



## Combining spatial and feature-based attention within the receptive field of MT neurons

Dieter R. Patzwahl<sup>a</sup>, Stefan Treue<sup>b,c,\*</sup>

<sup>a</sup> Multi Channel Systems MCS GmbH, Aspenhausstrasse 21, 72770 Reutlingen, Germany

<sup>b</sup> Cognitive Neuroscience Laboratory, German Primate Center, Kellnerweg 4, 37077 Goettingen, Germany

<sup>c</sup> Bernstein Center for Computational Neuroscience, Goettingen, Germany

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### ABSTRACT

This study investigates the effects of feature-based attention on responses of direction-selective neurons in the middle temporal area (MT) of macaque visual cortex to attended stimuli inside the receptive field. Redirecting attention between the preferred and null direction of transparent random dot motion patterns caused a mean modulation of responses of ~32%, about half of what was observed when the two directions of motion in the receptive field were spatially separated allowing feature-based and spatial attention to work in concert. This is consistent with models of visual attention that interpret the attentional modulation of a neuron as the combination of all attentional influences, treating stimulus location simply as another feature.

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### 1. Introduction

Visual attention is a process for enhancing the representation of attended aspects of the sensory input at the expense of unattended information. This endows us with faster and more accurate vision that is of higher spatial resolution and enhanced sensitivity for fine changes. Perceptually attentional modulation seems to manipulate the very appearance of our environment, increasing the apparent contrast of attended stimuli (Carrasco, Ling, & Read, 2004; Treue, 2004) and enhancing their perceptual strength along a multitude of dimensions (e.g. Anton-Erxleben, Henrich, & Treue, 2007; Lankheet & Verstraten, 1995; Liu, Fuller, & Carrasco, 2006; Turatto, Ves-covi, & Valsecchi, 2007).

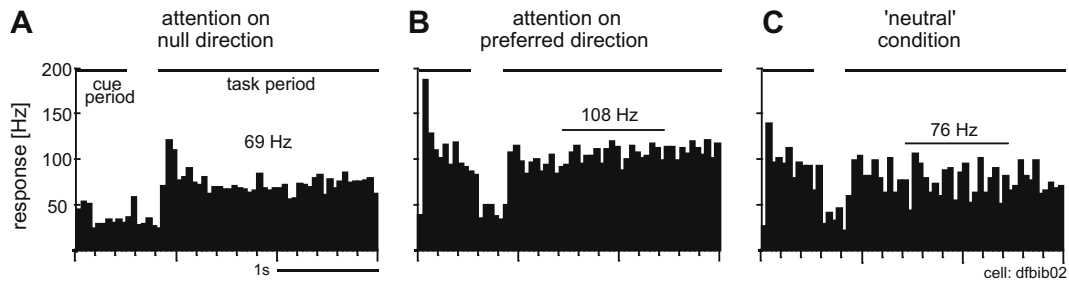
The physiological correlate of these effects appears to be an enhanced gain of neurons in visual cortex tuned to the stimulus dimensions that are relevant in the momentary context and preferring features (such as a particular stimulus location, direction, and orientation) that are currently attended. Correspondingly the sign and magnitude of attentional modulation of individual neurons are well predicted by the similarity between the attended stimulus properties and the preference of a given neuron for these features. While most studies of the neurophysiological correlate of attentional modulation have focused on spatial attention this feature-similarity gain

model was developed as a consequence of observing a direction-specific gain enhancement of neurons in area MT of macaque visual cortex across the visual field when the animal was attending to a stimulus moving coherently in one direction (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999). Such a feature-based response modulation of neurons, even though spatial attention was directed far outside their receptive field, was subsequently also observed in recordings in area V4 (Bichot, Rossi, & Desimone, 2005; McAdams & Maunsell, 2000), as well as fMRI and EEG studies (Saenz, Buracas, & Boynton, 2002; Stoppel et al., 2007) and psychophysical experiments (Saenz et al., 2002) and is consistent with the results of other recording studies of the effects of feature-based attention in the ventral processing pathway of primate visual cortex (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, & Desimone, 1993; Haenny, Maunsell, & Schiller, 1988; Haenny & Schiller, 1988; Mirabella et al., 2007; Motter, 1994a, 1994b).

While single-cell recording studies of spatial attention have addressed the changes in receptive field profiles (Anton-Erxleben, Stephan, & Treue, in press; Connor, Gallant, Preddie, & Van Essen, 1996; Connor, Preddie, Gallant, & Van Essen, 1997; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006; Womelsdorf, Anton-Erxleben, & Treue, 2008) when attention is directed in or near the receptive field, studies of feature-based attention have often maintained attention far outside the receptive field. The notable exception is a recent study by Wannig, Rodriguez, and Freiwald (2007), who have cued macaque monkeys to direct their attention onto one of two superimposed, transparently counter-rotating random dot surfaces. They interpret their finding of a non-spatial attentional modulation depending on the local direction of motion of the attended

\* Corresponding author. Address: Cognitive Neuroscience Laboratory, German Primate Center, Kellnerweg 4, 37077 Goettingen, Germany. Fax: +49 551 3851 183.

E-mail addresses: [patzwahl@multichannelsystems.com](mailto:patzwahl@multichannelsystems.com) (D.R. Patzwahl), [treue@gwdg.de](mailto:treue@gwdg.de) (S. Treue).



**Fig. 1.** Responses of a single cell in the three behavioral conditions of task 1. The x-axis represents time and the y-axis average firing rate across trials in 50 ms bins. The panels show post stimulus time histograms of the cell during the cue presentation, the task phase (when the transparent stimulus was presented) and the blank period in between. In each task period transparent motion (preferred and null direction) was presented inside the receptive field. In condition A attention was directed towards the null direction and in condition B towards the preferred direction. In condition C attention was on a dot at the fixation cross. The firing rate shown in each panel represents the average response rates during the interval indicated by the horizontal line (including only hit trials where the behaviorally relevant target change occurred after the analyzed interval). The stimulus during the cue period moved in the null direction in condition A and in the preferred direction in the other two conditions.

dot pattern as surface-based attention, while at least some of the data could also be accounted for by an expanded feature-similarity gain model of attention (Treue & Katzner, 2007).

Here we report the effects of feature-based attention directed into the receptive field of MT neurons in tasks designed to either isolate the effects of attention to a particular motion direction or to combine it with spatial attention. We find strong attentional effects based on the attended direction which was further enhanced by combining it with the modulation caused by selectively attending to one of two spatially separated patterns within the receptive field.

## 2. Methods

**Stimuli:** Task 1 was designed to study attentional modulation based solely on the direction of motion in the absence of any changes in spatial attention. The transparent motion stimulus consisted of two spatially superimposed random dot patterns (dot size  $0.03^\circ$ , density: 3 dots/deg<sup>2</sup>) moving in the preferred and null direction for the cell under study. The two dot patterns were red or green, respectively (approximately isoluminant) to make the perceptual separation easier (Croner & Albright, 1999) but the two possible color-direction combinations were randomized. Transparent motion stimuli pose a particular challenge for the visual system as they require the extraction and encoding of more than one stimulus property at a given visual field location and in that signal-to-noise ratios cannot be improved by enlarging the area of spatial averaging. Responses in area MT to the combination of multiple directions of motion in the receptive field fall in between the responses to the individual directions in isolation (Snowden, Treue, Erickson, & Andersen, 1991; Treue, Hol, & Rauber, 2000).

Task 2 was designed to investigate the effect of combining spatial location and motion direction. The two moving patterns were spatially separated half circles of moving white dots, and were placed side-by-side to form a circle, separated by a gap (1/10 of the stimulus diameter, see Fig. 3a). In both tasks the size (3–10° diameter), direction, and speed (2–20°/s) of the patterns were adjusted to the preferences of each recorded cell. In Task 2 the two half circles were aligned parallel to the preferred direction of the cell. The same dot density was used for the surfaces in tasks 1 and 2. Because of the smaller stimulus area in Task 2 that meant that fewer dots were present in the receptive field. This is unlikely to have any effect on responses given that MT neurons show response saturation at low number of dots in the receptive field (Snowden et al., 1991, 1992).

**Behavioral task:** tasks 1 and 2 were carried out in separate blocks, but within a given block all trial conditions were interleaved. In task 1 the monkey was instructed by a moving pattern which direction was relevant (target) in a given trial, and in task 2 the location of a static pattern indicated the relevant location (target). The other pattern was irrelevant (distractor). At the beginning

of each trial the respective cue was presented for 500 ms and was separated from the onset of the target and distractor stimuli by a gap of 350 msec<sup>1</sup>. During the following task period both target and distractor could change speed (duration: 200 ms, 340–2660 ms after onset, 70–120% faster than the base speed), and the monkey was rewarded only when he responded to a speed change of the target by releasing a lever. In a 'neutral' condition the monkey had to respond to a color change at the fixation cross. Failure to respond within the reaction time window (200–600 ms after the end of the speed change), responding to a change in the distractor or deviating the gaze by more than 1° from the fixation cross aborted the trial without reward. The monkey's performance was 86% (task 1), and 73% (task 2) of those trials that were not aborted due to eye movements.

**Data analysis:** Our recording methods have been described elsewhere (Treue & Maunsell, 1999). Cells were determined to be in MT by their directionality, receptive field position and size, and by the position of the electrode in the brain. Response rates were determined by averaging the firing rates across trials for 1 s starting 600 ms after task period onset to exclude motion onset responses (see Fig. 1). Only correctly completed trials and within those only trials where no stimulus change occurred within the period used for determining the response rate were included in the analysis. Data analysis was restricted to 46 cells for which more than 8 trials per condition were recorded. To quantify attentional modulation between two different attentional conditions an attentional index  $(R_p - R_N)/(R_p + R_N)$  was calculated ( $R_p$  = response when attending to preferred direction,  $R_N$  = response when attending to null-direction). *t*-Tests were used throughout to test for significant shifts of the index distribution from zero (no attentional modulation).

## 3. Results

### 3.1. Attention to motion direction

In task 1 the monkey had to attend either to the preferred direction, the null direction, or to a dot at the fixation cross. Fig. 1 depicts the responses of a typical MT cell under these three attentional conditions.

When attention was directed to the null direction (Fig. 1A) the firing rate was lowest (mean: 69 Hz). Under the same stimulus conditions but with attention directed to the cell's preferred direction (Fig. 1B) the firing rate increased substantially (108 Hz, an

<sup>1</sup> This delay is long enough for a decay of the activity evoked by the cue. Therefore a potential influence on the following stimulus period would consist of an adaptation effect that would reduce responses in the attention on preferred direction and vice versa for the attention on null direction. Rather than accounting for our observation such an effect would reduce the attentional modulation observed.

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