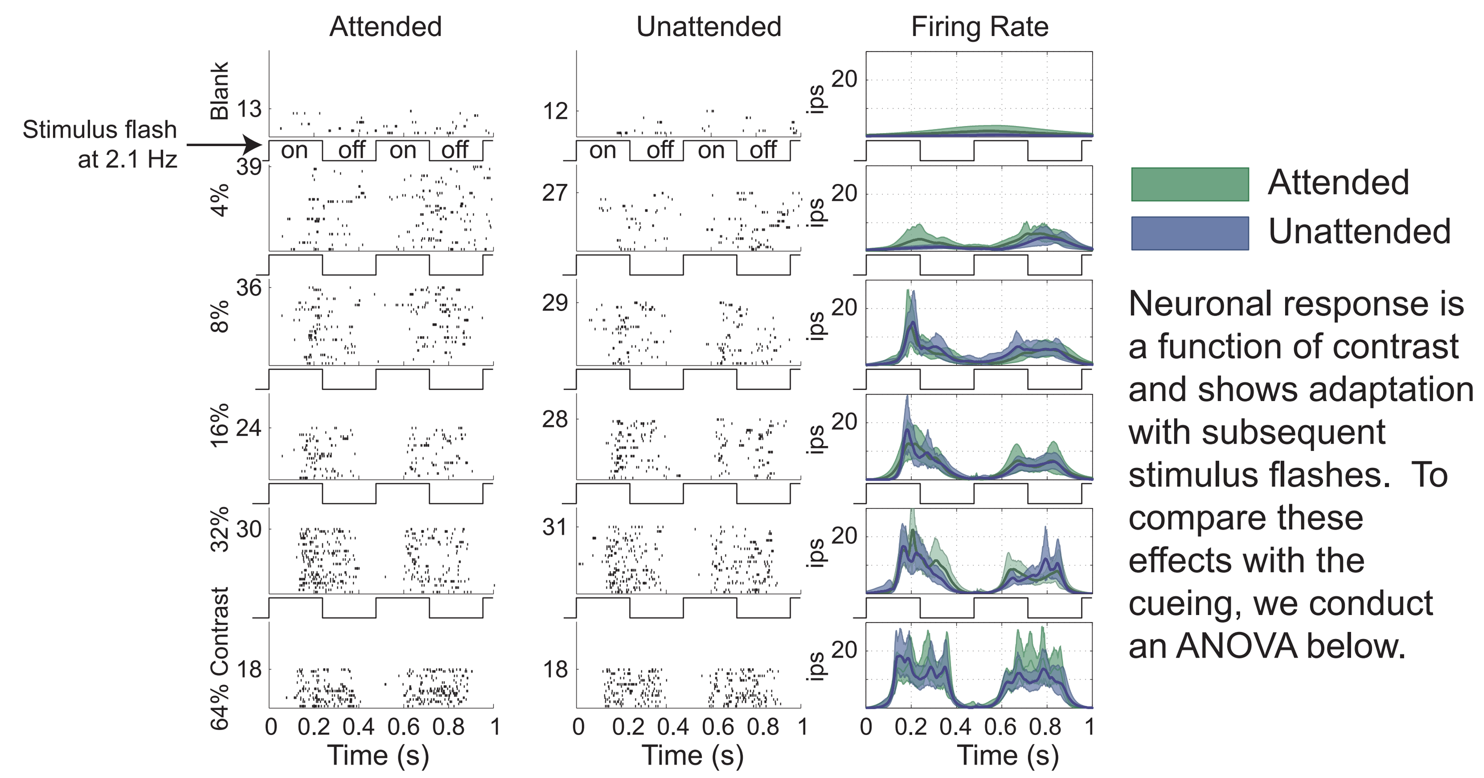




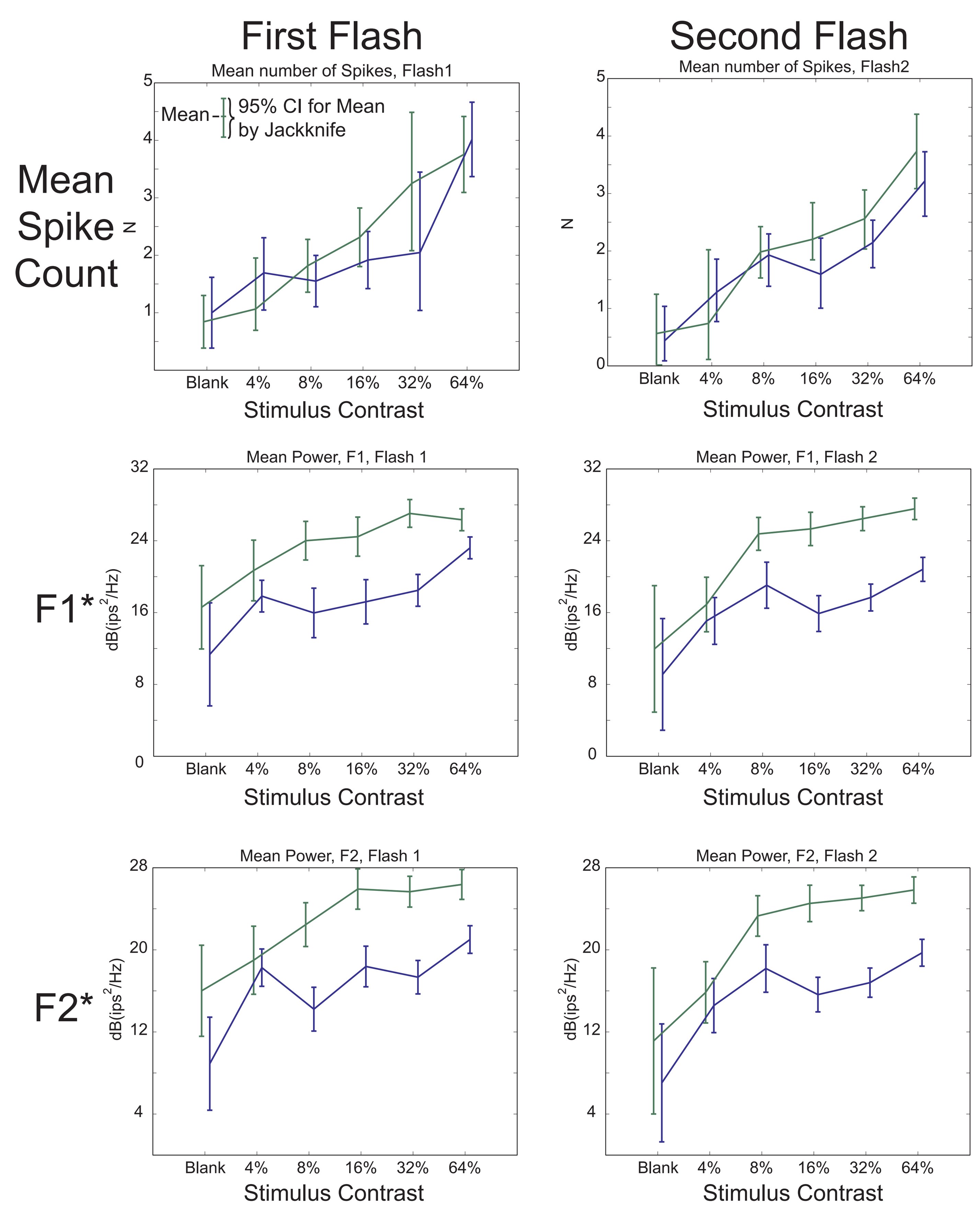
The behavioral task was controlled by a computer running TEMPO (Reflective Computing) under MSDOS 6.22 (Microsoft). Stimuli were presented by a VSG 2/3 (Cambridge Research) at 96Hz refresh on a 20 inch Sony CRT monitor positioned 57 cms from the monkey's eyes. Eye position was monitored by an IR video eye tracking system (ASL) operating at 120 Hz.

Neural activity was recorded using monopolar tungsten electrodes (FHC) referenced to a titanium strip secured by a skull screw in the implant. Rapid typing was conducted with hoop-discriminated spikes, and an attempt was made to maximize the driving of a single neuron. Neural data together with timing pulses were continuously streamed to disk at 20KHz for offline analysis.

Single Unit Example



Neuronal response is a function of contrast and shows adaptation with subsequent stimulus flashes. To compare these effects with the cueing, we conduct an ANOVA below.



ANOVA Results:
Contrast: P<1e-6 **
Flash Number: P<0.087
Cue: P<0.09

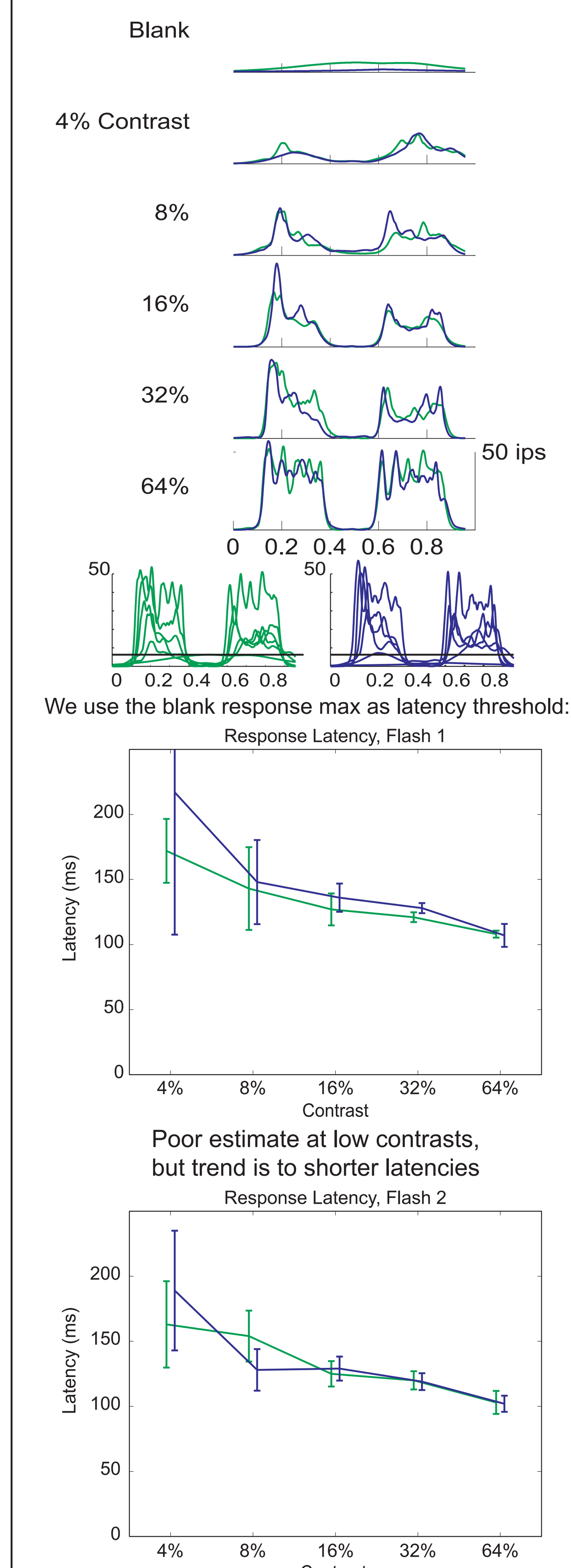
ANOVA Results:
Contrast: P<0.0035 *
Flash Number: P<0.49
Cue: P<1e-6 **

ANOVA Results:
Contrast: P<0.053
Flash Number: P<0.21
Cue: P<1e-6 **

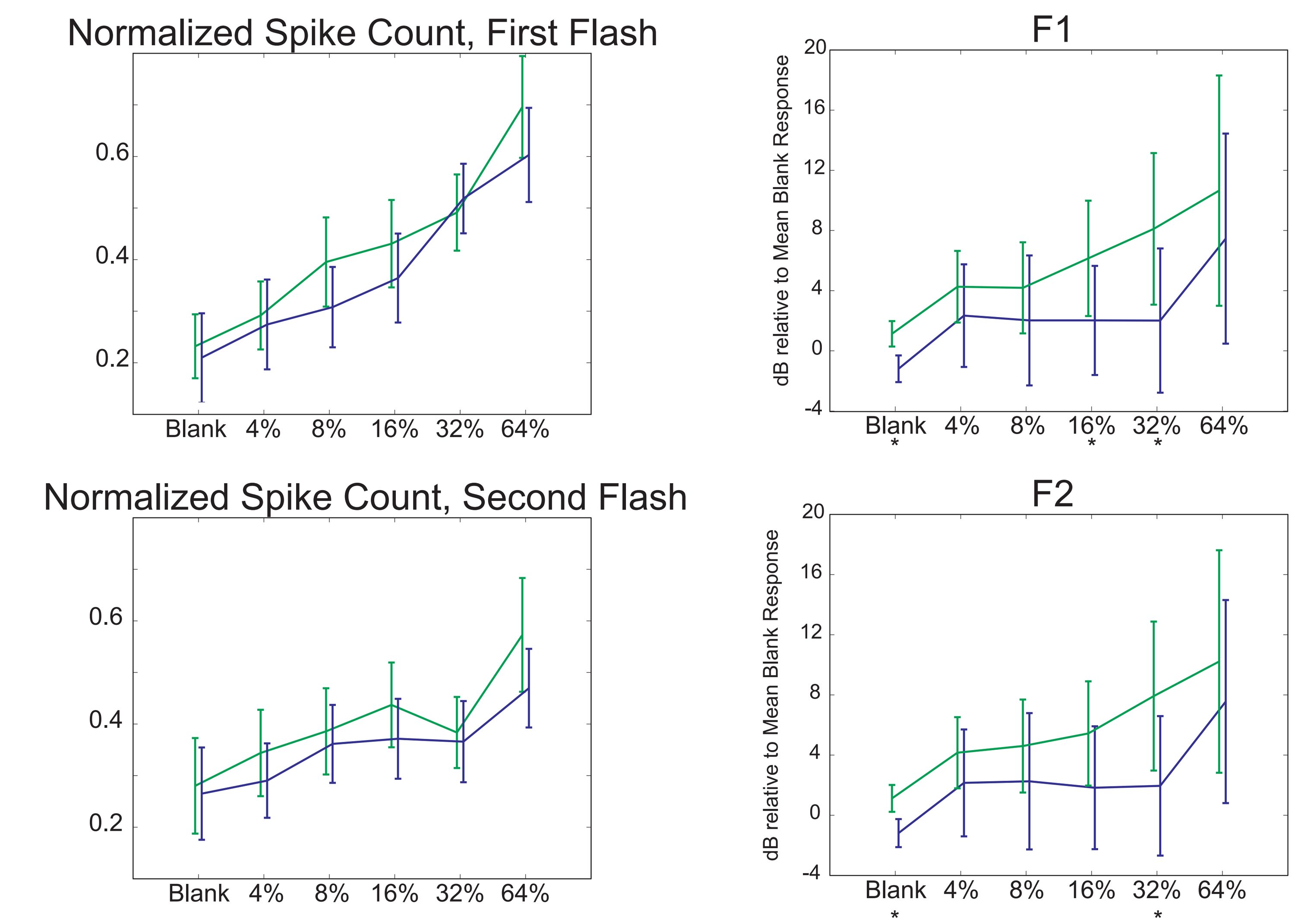
*Note: F1 and F2 are computed directly from the spiketimes on a trial-by-trial basis, using a Slepian tapered estimate with a frequency bandwidth of 2 Hz, so that the F1 and F2 estimates are uncorrelated. Thus these measures indicate patterning of spikes within single trials, and this patterning is more influenced by attention than the mean spike count. The apparent additive increase in power for all contrasts on a log scale is consistent with a multiplicative scaling of the response with attention (McAdams and Maunsell, 1999).

Attention and contrast-gain-control-like behavior in a single unit

Apply a narrow-bandwidth local likelihood Poisson estimator (locfit, C. Loader) to visualize dynamics.

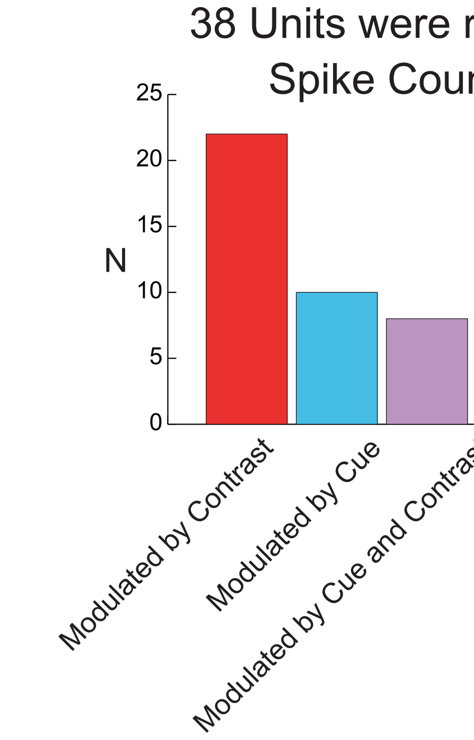


Population Average



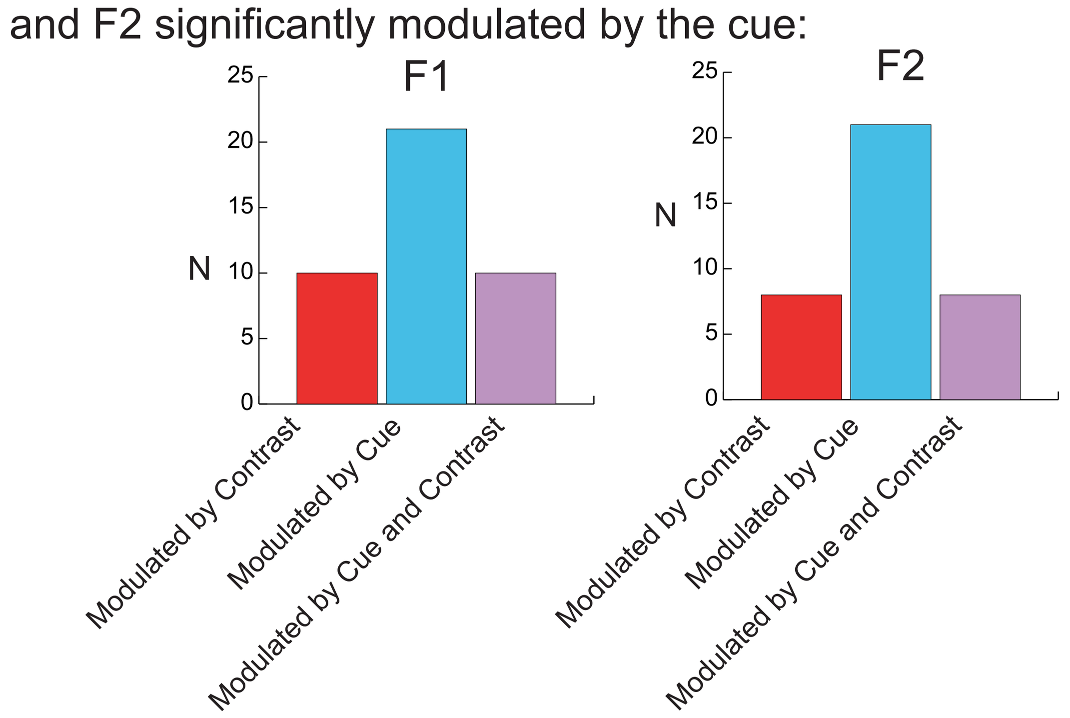
Ensemble Summary

38 Units were recorded in 20 locations



Significant Modulation defined as P<0.05 in an ANOVA against contrast, flash number, and cue

Of the 22 neurons that showed a significant contrast response in the mean firing rate, essentially all had F1 and F2 significantly modulated by the cue:



Conclusions

Attention influences the power in the F1 and F2 responses even more than the mean rate

Single units in V4 can show shifts in dynamics that are analogous to changes in contrast

References

Loader, C (2002). Local Regression and Likelihood (New York: Springer-Verlag).

McAdams CJ, Maunsell JHR (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. J Neurosci 19(1), 431-41.

Reynolds JH, Pasternak T, Desimone R (2000). Attention increases sensitivity of V4 neurons. Neuron 26(3), 703-14.

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