Spatial, feature and temporal attentional mechanisms in visual motion processing

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Sonia Baloni

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New Delhi (India)

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Thesis committee members:

Prof. Dr. Stefan Treue (Advisor, First Referee)
Cognitive Neuroscience Laboratory
German Primate Center
Kellnerweg 4
37077 Göttingen

Prof. Dr. Alexander Gail (Second Referee)
Sensorimotor Group, BCCN
German Primate Center
Kellnerweg
37077 Göttingen

Prof. Dr. Fred Wolf
Department of Nonlinear Dynamics & Network Dynamics Group, BCCN
Max Plank Institute for Dynamics and Self-Organization
37077 Göttingen

Additional Reviewers:

Prof. Hansjörg Scherberger
Research Group Primate Neurobiology
German Primate Center
Kellnerweg 4
37077 Göttingen

Prof. Dr. Melanie Wilke
Department of Cognitive Neurology
University Medicine Göttingen
Robert Koch Strasse 40
37075 Göttingen

Prof. Dr. Tobias Moser
Inner Ear Lab
Department of Otolaryngology
University Medicine Göttingen
Robert Koch Strasse 40
37075 Göttingen

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I hereby declare that this thesis has been written independently and with no other sources and aids than quoted.

Sonia Baloni

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CONTENTS

1. INTRODUCTION

In order to sustain ourselves in the environment we need to process the information present around us. Sensory organs act like an interface between the surroundings and us and help us to encode the information of the surroundings that are then propagated to higher processing centers for perception and action. Since it is difficult to process all of the information present in the environment at a given time, evolution has provided us with a mechanism known as ‘attention’, which helps us to direct our processing resources only to the behaviorally relevant aspects of the environment.

In my thesis I will be discussing the role ‘attention’ in visual motion processing, which is accomplished along the dorsal pathway. I will present my results through three projects; two physiology projects studying the spatial and feature-based attentional effects in visual motion processing with macaque monkeys as subjects and a psychophysics experiment which explores temporal aspects of visual motion processing in the human subjects.

This chapter is dedicated to provide a comprehensive introduction for the projects that I will be discussing in the following chapters. I have segregated the results of my projects into three chapters. The following chapter (chapter:2) investigates the physiology of spatial attention effects in area MSTd of macaque visual cortex. Chapter 3 involves experiments to study the physiological effects of feature-based attention in area MSTd and MT of the macaque visual cortex. In chapter 4, I discuss results from the psychophysics project, which studies attentional limitation in visual motion processing in the temporal domain.

1.1 Visual processing hierarchy:

Visual information gains access to our system through eyes and are transformed into the neural code by retina (a light sensitive tissue situated at the back of the eye), which are then further propagated to the three sub-cortical regions; lateral geniculate nucleus (LGN), superior colliculus, and the pretectum. LGN receives about 90% of the projections from the retina and in turns projects majorly to the primary visual cortex or area V1. Many anatomical, behavioral and physiological studies have identified at least 30 cortical areas in macaque, involved in visual processing (Van Essen and Maunsell 1983; Felleman and Van Essen 1991), which are interconnected (majority of them being reciprocal connections) by more than 300 distinct cortico-cortical pathways (Van Essen and Gallant 1994). Based on these projection studies a heuristic hierarchical model for visual processing was proposed (Van Essen and Maunsell 1983; For review see, Maunsell and Newsome 1987). A simplified version of this hierarchy developed by Van Essen (1985), is shown in figure 1. Further, lesion studies combined with the electrophysiology studies have contributed in understanding the functional properties of the neurons representative of different areas along the hierarchy, which suggests existence of two distinct pathways originating from the area V1, through which visual information processing is accomplished (Mishkin, Ungerleider et al. 1983). The two visual pathways (figure 2) are identified as i) Dorsal pathway which extends from area V1 via area V2, V3, MT, MST, LIP, VIP to the parietal cortex and is involved in motion processing, ii) Ventral pathway which extends from area V1 via area V2, V3, V4, IT to the temporal lobe and is specialized for color, shape and object recognition (For review see, Maunsell and Newsome 1987).
A notable trend of the organization of the visual cortical areas is the size of receptive field, which are arranged in a retinotopic manner and increases in size with successive stages of the hierarchy, with V1 neurons having the smallest receptive field (Van Essen and Maunsell 1983).

1.1.1 Stimulus selectivity

The hierarchical model of visual processing proposes a division of labor, where each area contributes by processing an aspect of the incoming visual information it is specialized for. Literature shows that neurons across the visual cortex are selective for not one but multiple stimulus dimensions e.g., area V1 shows selectivity for color (Gegenfurtner and Kiper 2003), orientation (Hubel and Wiesel 1968), direction and speed (Snowden, Treue et al. 1992), along the ventral pathway area V2 for color, orientation selectivity (Gegenfurtner, Kiper et al. 1996), V3 for color, orientation, binocular disparity selectivity (Gegenfurtner, Kiper et al. 1997; Adams and Zeki 2001) and V4 shows selectivity for color, orientation, direction (Schein and Desimone 1990). Along the dorsal pathway area MT shows selectivity for color (Seidemann, Poirson et al. 1999), direction

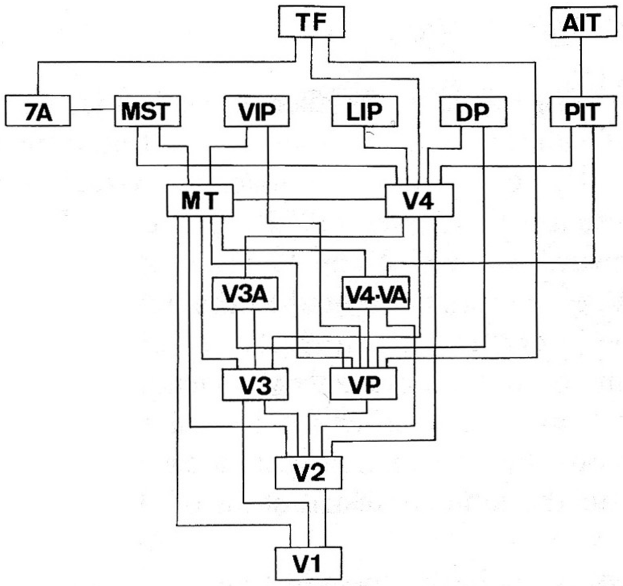

Figure 1: Visual processing hierarchy in macaque visual cortex (Maunsell et al, 1987)This figure shows only the major connections existing between different areas in the macaque visual cortex adapted from numerous neuroanatomical studies by Van Essen (1985). Each area is one level above the highest level from which it receives forward input, and below all levels from which it receives feedback. Similarly, each area is above all areas to which it sends a feedback projection, and below those to which it sends a forward projection. For clarity the feed-forward connections are not distinguished from feed-back connections.

and speed (Albright 1984), area MSTd for optic flow stimuli (Graziano, Andersen et al. 1994), eye movements (Kawano, Sasaki et al. 1984; Thier and Erickson 1992) etc. But in spite of demonstrating selectivity for multiple stimuli, each area has one stimulus dimension for which they show 'best' selectivity marked by response strength, frequency of feature selective neurons, tuning characteristics (e.g., orientation selectivity for V1 (Hubel and Wiesel 1968), color for V4 (Schein and Desimone 1990), direction for MT (Albright 1984), components of optic flow for MSTd (Graziano, Andersen et al. 1994) etc.).

Moreover, there are neuroanatomical evidences showing reciprocal connections not only amongst different areas within a processing pathway, but also amongst areas at the same hierarchical level between the two pathways e.g., existence of inter-connections of V4 of the ventral pathway with MT and MST of the dorsal pathway (Figure1,For review see, Maunsell and Newsome 1987), suggesting that these two processing pathways are not mutually exclusive of each other.

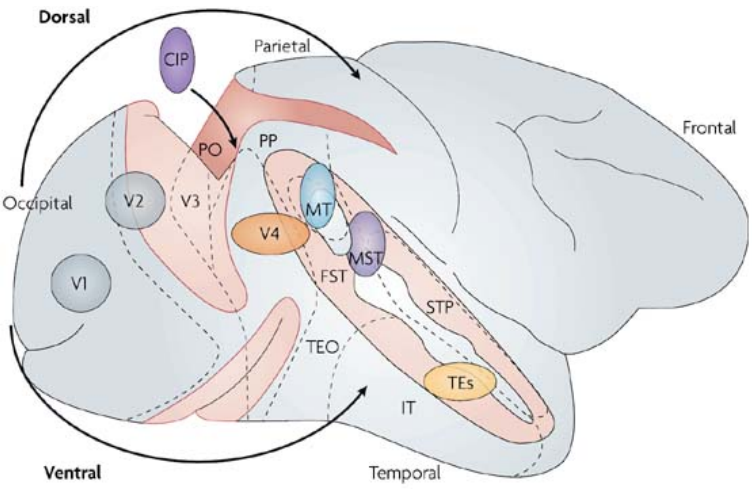

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Figure 2: Schematic diagram of visual processing pathways in Macaque cortical areas.

The two visual processing pathways; dorsal and ventral pathways are marked by arrows. The ventral visual areas are highlighted with horizontal ellipses of red/orange colors, the dorsal visual area highlighted with vertical ellipse of blue/ purple colors, the early visual areas V1 and V2 are shown with gray circles.

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1.2 Visual motion processing

1.2.1 Origin of motion processing

Motion processing is largely accomplished along the dorsal pathway, which originates from the area V1 (figure 2), the first area in the visual cortex to demonstrate direction selectivity (Hubel and Wiesel 1968). The direction selective cells in area V1 are represented in the layer 4B, but their origin can be back traced to the M pathway in sub-cortical area LGN. Area MT, the next area along the dorsal pathway to demonstrate strong direction selectivity receives direct and indirect (via V2 and V3) projections of the direction selective cells in the layer 4B from area V1 (Lund, Lund et al. 1975; Ungerleider and Mishkin 1979; Nakayama 1985).

1.2.2 Motion processing areas:

Medial Temporal lobe (MT)

Medial temporal Area (MT or V5) is located in the lower banks of the superior temporal sulcus and receives direct inputs from the area V1 (figure 2). The receptive field of MT neurons are almost 10 times larger than the V1 neurons and are retinotopically organized (Nakayama 1985; For review see, Born and Bradley 2005). Majority of its neurons show strong direction (Albright 1984) and binocular disparity selectivity and are organized into a systematic columnar structures (DeAngelis and Newsome 1999). The direction tuning profiles of the neuron in area MT for translation motion (linear motion stimuli) are well approximated by the Gaussian functions. The critical role of area MT in motion perception was elucidated by lesion (Newsome and Pare 1988), behavioral (Britten, Newsome et al. 1996) and electrical stimulation studies (Salzman, Britten et al. 1990). Majority of inputs from the area MT are propagated to area MST the next stage in visual processing hierarchy (Maunsell and van Essen 1983).

Medial Superior Temporal Area (MST):

Area MST is located in the anterior banks of the superior temporal sulcus (figure 2) and is further divided into two distinct areas; the lateral ventral region (MSTl) and the dorsal region (MSTd) (Komatsu and Wurtz 1988; Newsome, Wurtz et al. 1988; Born and Tootell 1992). MSTd is represented by neurons with large receptive field than MT (covering most of the contralateral visual hemi-field) and shows selectivity for a complex stimuli like spiral motion space (SMS) and linear motion stimuli (LMS) (Graziano, Andersen et al. 1994). Spiral motion space is a kind of optic flow stimuli, where expansion, contraction, clockwise and counterclockwise rotation forms the cardinal axis and the combination of rotation stimuli with expansion, contraction (known as spiral motion stimuli) represents a smooth continuum between these cardinal axes. Optic flow stimuli are generated in the retina when an observer navigates through the environment (the surroundings appear to expand). Since MSTd receives pursuit eye signals and also shows selectivity for SMS, suggest that this area might be involved in computing heading directions thereby helping in visual navigation (Sakata, Shibutani et al. 1983; For review see, Andersen, Snyder et al. 1997).

The lateral ventral part of MST (MSTl) is known to contribute in analysis of object motion. The receptive fields of MSTl though larger than MT, but are smaller than MSTd (Eifuku and Wurtz 1999).

1.3 Visual Information Processing: Attention

Not all visual information that gains access to our system is perceived. Rather, perception is limited only to the behaviorally relevant visual information (signal), which is selectively channeled out from the surrounding noise, by employing a filter mechanism called 'Attention'. Allocation of attention can be achieved either via voluntary top-down (goal driven) or automatic bottom-up (stimulus driven) mechanisms. Neural correlates of attention have been demonstrated by both behavioral and neurophysiological experiments along the dorsal and the ventral pathways. The results from many studies indicate that attention enhances visual processing, by combining top-down and bottom-up signals generating a saliency map of the visual environment, which highlights the behavioral relevant aspects of the environment, which then can be preferentially processed (Treue 2003). The saliency map could be either location dependent (spatial attention), or location independent (feature-based, object-based attention) or in a particular instant of time (temporal attention).

1.3.1 Different modalities of attention:

Spatial Attention

Spatial attention is the most widely studied form of attention. Behavioral studies have shown that when attention is directed to a location in the visual space, the efficiency and the accuracy of visual processing is increased at the attended location (Posner 1980). Effects of spatial attention have been demonstrated in almost all areas of the visual cortex, by recording from single neurons while monkey's attention was switched between two stimuli placed inside and outside the receptive field of a neuron (Treue and Maunsell 1996; McAdams and Maunsell 1999). The responses of neurons were on average significantly higher when attention was directed to the stimulus inside the receptive field of the neuron. Similar spatial attention effects have also been reported in the sub-cortical area LGN (O'Connor, Fukui et al. 2002). The magnitude of attentional modulation varies not only amongst neurons within an area but also between areas in the visual cortex (figure 3) (Cook and Maunsell, 2002). Across the visual processing hierarchy there is a general trend of increase in the magnitude of attentional modulation as we go higher in the visual processing areas, while within an area the modulation effects are suggested to depend upon the task demands (figure 4) (Spitzer, Desimone et al. 1988).

Neural correlates of spatial attention can be classified into multiplicative (figure 4), non-multiplicative (figure 5) and the contrast gain effects (figure 6). The multiplicative effects are characterized by enhancement of the response gain of neurons across the tuning curve by a constant factor without affecting the selectivity (tuning width) of the neuron and have been demonstrated for the orientation tuning curves in the area V4 (McAdams and Maunsell 1999) and direction tuning curves in the area MT (Treue and Maunsell 1996).

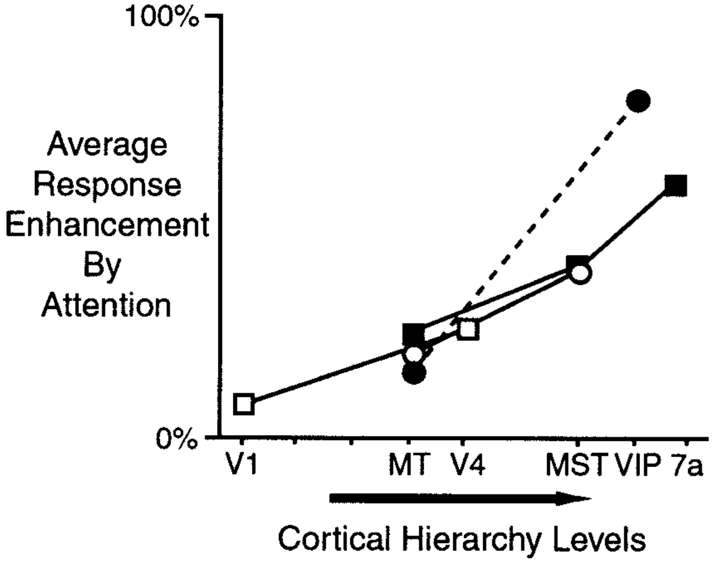

Figure 3: Magnitude of attentional modulation as a function of visual processing hierarchy.

The attentional modulation values were pooled from different studies. Filled circles corresponds to Cook and Maunsell (2002); open squares represents data from McAdams and Maunsell (1999); open circles are values from Treue andMaunsell (1999); and filled squares are from (Ferrera, Rudolph et al. 1994). *Maunsell, J. H. and E. P. Cook, "The role of attention in visual processing." Philosophical transactions of the Royal Society of London. Series B, Biological sciences, (2002),* ***357(1424):*** *1063-1072, by permission of the Royal Society.*

Conversely, the non-multiplicative effects are described by enhancement of both the response gain and the selectivity (narrowing of the tuning width), as a function of task difficulty (Spitzer, Desimone et al. 1988). These multiplicative and non- multiplicative effects were demonstrated on the feature selectivity of a neuron like direction, color or orientation, but non- multiplicative attentional effects have also been reported for spatial tuning domain in area MT and V4, where attending to a location tends to shift the center of the receptive field and width of the spatial responsitivity towards the attended location (Moran and Desimone 1985; Womelsdorf, Anton-Erxleben et al. 2006). This mechanism might contribute to enhance the spatial resolution and thereby enhancing the visual processing at the attended location. The third kind of attention effect; the contrast gain effects corresponds to a shift in the contrast-response functions in a direction to cause reduction in neuron's contrast-response threshold (Reynolds, Pasternak et al. 2000; Martinez-

Trujillo and Treue 2002), though these effects were very similar to the multiplicative response gain effects (For review see, Reynolds and Chelazzi 2004). Chapter 2 of my thesis investigates the spatial attention effects in the area MSTd across the tuning curves for SMS (preferred stimulus dimension) and compares them to the previous effects reported in the same area but with LMS (Treue and Maunsell 1996). For a separate data-set (discussed in chapter 3) spatial attention effects for SMS and LMS were recorded from the same neuron, in order to get better estimation of spatial attention effects across the two dimensions.

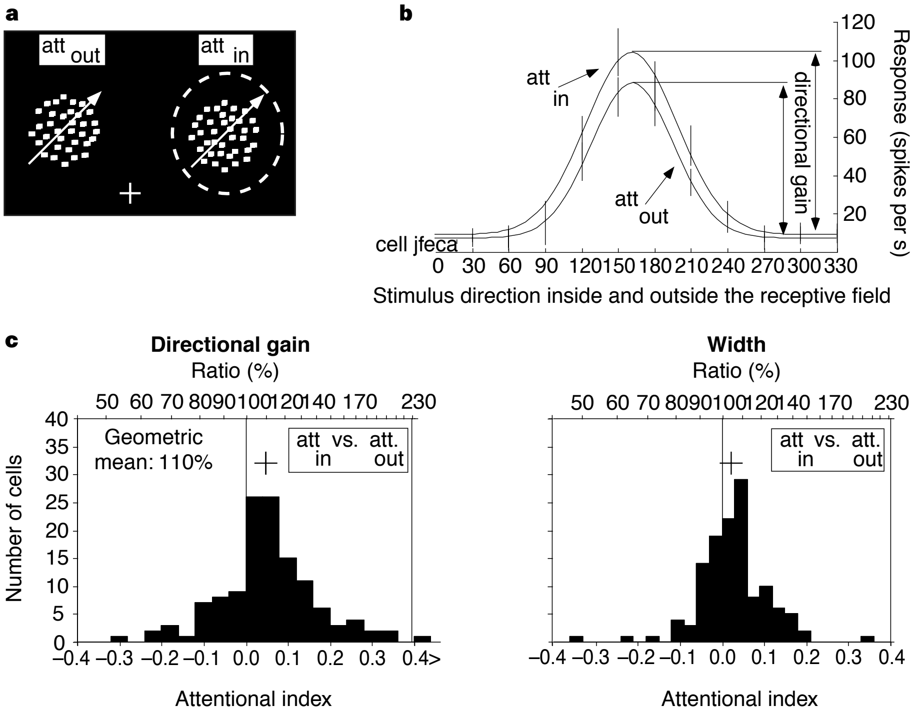

Figure 4: Multiplicative effect of attention in area MT (Treue and Martinez Trujillo 1999)

A. The task involved presentation of two random dot patterns simultaneously inside the classical receptive field (dashed circle) or outside the receptive field, while the monkeys were supposed to report the speed increment at the cued random dot pattern.

B. tuning curves of a example neuron when attention was directed inside the receptive field (att_{in}) and outside the receptive field (marked as att_{out})

C. Histogram showing distribution of the attentional index of directional gain and the width of the tuning curve for a population of MT neurons. There was a significant directional gain of 10% (mean marked by plus sign), but no change in width of the tuning curve when attention was directed inside the receptive field than outside, indicating a multiplicative effect.

*Reprinted from permission from the author, Nature, Treue, S. and J. C. Martinez Trujillo, (1999) "Feature-based attention influences motion processing gain in macaque visual cortex." **399**(6736): 575-579*

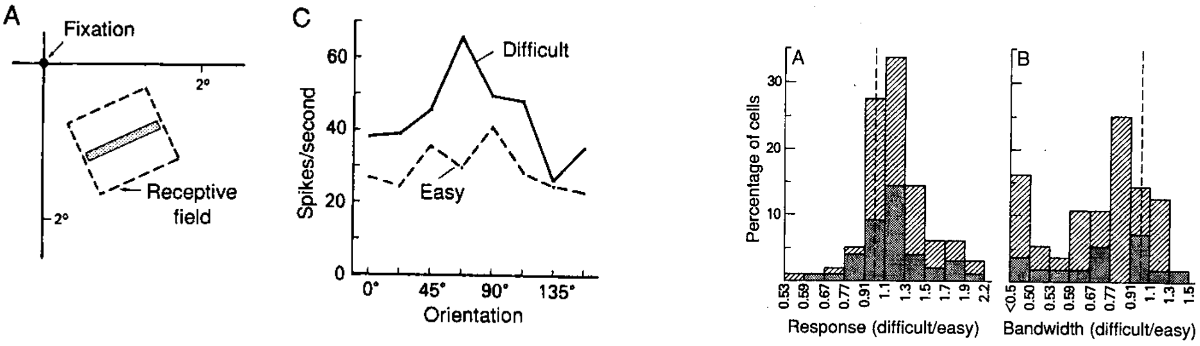

Figure 5: Non- multiplicative effects of attention in V4 neurons

A. The task which involved orientation discrimination task, the square area corresponds to the receptive field of the neuron
B. Orientation tuning curves for a example V4 neuron, which shows that the firing rates of the neurons were higher for difficult than easy discrimination task.
C. Distribution of the response ratio of the of V4 neurons for difficult and easy discrimination task, shows that for majority of the population the response of the neuron was higher in the difficult conditions.
D. Distribution of the tuning width ratio for the difficult and easy discrimination task, which shows that the selectivity of the neurons for majority of the population was enhanced (tuning width narrower) for the difficult conditions.

Spitzer, H., R. Desimone, et al. (1988). "Increased attention enhances both behavioral and neuronal performance." Science ***240****(4850): 338-340. Reprinted with permission from AAAS."*

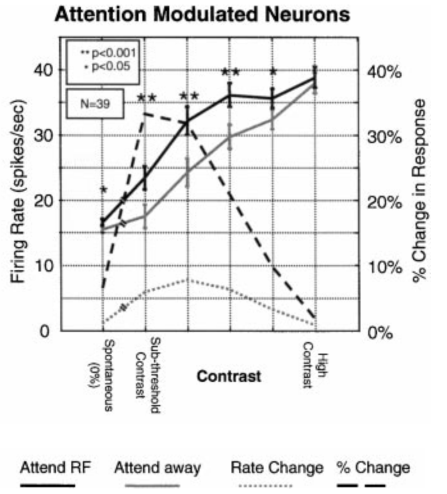

Figure 6: Contrast gain change in area V4

Population response of neurons in area V4 as a function of contrast when the monkey was performing a target detection task, by attending either inside (thick line with black circles) or outside the receptive field (thin line with open circles). Target stimuli (Grating stimuli) at five different contrast values spanning the dynamic range of each neuron were presented inside and outside the receptive field. The dashed and the dotted lines shows the percent and absolute difference in firing rate across the two attentional conditions respectively. *Reprinted Neuron, 26, Reynolds, J. H., T. Pasternak, et al., "Attention increases sensitivity of V4 neurons.", 703-714, Copyright (2000), with permission from Elsevier.*

Feature-based attention

This form of attention refers to directing attentional resources to a stimulus feature (like color, direction of motion, orientation etc.). Psychophysical studies have shown that unlike spatial attention that facilitates visual processing at the attended location, feature-based attention enhances processing of the attended feature across the visual field (Rossi and Paradiso 1995; Found and Muller 1996; Cohen and Magen 1999; Kumada 2001; Saenz, Buracas et al. 2003). Neural correlates for feature-based attention have been demonstrated in both the visual processing pathways (Treue and Martinez Trujillo 1999; McAdams and Maunsell 2000).

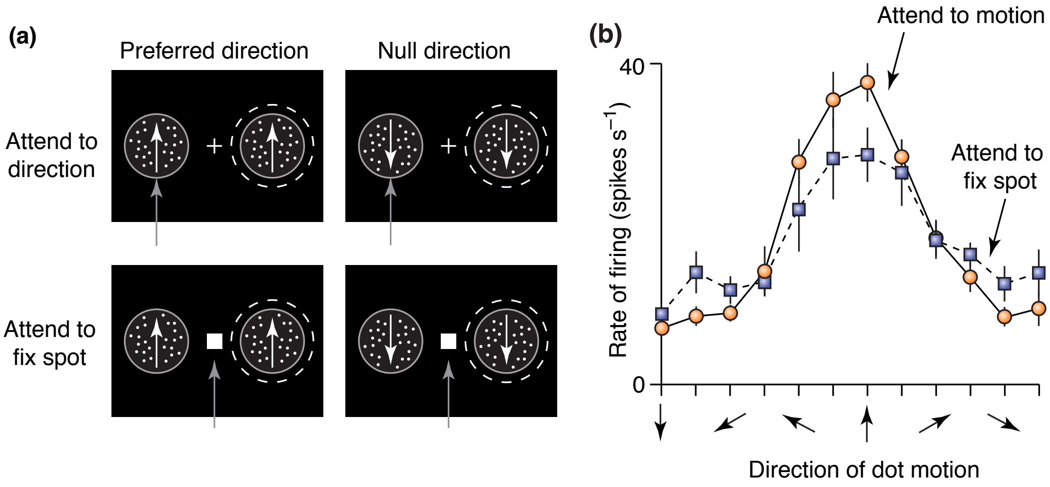

Figure 7: Feature-similarity gain model (Maunsell and Treue 2006)

(a) Schematic representation of the task. Two random dot pattern (RDP) were presented inside and outside the receptive field. The RDP inside and outside the receptive field were similar and could be either the preferred direction or the null direction of the neuron. In Attend motion trials monkeys were supposed to detect speed change in the stimuli outside the receptive field, while in attend to fix spot, the monkeys were instructed to detect the change in the luminance at the fixation spot at the center of the screen.

(b) Responses of MT neurons to different directions of motion under the two attentional conditions. It can be seen that responses of the neuron was increased when attention was directed to the preferred direction and decreased when directed to null direction. This effect was described as a push-pull effect, according to which when attention is directed to a feature, response of the neurons having feature similar to the attended feature are preferentially activated, while the response of other neurons are suppressed.

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The feature-based attentional effects were formulated into a 'feature-similarity gain model', according to which attention modulates responses of a neuron in a multiplicative fashion, and the magnitude of the modulation depends upon the similarity between the attended stimulus feature and neuron's preferred feature (Treue and Martinez Trujillo 1999). Therefore, feature-based attentional mechanisms improve the signal to noise ratio by selectively enhancing the response of the neurons in a multiplicative fashion across the visual cortex whose preferred feature is similar to the attended feature, and suppressing the response of neurons whose preferred feature is not similar to the attended feature.

Chapter 3 demonstrates feature-based attention effects in the area MSTd of macaque visual cortex for the two stimulus dimensions SMS and LMS and its comparisons with the area MT.

Object-based attention:

This form of attention refers to directing attention to coherent forms or features in the visual space and its neural correlates have been shown by range of psychophysical, physiological and imaging studies. A study (O'Craven, Downing et al. 1999), showed that directing attention to a feature of an object, resulted in the increase of responses in cortical areas that responded also to the task-irrelevant features of the attended object, but not for the features for the unattended overlapping objects. This result supported by many other studies (Mitchell, Stoner et al. 2003; Reynolds, Alborzian et al. 2003) indicated that attending to a feature of an object causes all of the object's feature to be selected together.

Temporal Attention

Since the visual inputs gaining access to our system is dynamic, we not only need to deploy attention to the most relevant location and feature but also to the relevant instance of time (temporal attention). Psychophysical study employing temporal analogue of Posner's (1978) spatial cue attentional task showed that just like spatial attention enhances visual processing at the cued location, visual processing is enhanced (Coull and Nobre 1998) and temporal resolution is improved (Correa, Sanabria et al. 2006) when attention is directed to the cued instant of time.

Visual search tasks involving processing of two targets when presented in close temporal proximity showed that the processing of the first target interferes and thereby degrades the processing of the second target. These interference pattern were independent of the spatial location of the two targets and were strictly time locked i.e. the processing of the second target was degraded no matter it was presented at the same spatial location as that of the first target (Kanwisher 1987; Raymond, Shapiro et al. 1992) or at different spatial location (Duncan, Ward et al. 1994). But this temporal interference was not there when the two targets belonged to different modalities (e.g., audio and visual) (Duncan, Martens et al. 1997).

Temporal interference in processing the two target stimuli presented at close temporal proximity at the same spatial location is most widely studied phenomena and is known as ‘Attentional Blink’. It has been described by several informal theories (Broadbent and Broadbent 1987; Raymond, Shapiro et al. 1992; Chun and Potter 1995) and computational model (Olivers and Meeter 2008; Shih 2008; Dux and Marois 2009). Almost all of the experiments studying attentional blink involved stationary stimuli like letters, digits, computer symbols etc., but none of the study looked into its profile in motion domain. Chapter 4 of my thesis involves extension of the attentional blink paradigm in the motion domain.(Maunsell and Cook 2002)

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1.4 Original articles and manuscripts

This thesis contains following research articles and manuscripts:

- **Characterization of spatial attention effects in area MSTd of macaque visual cortex for spiral motion stimuli.** Sonia Baloni, Daniel Kaping, Stefan Treue, in preparation

- **Relationship of the tuning properties with the spatial and feature-based attentional modulation in area MSTd of macaque visual cortex.** Daniel Kaping, Sonia Baloni, Stefan Treue, in preparation.

- **Attentional blink in visual motion processing.** Sonia Baloni, Janina Heuer, Nils Mueller, Stefan Treue, in preparation.

Chapter 2: Spatial Attention

In this chapter we studied the effects of spatial attention in area MSTd of macaque visual cortex with spiral motion stimuli. We sho that spatial attention modulates the responses of neurons in area MSTd multiplicatively across the tuning curve. The population of neurons recorded showed over-representation of the cells preferring expansion spiral motion space. These sub-population of neurons also showed significantly higher attentional modulation than cells preferring contraction spiral motion space. We also divided the population of neurons on the basis of waveform duration into putative narrow spiking and broad spiking neurons. These two population of neurons did not show any difference in the spatial attention modulation.

Author's contribution:

Daniel Kaping and Stefan Treue designed the experiment. Data collection and analysis was done by Daniel Kaping and Sonia Baloni. The manuscript was written by Sonia Baloni and Daniel Kaping and was edited by Stefan Treue. All authors discussed the results and worked upon the manuscript at all stages.

Characterization of spatial attention effects in area MSTd of macaque visual cortex for spiral motion stimuli

Daniel Kaping [1], Sonia Baloni[2,3], Stefan Treue[2,3]

[1]Laboratory for Attentional Control and Neural Circuits, York University, Department of Biology,Toronto,ON,Canada

[2]Cognitive Neuroscience Laboratory, German Primate Center, Goettingen, Germany

[3]Bernstein Center for Computational Neuroscience, Goettingen, Germany

ABSTRACT

Spatial attention modulates the responses of neurons across the visual cortex. Previous studies have shown multiplicative spatial attention effect in the dorsal region of medial superior temporal area (MSTd), with linear motion stimuli (LMS). We in this study report multiplicative spatial attention effect in the area MSTd with the more preferred stimulus dimension; spiral motion stimuli (SMS). The previously reported attentional effects with LMS were comparable to our results with SMS, suggesting that spatial attention modulates the responses of neurons irrespective of the stimulus dimension. MSTd neurons were characterized on the basis of their preferred direction in expansion and contraction spiral motion space, as well as on the basis of waveform duration into putative broad-spiking and narrow-spiking neurons. In agreement to previous studies we found a predominance of cells preferring expansion in MSTd, which additionally also had a significantly higher magnitude of attentional modulation than contraction preferring cells, which could be attributed to the involvement of MSTd in optic flow analysis. On the other hand no attentional differences were observed between putative broad-spiking and narrow-spiking neurons.

INTRODUCTION

Covertly directing the focus of attention to a stimulus placed within a predefined location has been a core tool to study the effects of spatial attention (Treue and Maunsell 1996; Luck, Chelazzi et al. 1997; Brefczynski and DeYoe 1999). This voluntary selection of the behaviorally most relevant location/stimulus prompts a top-down filtering process that enables us to overcome our limited visual information processing capacity. The perception of stimuli captured within the focus of attention is known to be facilitated; these stimuli are perceived more rapidly, accurately, with higher spatial resolution and sensitivity to fine changes while non-attended information appears lower in contrast, size and is sometimes not perceived consciously at all (Duncan 1984; Carrasco, Ling et al. 2004; Anton-Erxleben, Henrich et al. 2007). The quantitative effects of spatial attention on neuronal responses have been studied in a number of neurophysiological studies. One study recording from the dorsal part of the medial superior temporal area (MSTd), part of the dorsal motion processing pathway in the macaque, found that spatial attention modulates linear motion stimuli (LMS) responses of individual neurons by multiplying the firing rate by a constant factor (Treue and Maunsell 1996). This finding is consistent with the multiplicative gain model of attention and has been demonstrated in several extrastriate visual cortical areas (McAdams and Maunsell 1999; Treue and Martinez Trujillo 1999; Treue and Maunsell 1999). These studies typically characterize the attentional modulation employing the cell's "best" response selectivity produced by a collection of optimized stimuli belonging to a continuous set e.g., orientation studies in area V1, linear motion stimuli in area MT. A number of electrophysiological studies have shown that neurons within the dorsal region of MSTd respond preferentially to radial expansion, contraction and rotations (Duffy and Wurtz 1991; Graziano, Andersen et al. 1994). Although attention is known to progressively increase response gain from one visual area to the next along the dorsal motion processing hierarchy (Maunsell and Cook 2002), it remains uncertain whether the magnitude of enhancements is stimulus dependent. We intend to extend the previously described results of spatial attention induced response modulation in MSTd (Treue and Maunsell 1999) by (I) utilizing optimized complex global motion patterns and (II) additionally exploring the effects of spatial attention on MSTd microcircuitry. Recent studies have claimed to distinguish varying contributing cell types of local cortical microcircuits based upon the waveform duration of the recorded extracellular action potential waveform durations (Mitchell, Sundberg et al. 2007). The dynamic interplay of glutamatergic broad-spiking pyramidal cells and narrow-spiking GABAergic interneurons (Connors and Gutnick 1990; Wonders and Anderson 2006) ensures a balance of excitation and inhibition in cortical circuits. Here we sought to investigate and quantify the effect of spatial attention with an optimized complex global motion patterns on classified putative cell types in MSTd.

MATERIALS AND METHODS

We recorded the responses of 123 well-isolated motion-selective neurons from area MSTd of the visual cortex in two hemispheres of two macaque monkeys (monkey N: n = 65 and monkey W: N = 56) engaged in a spatial attention task. Experiments were performed in a dimly lit room. During the experiment, a custom computer program running on an Apple Macintosh PowerPC controlled the stimulus presentation, and monitored and recorded eye positions, neural and behavioral data. Eye positions were determined using video-based eye tracking (ET49, Thomas Recording, Giessen, Germany). Monkeys sat in a custom-made primate chair viewing visual stimuli on a computer monitor (distance of 57 cm). The monitor covered 40º x 30º of visual angle at a resolution of 40 pixel/deg.

Stimuli

We used random dot patterns (RDPs) of small bright dots (density: 8 dots per degree, luminance 75 cd/m^2) plotted within a stationary circular aperture on a gray background of 35 cd/m^2. Stimuli were spiral motion space (SMS) patterns considering expansion, clockwise rotation, contraction and counterclockwise rotation as neighboring stimuli with a continuum of stimuli in between these cardinal directions. The direction of SMS was determined by the angle that the individual dot formed with radial reference lines. By varying the angle we were able to create smooth transitions between neighboring directions within spiral motion space. Movement of the dots was created by the appropriate displacement of each dot at the monitor refresh rate of 75Hz.

Animal preparation and neural recordings

Following initial training, monkeys were implanted with a custom-made orthopedic implant preventing head movements during training and extracellular recordings. A recording chamber was placed on top of a craniotomy over left (monkey N: 3.25 mm posterior/16.3 mm lateral; Crist Instruments, CILUX Recording Chamber 35º, Hagerstown, MD) or the right (monkey W: 3 mm posterior/ 15.5 mm lateral; custom-fit computer-aided milled magnetic resonance imaging (MRI) compatible chamber, via digitized monkey skull surface reconstruction, 3di, Jena, Germany) parietal lobe. Pre-surgical MRI was used to position the chambers; post-surgical MRIs verified correct positioning and precise targeting of area MSTd. All surgeries were performed under general anesthesia and sterile conditions. Animal care and all experimental procedures were conducted in accordance with the German laws governing animal care and approved by the animal ethics committee of the district government of Braunschweig, Lower Saxony, Germany.

For extracellular recordings we simultaneously used up to three microelectrodes in a three-electrode twelve channel system (Mini-Matrix, Thomas Recordings, Giessen, Germany). The dura mater was penetrated with sharp guide tubes so that the electrodes could be inserted into the brain. The raw signal of the electrodes were amplified (gain range 1000 - 32000) and filtered (frequency range 40kHZ). Action potentials were online-sorted (waveform window discrimination, Sort Client, Plexon Inc., Dallas, TX) and recorded.

The receptive field (RF) of each well-isolated MSTd cell was identified by its responses to a stationary RDP stimulus manually swept across the screen. To characterize preferred SMS direction and speed of the individual cell the monkey performed a luminance task on a central positioned fixation point, while a RDP was presented within the estimated MSTd RF. The size of the RDP was matched to allow the placement of two RDPs at equal eccentricity to the fixation point (inside & outside the RF). Twelve SMS directions (in the steps of 30°) at a maximum velocity of 8 degrees per second for the dots furthest away from the center (central dots maintaining their position giving an impression of self motion) were randomly chosen in intervals of 800ms. Responses to each SMS direction were defined as mean firing rates in an interval of 80-800ms after the onset of a particular SMS direction. An direction tuning curve was fitted online with a circular Gaussian. The SMS direction yielding the highest mean firing rate was presented at eight different speeds (spaced between 0.5 and 64 deg/sec) to determine the preferred speed of the individual neuron.

Tuning for linear motion stimuli (LMS) was also measured for a sub-population of 61 neurons, using a similar protocol as described above, with 8 directions (in steps of 45°) used as opposed to SMS for which 12 directions (in steps of 30°) were used.

Behavioral Tasks

For the main experiment, two monkeys were trained in a spatial attention task (Figure 1) to attend one SMS RDP target stimulus in the presence of another distractor RDP. A single trial started with the presentation of a fixation point (0.2º x 0.2º) placed in the center of the computer screen and a stationary cue RDP (4°stimulus, dot density of 20 dots / degree) positioned at the location to be attended throughout the trial. Once the animal foveated the fixation point and touched the response lever the cue RDP turned off. While maintaining their gaze on the fixation point a brief blank period (225 ms) was followed by the onset of two simultaneously presented random motion RDPs (375 ms). One RDP was placed inside the RF while the other was placed at equal eccentricity to the fixation point outside the RF (opposite hemifield). In a given trial the two RDPs were replaced by coherent SMS motion, moving in the same direction, picked randomly from one of the twelve directions in SMS. This ensures that feature-based attention was equated between any pair of conditions. The monkeys had to report a speed change within the cued target stimulus while ignoring all changes within the distractor stimulus. The target was either the stimulus inside (attention-in condition) or outside (attention-out condition) the RF. Changes in the target stimulus and distractor stimulus occurred at random times between 150 ms and 2400 ms after the onset of coherent SMS motion (total possible trial length 3000 ms). Our experiment allowed us to compare the neuronal responses across the tuning curve during the sustained state of selective spatial attention to the stimulus inside the RF when it was behaviorally relevant (attended target stimulus) vs irrelevant (unattended distractor). The baseline spontaneous firing rate was obtained from fixation-only trials, in which the monkey performed a luminance detection task at the fixation point, while no stimulus was presented in the visual space.

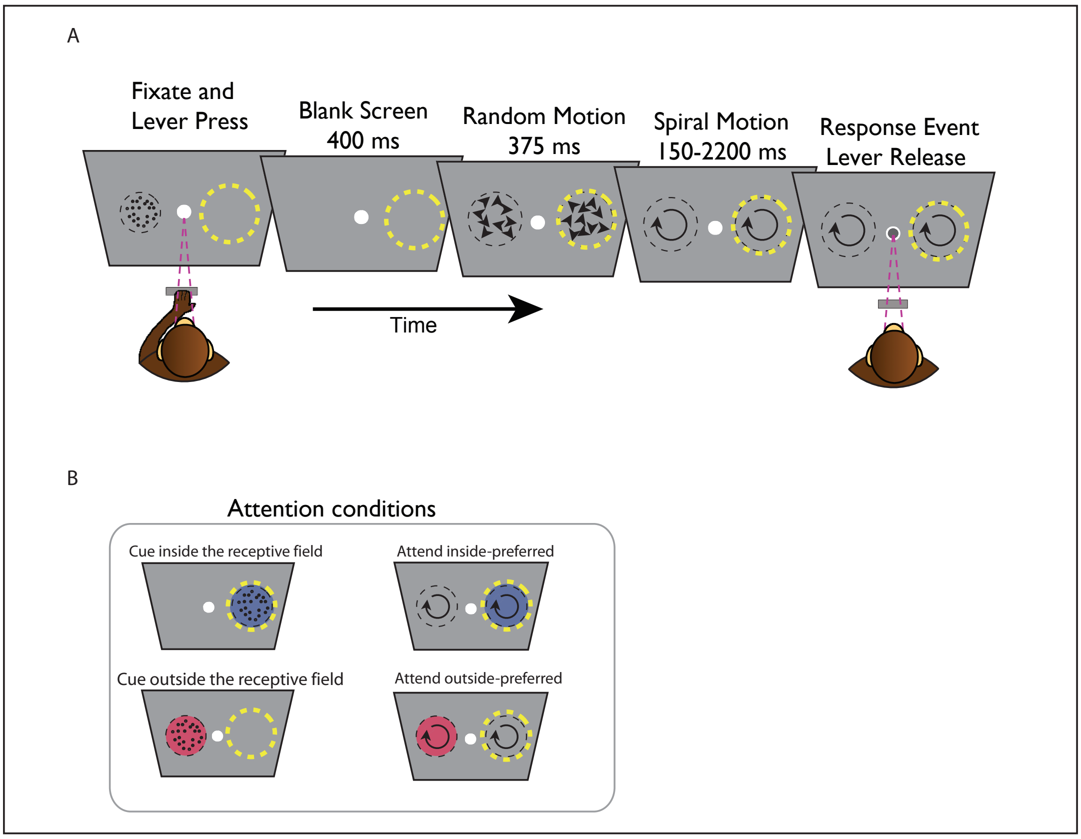

Figure 1:

A. Trial Course: Each trial began when the monkey attained fixation at the central fixation point (FP) and touched the lever. A cue (static random dot pattern) was the presented either inside or outside the receptive field for 80ms (dashed yellow circle) for 80ms. This was followed by a blank period for 400ms and then two random motion RDPs were simultaneously presented both inside and outside the receptive field for 375ms. The random motion period was followed by the onset of coherent motion stimuli (SMS or LMS) and within a time period of 200-2000ms there was a speed increment either in the target (stimulus at the cued location) or the distractor. The monkey's task was to release the lever after detecting a speed increment in the target and ignore speed changes in the distractor.

B. Attentional conditions: The two attentional conditions for which responses of the neurons were measured and analysed. The preferred direction was always presented both inside and outside the RF. Spatial attention was allocated with the help of the cue, which was presented either inside the RF (attend inside-preferred) or outside the RF to the (attend outside-preferred).

Data Analysis

Data was analyzed offline with custom scripts using MATLAB (The Math Works, Natick, MA). For the analysis of neuronal data only correctly performed, completed trials were included. Spike density functions (SDF) were obtained by convolving each spike with a Gaussian function (σ =

30°). Response rates were determined by averaging the frequency of action potentials over 850 ms of stimulus presentation starting 267 ms after coherent SMS onset and then pooling across trials of the same SMS directions. The resulting tuning curves of averaged responses across 12 discrete SMS directions are generally well represented by a Gaussian function (equation 1) (Graziano, Andersen et al. 1994). We constructed SMS tuning functions for each task (attention-in and attention-out) by fitting the averaged responses of the neuron with the Gaussian function (equation 1). The function has four free parameters: a = asymptote, b = amplitude, c = tuning width, d = direction and one fixed parameter, s = spontaneous firing rate of the neuron obtained from fixation-only trials. Direction was used as a measure of preferred SMS direction of the cell.

$$f(x)=s+a+b\cdot e^{\left(-\frac{(x-d)^2}{2c^2}\right)} \quad \text{.................... Equation1}$$

For population analysis responses of each neuron for the two attentional conditions (attend-in and attend-out) were normalized with respect to the response in the attention-in condition. Population responses were computed by averaging across the normalized responses.

Tuning Properties

Each neuron’s preferred direction and speed were assessed before starting the experiment, by fitting a Gaussian function to the responses of a neuron collected by presenting different SMS or LMS directions randomly in the RF. To further assess the selectivity of a neuron to LMS or SMS, a directionality index (DI) was evaluated using equation 2. DI gives a good measure of the selectivity of a neuron as it captures the relative difference in firing rates between preferred and anti-preferred directions.

$$DI = 1-(\text{Response}_{\text{Anti-preferredDirection}}/\text{Response}_{\text{PreferredDirection}}) \quad \text{....... Equation 2}$$

We also wanted to study whether there is a difference in the strength of response of a neuron to different stimulus dimensions (SMS and LMS), for which a response index (RI) was calculated (equation 3), which measures the relative difference in the firing rate of the preferred direction for SMS and LMS.

$$RI = 1-(\text{SMS}_{\text{preferredDirection}}/ \text{LMS}_{\text{preferredDirection}}) \quad \text{.... Equation 3}$$

For studying the tuning properties of MSTd neurons, the current data-set of 123 neurons was pooled with the data-set of 105 neurons from another set of experiments. Current data-set of 123 neurons had tuning curves for 123 SMS and 61 LMS. While the other data-set of 105 neurons had tuning curves for 103 SMS and 42 LMS. Hence by merging the two data-set for tuning analysis we had 226 neurons for SMS and 103 neurons for LMS.

Attentional modulation:

The effects of spatial attention were analyzed during the sustained response after the onset of coherent SMS stimuli. During all trials the RDPs (inside and outside the RF) moved in the same direction. For each recorded neuron the differences in response between the attention-in and attention-out conditions were quantified by computing an attentional index (AI, equation 4), across the four parameters used for fitting the Gaussian equation, namely amplitude, asymptote, width and direction, represented by the variables a, b, c and d in equation 1. The variables param_in and param_out in equation 2 refers to the four Gaussian parameters when attention was inside and outside the RF respectively, for which the AIs were evaluated.

$$AI = (Param_{in} - Param_{out}) / (Param_{in} + Param_{out}) \qquad \text{………. Equation 4}$$

Waveform characterization:

The waveforms of 118 of 123 recorded single units were characterized into putative narrow-spiking and broad -spiking neurons. The classification was done on the basis of waveform duration, defined as the time in micro-second (μs) between the waveform trough-to-peak (Mitchell, Sundberg et al. 2007) obtained by aligning all of the recorded action potentials by their troughs.

The distribution of waveforms duration so obtained was tested for bimodality by applying Hartigan's dip test (Hartigan and Hartigan 1985; Mitchell, Sundberg et al. 2007). The units having mean trough-to-peak duration between 100-195 μs were defined as putative fast-spiking neurons, while the ones having mean trough-to-peak duration between 196-600μs were classified to putative narrow-spiking neurons.

Fano-factor:

Fano-factor is a measure of spike-rate variability and is evaluated as a ratio of spike-count variance to the mean spike-count (Equation 5). We used fano-factor as a mean to study quantitative variability in the firing rates between two cell type classifications namely: cell types classified on the basis of waveform durations(putative narrow-spiking and broad-spiking neurons) and cell types

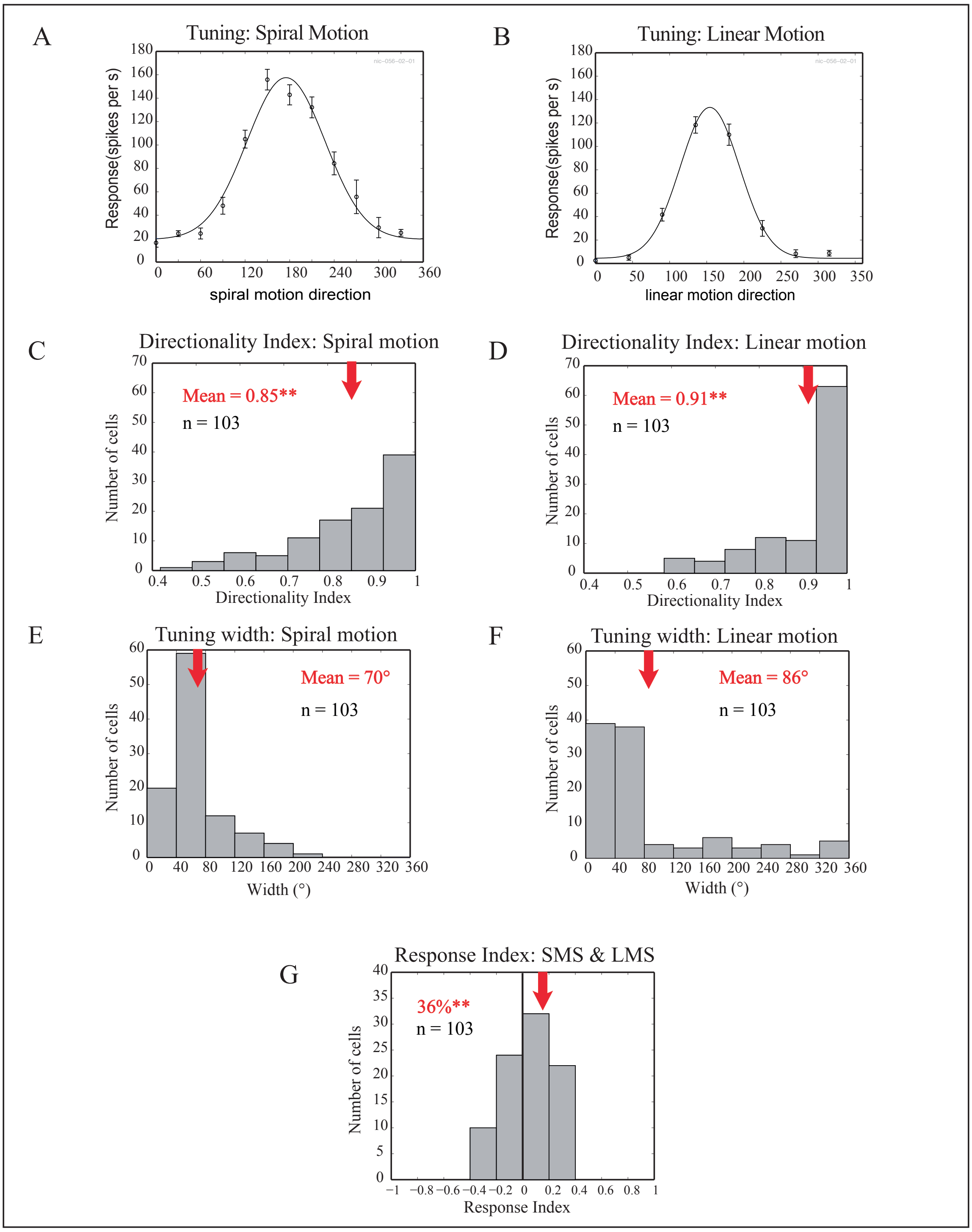

Figure 2: Tuning properties of MSTd neurons

A and B show example tuning curves for SMS and LMS respectively. The x-axis represents the SMS / LMS directions presented and the y-axis corresponds to the response of the neuron (spikes/sec).

C and D depict the distributions of the directionality indices evaluated using equation 2 (materials and methods) for SMS and LMS respectively.

E and F show the distribution of width of tuning curves for SMS and LMS respectively obtained from Gaussian fits.

G Distribution of the response index for MSTd neurons evaluated using equation 3.

characterized on the basis of the preferred SMS (expansion and contraction cells). Fano-factor was evaluated for the two attentional conditions i.e when attention was directed to the preferred spiral motion direction either inside (FF_{in}) or outside (FF_{out}) the receptive field . To access if fano-factor is attentional dependent we evaluated fano-factor index (Equation 6).

Fano-factor (FF) = $\text{Variance}_{\text{spike-count}} / \text{Mean}_{\text{spike-count}}$ .... Equation 5

Fano-factor index (FFI) = $(FF_{in} - FF_{out}) / (FF_{in} + FF_{out})$ ………. Equation 4

RESULTS

Tuning Properties

We determined sensory response selectivity of MSTd neurons to unattended SMS and LMS RDP stimuli. Both monkeys were engaged in a luminance change detection task at the central fixation point while one of the SMS or LMS directions was randomly presented in the periphery in the form of two simultaneously presented RDP stimuli, one positioned inside the RF of the neuron under study and the other in the opposite hemifield (Figure 1). To ensure that the monkeys were correctly attending to the luminance change and ignored all changes in either RDP, randomized in time and order, the RDPs could increase their speed, which marks the change presented in the attentional condition. The resulting tuning curves were plotted in Cartesian coordinates (fit with a Gaussian function, equation 1) with the mean highest firing rate corresponding to the preferred direction. Repeated presentation of the set of SMS/LMS directions to individually recorded MSTd neuron allowed for a discrete designation of the preferred direction. Figure 2A and 2B represents sensory tuning curves of example neurons for SMS and LMS respectively.

The selectivity of MSTd neurons for the two stimulus types SMS and LMS was characterized for 103 neurons for which tuning curves for both SMS and LMS were recorded. Figures 2C and 2D show the distribution of directionality index (DI) for SMS and LMS respectively. The mean index of 0.83 ($p << 0.01$, signrank test) for SMS and 0.91 ($p << 0.01$, signrank test) for LMS, indicates that the responses of MSTd neurons to preferred direction (SMS or LMS) is on average more than five times higher than their response to anti-preferred direction, indicating strong selectivity to both stimulus types.

Although having comparable direction selectivity, there was a significant difference (ranksum test,

$p<0.05$) in tuning width (obtained from the Gaussian fits) for the 103 neurons for SMS (mean width = 70°, figure 2E) and LMS (mean width = 86°, figure 2F) with the former being narrower. We then evaluated the response index (equation 3) over the preferred direction for the same 103 units, and found that MSTd neurons exhibit 36% higher responses to the preferred SMS than preferred LMS direction (Figure 2G).

Moreover, almost all the neurons that were tested were tuned to SMS, while only 49% (61 neurons) from the current data set of 123 neurons and 45% (48 neurons) from another data-set of 105 neurons were tuned to LMS.

MSTd Spatial Attention

We tested spatial attention induced activity changes for discrete SMS directions of 123 MSTd neurons. Recording the responses for identical stimuli for two different attentional conditions (attention-in and attention -out) allowed us to evaluate changes across the tuning curve of 12 SMS directions. In the population tuning curves (figure 3A), a modulation of responses was observed when attention was directed inside the RF (blue curve) compared to when attention was directed outside the RF (red curve). To compare the attended and unattended tuning curves we isolated four main fitting parameters: direction, width, asymptote and amplitude. The spatial attention induced response modulation of these parameters was computed using equation 4. The distribution of the attentional indices for the four parameters are shown in figures 3B-E. The x-axis represents the attentional indices for figure 3B-D and difference in direction (under two attentional conditions as obtained from Gaussian fit) for figure 3E, with the black line at zero corresponding to no modulation and the red arrow marks the mean for each distribution.

The amplitude parameter (figure 3B) corresponds to the firing rate for the preferred direction of the neuron and a significant modulation of 30% ($p<0.01$, ranksum test) indicates enhancement of responses of MSTd neurons when attention was directed inside vs. outside the RF.

The asymptote parameter on the other hand corresponds to the firing rate for the anti-preferred direction of a neuron and the distribution of the modulation indices for this parameter is plotted in figure 3C. A significant modulation of 10% ($p<0.01$, ranksum test) for the asymptote parameter suggests that there is modulation of responses across the whole tuning curve.

To assess if this modulation was multiplicative, we evaluated modulation indices for each neuron for width and the direction parameter. We found no significant modulation across width (figure 3D) or direction (figure 3E) parameters, indicating that indeed the modulation across the tuning curves for MSTd neurons is multiplicative.

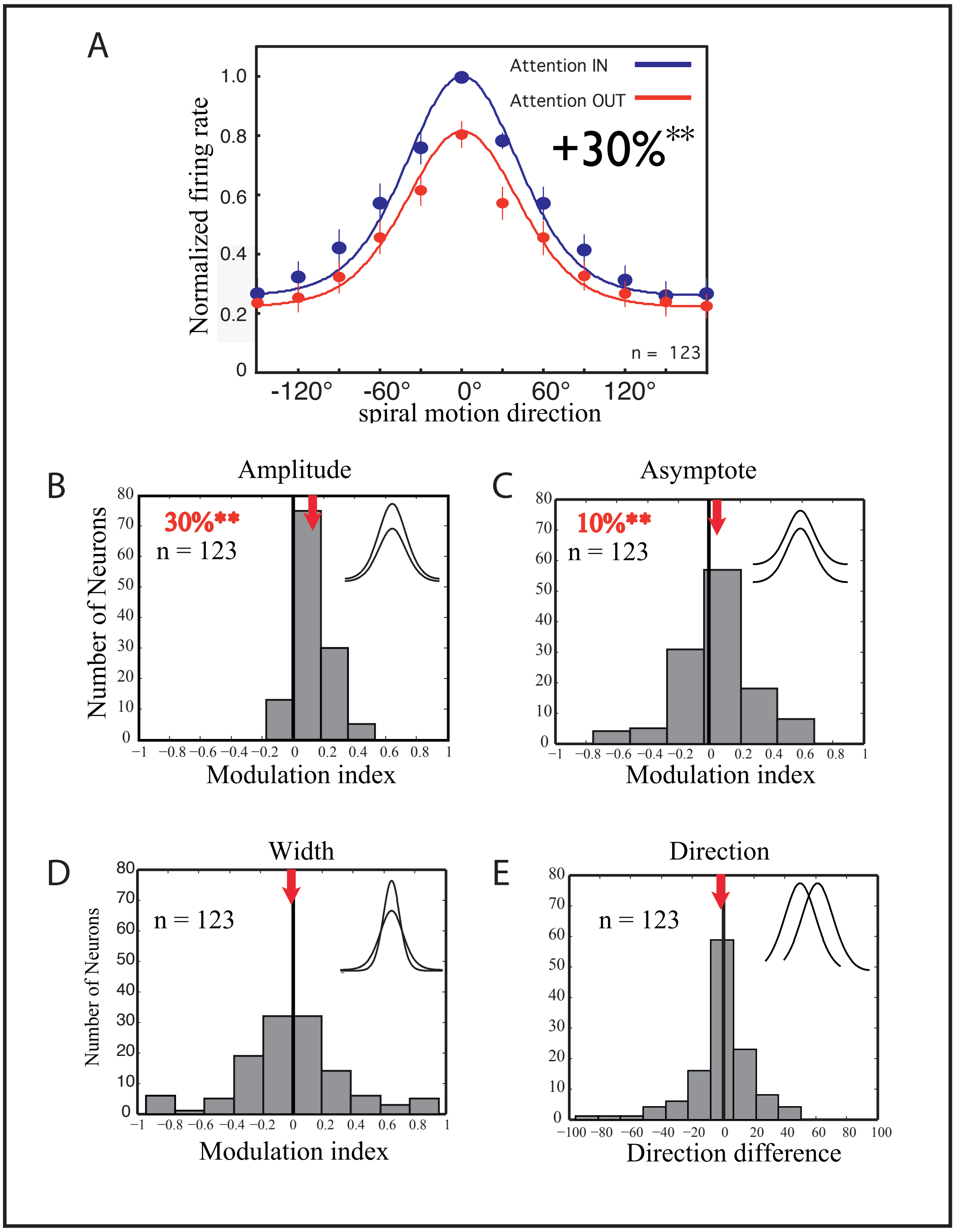

Figure 3: Spatial attention modulation in MSTd

A. Population tuning curves of 123 neurons in area MSTd. The x-axis represents the SMS direction plotted with respect to its relative difference from the preferred direction (center point 0°), while the y-axis represents the normalized firing rate. The blue and red curves marks the population response to different SMS directions when attention was directed inside and outside the RF respectively. Error bars correspond to standard error of mean.

B - D Distribution of the modulation indices (equation 2) for the four parameters, namely amplitude (B), asymptote (C), width (D), and direction (E), obtained from Gaussian fits of the tuning responses of the 123 neurons recorded under two different attentional conditions. The percent modulation value for each parameter tested is provided, the distributions which were significantly modulated are marked by an asterix (*).

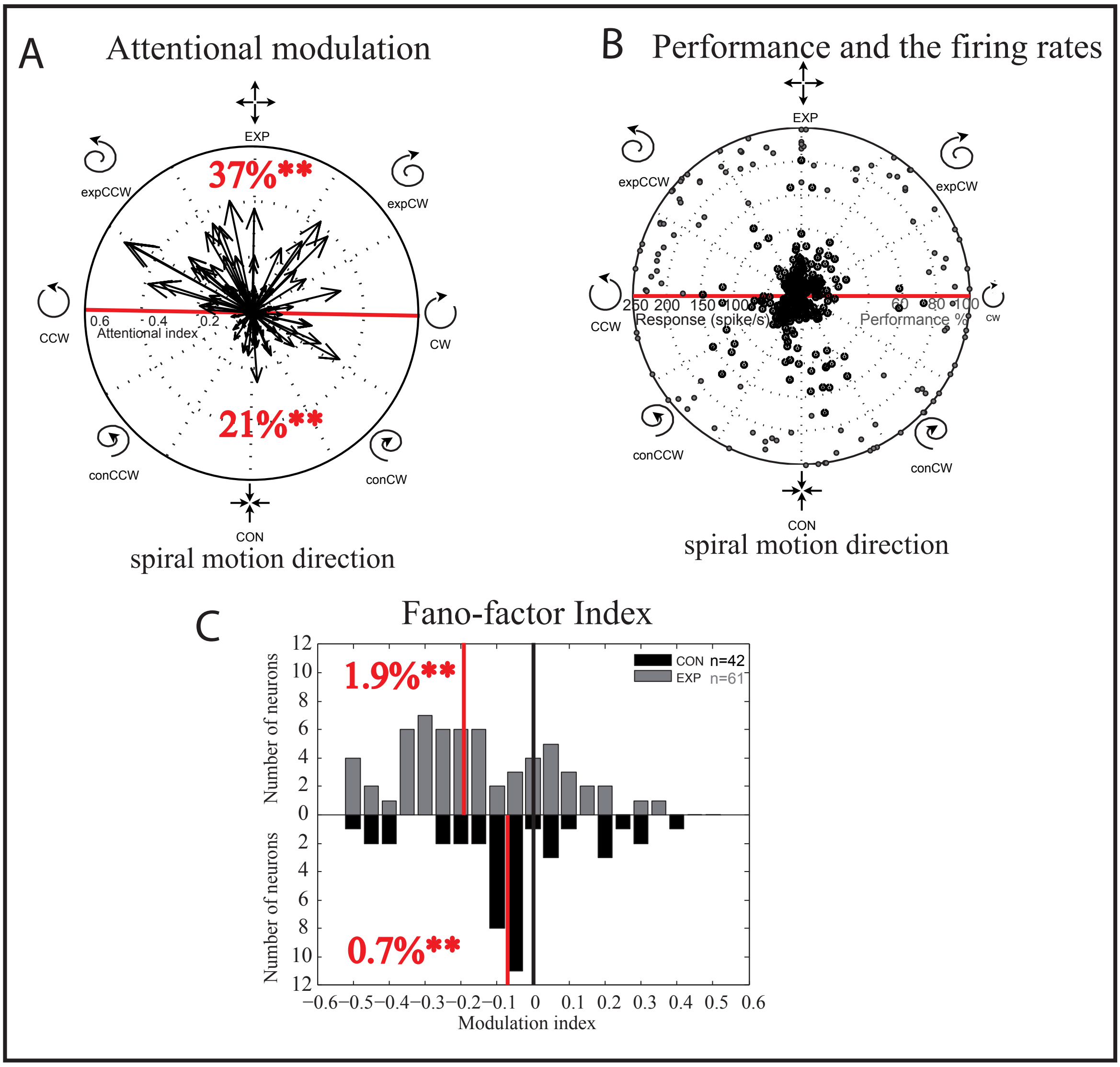

Figure 4: Direction-dependent attentional modulation

A. Polar plot showing the distribution of cells preferring expansion and contraction spiral motion space. Each arrow in the plot corresponds to a neuron, the arrowhead points to the preferred direction in the spiral motion space, while the length of the arrow marks the magnitude of the attentional index. The polar plot was bisected in the center along the clockwise-counter-clockwise axis, and neurons with preferred direction between >0° and <90° or >270° and <360 were classified as expansion neurons, while those neurons with preferred direction between >90° and <270° were classified as contraction neurons. 20 cells preferring pure rotation directions (90° or 270°) were excluded from the analysis, giving a data-set of 103 neurons.

B. The performance of the monkeys (dark dots) and the firing rates (light color dots) of the neuron for each neuron are plotted as a function of the preferred direction in the polar coordinates.

C. The distribution of fano factor index for expansion (light gray bars) and contraction cell (black bars). The dotted line marks the point of zero modulation, and the red lines correspond to the mean of each fano-factor index distribution.

Direction dependent anisotropy: Expansion and Contraction

On the basis of the preferred direction of a neuron we classified 123 neurons into two classes: expansion and contraction cells. To do this, we took the clockwise (CW) – counterclockwise (CCW) direction axis (red line in figure 4A) as the reference and neurons falling above this axis (with preferred direction falling between >0°and <90° or >270° and <360°) were classified as expansion cells, while cells falling below this axis (with preferred direction falling between >90°and <270°) were classified as contraction cells. 20 neurons were excluded from this axis, since these neurons had pure rotation (90° or 270°) as their preferred directions and were difficult to classify into either expansion or contraction classes. The distribution of preferred SMS directions along with the associated AI in the polar coordinates are depicted in Figure 4A. The length of the individual direction vector marks the magnitude of the cells attentional modulation. More than half of these cells (approximately 60%) preferred stimuli composed of some combination of CW or CCW motion with expansion or pure expansion. This asymmetry in our MSTd directional preferences is consistent with previous reports (Graziano, Andersen et al. 1994; Geesaman and Andersen 1996; Heuer and Britten 2007). Further, we report that this anisotropy not only typifies the tuning preferences of MSTd but also their attentional modulation. The 61 cells responding preferentially to some form of expansion were significantly ($p < 0.05$) modulated by spatial attention, nearly twice as much (37%, AI = 0.16) as cells responding to contracting SMS stimuli (21%, AI = 0.095) as seen in the comparatively longer direction vectors for the expansion neurons in figure 4A. However, the performance of the monkeys and the firing rate for neurons for these two classes of neurons did not significantly differ (figure 4B, $p<0.05$, t-test). The measure of firing-rate variability (figure 4C) revealed that MSTd neurons preferring expansion SMS showed a significant reduction in Fano-factor (increased reliability of firing rate) with attention (mean attended expansion = 1.9, mean attended contraction = 0.7, $p < 0.02$).

Waveform duration: Broad-spiking and Narrow Spiking neurons

Out of 123 well isolated neurons we analyzed 118 neurons and identified two distinct clusters based upon their waveform duration, which we treat as putative narrow-spiking interneurons and putative broad-spiking pyramidal neurons (Figure 5a). The overall population of waveforms durations ranged from 115 to 550 µs. A Hartigan's Dip test ($p<0.05$) confirmed two populations of waveforms. Narrow-spiking interneurons had a mean trough-to-peak duration of 146.1µs while broad-piking neurons had mean trough to peak duration of 304.6µs.

The distribution of waveforms was significantly bimodal (Hartigan dip test, $p < 0.05$, Figure 5B),

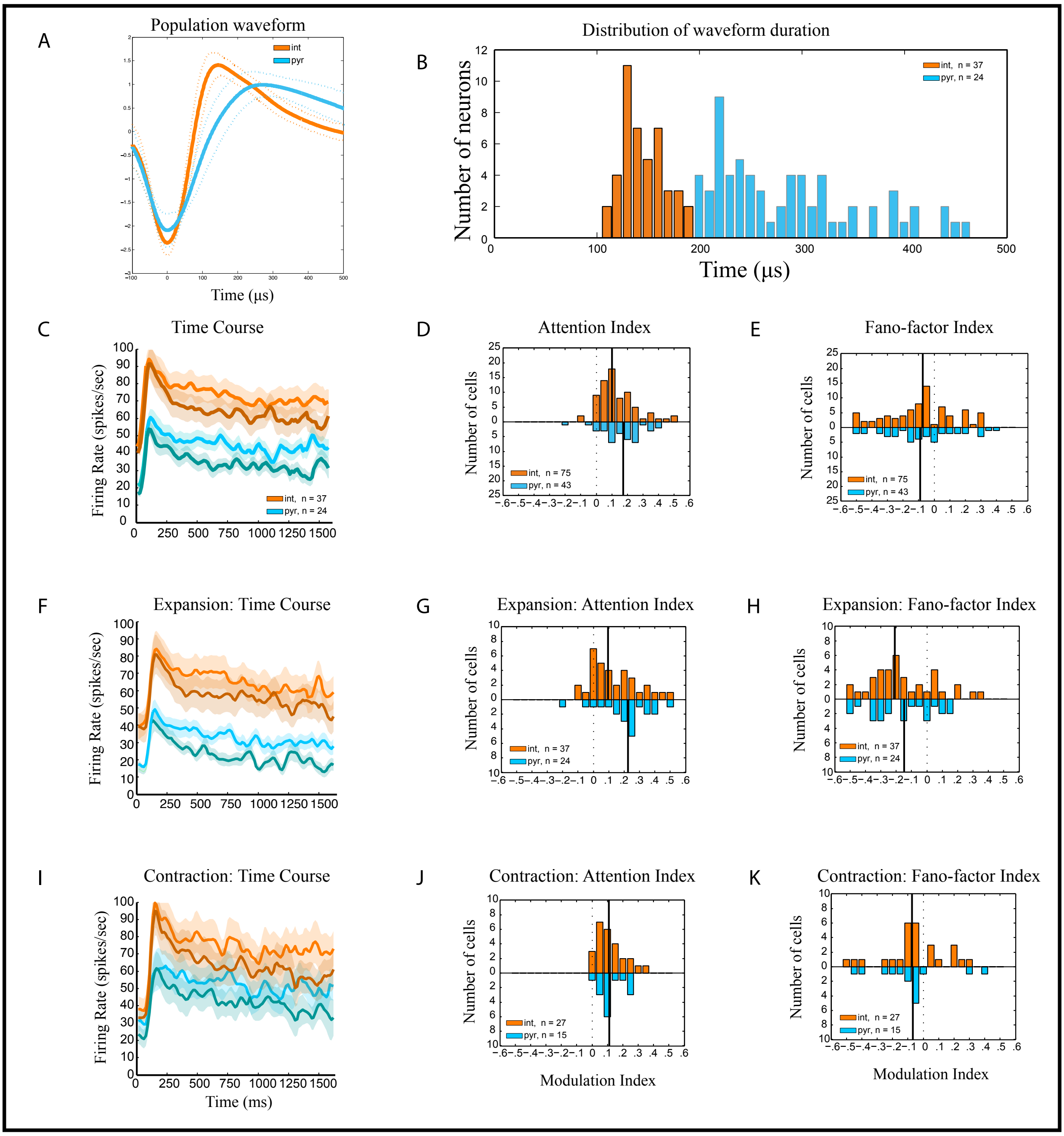

Figure 5: Classification of neurons by waveform duration

A. Population waveform for the broad-spiking (Blue) and narrow-spiking (orange) neurons.

B. Distribution of waveform durations for the broad-spiking (Blue) and narrow-spiking (orange) neurons. C-E: Times course, attentional indices and fano-factor indices for 123 broad-spiking (Blue) and narrow-spiking (orange) neurons.

F-H: Times course, attentional indices and fano-factor indices for 61 broad-spiking (Blue) and narrow-spiking (orange) neurons preferring expansion stimuli.

I-K: Times course, attentional indices and fano-factor indices for 42 broad-spiking (Blue) and narrow-spiking (orange) neurons preferring contraction stimuli.

though we did not observe any bias towards over-representation of putative pyramidal neurons as reported by other studies (Connors and Gutnick 1990; Markram, Toledo-Rodriguez et al. 2004; Mitchell, Sundberg et al. 2007). According to the bimodal distribution, narrow-spiking neurons were defined as those with duration from 100 to 195µs and broad-spiking neurons were defined as those with duration from 196 to 600µs (figure 5B). In agreement to previous studies (Mitchell, Sundberg et al. 2007), we found (figure 5C) narrow-spiking neurons (brown curve) had firing rates significantly higher than broad-spiking neurons (blue curve). However, the spatial attentional modulation (figure 5D) for these two classes was not significantly different (ttest, p>0.05).

We next divided the narrow-spiking and broad-spiking neurons into sub-population of expansion and contraction and compared the spatial attention modulation and Fano factor between these sub-populations of neurons (figure 5 F-K). For both narrow-spiking and the broad-spiking neurons, the distribution of spatial attention modulation between expansion cells (figure 5G average modulation for narrow spiking = 36% and average modulation for broad spiking = 47%) and contraction cells (figure 5J) (average modulation for narrow spiking = 25% and average modulation for broad spiking = 26%) did not significantly differe (ranksum test, p>0.05). The same trend was observed for Fano factor analysis, that is for both narrow-spiking and broad-spiking neurons, the distributions of Fano factor indices for expansion (figure 5H) and contraction cells (figure 5K) did not significantly differ (ttest, p>0.05).

DISCUSSION

Our results show that neurons in area MSTd are preferentially tuned to SMS and their responses across the tuning curve are modulated in a multiplicative manner by spatial attention. The population of neurons also showed bimodal distributions on the basis of preferred direction (expansion and contraction preferring neurons) and extracellular action potential widths (putative broad-spiking and narrow-spiking neurons).

The neurons preferring expansion SMS were over-represented and were modulated significantly higher by spatial attention than those preferring contraction SMS (figure 4A). However, there was no significant difference in spatial attention modulation between the putative broad-spiking and narrow-spiking neurons (figure 5D), though the firing rates of the putative narrow-spiking neurons were significantly higher than the putative broad-spiking neurons (figure 5C).

Tuning properties

Tuning to multiple stimulus dimensions is not uncommon in visual cortex eg, area V1 neurons are selective for color (Cumming and DeAngelis 2001; Johnson, Hawken et al. 2001; Sincich and Horton 2005), orientation (Hubel and Wiesel 1968) and other features. Area MT also shows selectivity for color, motion direction and orientation (Croner and Albright 1999; Seidemann, Poirson et al. 1999; Born and Bradley 2005), and area V4 neurons are tuned to color (Zeki 1980; Schein and Desimone 1990), orientation, and motion direction (Desimone and Schein 1987). This aspect of multiple stimulus selectivity could be very useful in solving the binding problem (Treisman 1996; Reynolds and Desimone 1999; Di Lollo 2012) and would help in coding different stimulus attributes of an object, thereby enhancing an object's representation (Andersen 1997; Treue 2003) when attended (object-based attention). On the other hand, visual processing has been characterized as hierarchical processing, in which each area contributes by processing a single attribute of the incoming visual information (Andersen 1997) and accordingly should code for only one stimulus dimension.

We compared the tuning characteristics of MSTd neurons for the two stimulus dimensions it is known to show selectivity for LMS and SMS. We found similar directionality indices for both stimulus types (figure 2C and 2D), but MSTd neurons differed in their response properties in other factors evaluated, namely they demonstrated 36% higher response for SMS than LMS. Moreover, out of the total neurons recorded we found only 50% were tuned to LMS, though almost all neurons were tuned to SMS. Even the tuning width for the two types of stimuli differed significantly, with the same set of neurons showing narrower tuning width (mean width = 70°) for SMS than for LMS (mean width = 86°). Taken together, our results suggest that SMS is the more preferred stimulus space for MSTd neurons in agreement with a previous study (Graziano, Andersen et al. 1994).

This variability in stimulus selectivity has also been shown in other areas of the visual cortex. Area V1 is known to show more selectivity for orientation and spatial frequency (Hubel and Wiesel 1968) than for other stimulus dimensions; similarly MT is known to show superior tuning to LMS (Albright 1984; Born and Bradley 2005) and V4 to color (Schein and Desimone 1990). It may be the case that this presence of selectivity to multiple stimuli across the visual cortex is a mechanism to facilitate the association of different stimulus attributes to an object, and enhance its representation in the visual cortex when attention is directed to it. However, whether all of these stimulus attributes are functionally processed in each area is still an open question.

Spatial Attention

Directing attention to a location in a space enhances the response of neurons in a multiplicative fashion across the visual cortex (Treue and Maunsell 1996; McAdams and Maunsell 1999; Maunsell and Cook 2002). We found such multiplicative effect of spatial attention for the tuning curves in area MSTd for the most preferred stimulus dimension, SMS. In addition, these multiplicative attentional effects have also been demonstrated previously with LMS (Treue and Maunsell 1996), another stimulus for which neurons in MSTd show selectivity, suggesting that multiplicative response enhancement occurs irrespective of the stimulus dimension at the spatially attended location.

The 30% response modulation observed in area MSTd for SMS and LMS (Treue and Maunsell 1996), is twice the magnitude reported in a preceding area in the visual processing hierarchy, area MT. But in our control experiment we recorded spatial attention task from the same two monkeys from area MT for 56 neurons (data shown in chapter 3). Average spatial attention was found to be 23% for 56 neurons recorded and was not significantly different from the 30% modulation observed in area MSTd. These results are in disagreement with the studies showing stronger attentional modulation in higher visual cortical areas (Maunsell and Cook 2002).

Direction dependent attentional modulation

We segregated our data set on the basis of the preferred direction of the neuron and found an over-representation of expansion-preferring neurons (previously reported by Graziano et al 1994), accompanied by a significantly higher attentional modulation of neurons preferring expansion (figure 4A) than contraction spiral motion space.

The presence of a higher frequency of cells preferring expansion could be due to the involvement of MSTd neurons in analyzing optic flow stimuli, which along with extra-retinal inputs helps in estimating self-motion (Duffy and Wurtz 1995; Bradley, Maxwell et al. 1996; Shenoy, Bradley et al. 1999). Optic flow is generated by a combination of an observer’s eye and head movements as they navigate in the environment, and give that primates usually move forward, visual space is typically encoded as an expanding stimulus. Thereby, having a high number of expansion cells in MSTd could be an evolutionary advantage to facilitate optic flow processing by coding a large area of visual space when an individual is moving forward in his environment, which would lead to better estimation of self- motion.

In line with this idea, Takeuchi (1997) reported shorter reaction times for expansion than contraction stimuli for visual search task in human subjects. We also observed significantly lower Fano-factor index (figure 4C) and higher attentional modulation (figure 4A) for the expansion spiral motion space. The lower Fano-factor index corresponds to a decrease in variability (increase in reliability) of the firing rates while attending to the expansion spiral motion space, indicating higher precision of its representation. Lower variability in firing rates coupled with higher attentional modulation demonstrates that attention strengthens the stimulus representation, not only by increasing the gain change but also by increasing the precision of representation (Mitchell, Sundberg et al. 2007). Hence, not only there more cells preferring the expansion spiral motion space in MSTd, but they are also more precisely encoded.

Waveform duration: Broad-spiking and Narrow Spiking neurons

We also characterized neurons on the basis of their extra-cellular waveform duration into putative inter-neuron (narrow-spiking) and pyramidal neurons (broad-spiking) cell classes. We did not find any bias in terms of over-representation of the pyramidal over the narrow-spiking neurons as reported in other studies (Connors and Gutnick 1990; Markram, Toledo-Rodriguez et al. 2004; Mitchell, Sundberg et al. 2007). This maybe due to our online sorting method, which prioritizes neurons with a high firing rate and sharp waveform (characteristics of the narrow spiking neurons). Hence our data-set may have more number of narrow spiking neurons due to our sampling criteria.

These two putative classes of neurons have contrasting mechanisms of action. While the broad–spiking pyramidal neurons are excitatory, narrow-spiking inter-neurons have suppressive mode of action, which suggests that they may contribute differently to information processing. Mitchell et al, 2007 showed that though the magnitude of spatial attentional modulation did not differ between the two classes, the Fano-factor attentional index for putative inter-neurons was on average significantly higher than that for putative pyramidal neurons. They explained that the difference in the attentional modulation between neurons in a given area could be due to the presence of these two types of neurons. We did not observe any significant difference between the two classes of neurons for either attentional modulation or the Fano-factor index between the two classes of neurons (Figure 5C-E). These differences were not there even when we segregated the data into expansion and contraction preferring neurons (figure 5F-K).

CONCLUSION

In conclusion, the current study adds to the evidence that neurons across the visual cortex are tuned to a number of stimuli, which might help in better representation of different feature attributes of an object, possibly circumventing the binding problem. However, in spite of the existence of multiple stimulus selectivity, each area shows superior selectivity for a given stimulus dimension: area V4 for color, MT for direction and speed, IT for complex shapes, MSTd for complex motion stimuli. The sensory responses to all the stimuli an area shows tuning for can be modulated multiplicatively by spatial attention, as indicated by the multiplicative spatial attention modulation in area MSTd for both SMS and LMS. Interestingly, the spatial attention modulations in area MSTd for SMS are direction-dependent. Since neurons in this area analyze optic flow, which bring about self-motion perception, MSTd is equipped with more expansion spiral motion space preferring neurons.

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Chapter 3: Feature-based Attention

In this chapter we compare the effects of feature-based attention in area MSTd of macaque visual cortex across two stimulus dimensions (spiral motion stimuli and linear motion stimuli). Feature-based attention modulations were restricted to the spiral motion stimuli only, although neurons in area MSTd also shows selectivity for linear motion stimuli also. Our results provides evidence for recruitment of the MSTd neurons in perceptual processing of the spiral motion stimuli.

Author's contribution:

Daniel Kaping and Stefan Treue designed the experiment. Data collection and analysis was done by Daniel Kaping and Sonia Baloni. The manuscript was written by Daniel Kaping and Sonia Baloni and was edited by Stefan Treue. All authors discussed the results and worked upon the manuscript at all stages.

Relationship of the tuning properties with the spatial and feature-based attention attentional modulation in area MSTd of macaque visual cortex

Daniel Kaping[1], Sonia Baloni[2,3], Stefan Treue[2,3]

[1]Laboratory for Attentional Control and Neural Circuits, York University, Department of Biology,Toronto,ON,Canada

[2]Cognitive Neuroscience Laboratory, German Primate Center, Goettingen, Germany

[3]Bernstein Center for Computational Neuroscience, Goettingen, Germany

ABSTRACT

Neurons in the visual cortex respond preferentially to certain sets of stimuli over others. But it is not clear if all the features, for which an area shows selectivity for, are also processed there. Attention is known to enhance processing of relevant information at expense of irrelevant sensory input. We made use of these response enhancements (spatial and feature-based) to gain insight into the functional recruitment of motion processing neurons within dorsal region of the medial superior temporal area (MSTd) and the middle temporal area (MT). While motion processing neurons in MT are specialized for linear motion stimuli (LMS), neurons in MSTd respond selectively to both, LMS and spiral motion stimuli (SMS). Measuring responses during different attentional states (location or feature dependent) we found that spatial attention influences MT and MSTd responses and reaction times irrespective of stimulus type. Feature-based attention on the other hand influenced MSTd responses and reaction times only when complex motion features where attended, while attending to linear motion directions had no significant effect. The results indicate a disassociation of neuronal task related functional recruitment and the tuning preferences. Similarity between the attended feature and preferences of a neuron alone is un-predictive of the functional involvement of a neuron during visual feature processing.

INTRODUCTION

When presented with a set of stimuli belonging to a stimulus dimension, neurons in the visual cortex illicit graded responses. These response profiles helps in characterizing their selectivity along that stimulus dimension. Traditionally, stimulus evoked response-tuning profiles allowed to label localized regions in visual cortex on the strength of their responses to a given stimulus set e.g. primary visual cortex (V1) tuned for elementary features of visual stimuli, such as oriented contours (Hubel and Wiesel 1968); middle temporal area (MT) tuned for motion direction (Dubner and Zeki 1971); dorsal region of the medial superior temporal area (MSTd) responding to linear motion in similar fashion as preceding area MT as well as to be the first known area to preferentially respond to complex spiral motion patterns (Graziano, Andersen et al. 1994; Geesaman and Andersen 1996). But neurons across the visual cortex are tuned not only to one stimulus, but to a range of stimulus dimensions, amongst which there is usually one modality to which they show relatively good selectivity assessed by either their response profiles, directionality index, frequency of neurons tuned to a modality etc. Neurons in area V1 shows best selectivity for orientation stimuli but nonetheless they also demonstrates, direction & color tuning (Cumming and DeAngelis 2001; Johnson, Hawken et al. 2001; Sincich and Horton 2005), similarly area MT represents neurons which are not only direction & speed selective (Albright 1984; Born and Bradley 2005), but also show tuning to stereoscopic disparity & orientation (Croner and Albright 1999; Seidemann, Poirson et al. 1999; Born and Bradley 2005). Therefore, neurons across the visual cortex show selectivity for range of stimulus dimensions, with one of them being the best dimension.

Stimulus selectivity helps in effective encoding of visual information by a neuron, but can it be taken as a stand alone criteria for a neuron to be engaged in the perceptual processing of the stimuli it shows tuning for? Lesion (Newsome and Pare 1988) studies have been useful in understanding the role played by different cortical areas in perception (Newsome and Pare 1988; Marcar and Cowey 1992; De Weerd, Peralta et al. 1999). Evidence for the contribution of a neuron in perception has been shown by studies comparing behavior of the subjects with the neuron's response. One line of study compared psychophysical performance of the monkeys to the neuron's performance (generated by ROC analysis) in area MT and MST of macaques, while they were performing a direction discrimination task (Britten, Shadlen et al. 1992; Celebrini and Newsome 1994). They reported that the psychophysical performance of the monkeys could be reliably estimated by the neuronal performance, showing direct evidence of participation of the neuron in direction discrimination task. They also found trial-by-trial correlation of the neuron's firing rate to the behavioral judgment of the monkeys in area MT (Britten, Newsome et al. 1996). Further, trial-by-trial correlation of the neuron's firing rate to the reaction times (another measure of behavioral performance) have added to the role played by MT and VIP in motion perception (Cook and Maunsell 2002), LIP (Janssen and Shadlen 2005) and FEF (Everling and Munoz 2000) in saccadic eye movement.

Attention is known to enhance behavioral performance as attended sensory inputs are processed more rapidly and accurately and with higher spatial resolution and sensitivity for fine changes, while non-attended information appears lower in contrast, size and is sometimes not perceived consciously at all (Carrasco, Ling et al. 2004; Anton-Erxleben, Henrich et al. 2007). Stimulus location (spatial attention) or specific stimulus attributes (feature-based attention), like a particular direction of motion (Treue and Martinez Trujillo 1999; Maunsell and Treue 2006) serve as key components to allow for an organization of a saliency map (Treue 2003) reflecting the behavioral relevance of visual stimuli.

Spiking activity of individual neurons in the visual cortex can be modulated (Treue 2003; Gilbert and Sigman 2007) by: (i) stimulus location dependent spatial attention (Luck, Chelazzi et al. 1997;

Brefczynski and DeYoe 1999; Treue 2003) and irrespective of stimulus position via (ii) feature-based attention (Treue and Martinez Trujillo 1999; Saenz, Buracas et al. 2002; Saenz, Buracas et al. 2003). Spatial attention enhances all graded responses, characterizing a neuron's selectivity along a continuous feature space (e.g. motion direction; (Dubner and Zeki 1971; Saito, Yukie et al. 1986; Tanaka, Hikosaka et al. 1986; Orban, Lagae et al. 1992; Geesaman and Andersen 1996) in a multiplicative way. The response tuning curves are multiplied by a factor (McAdams and Maunsell 1999; Treue and Martinez Trujillo 1999) without broadening or sharpening the selectivity of a neuron. Contrastingly, feature-based attention is not restricted to the encoded parts of the visual world of a particular neuron but also to its response profile. Operating across the entire visual field, feature-based attention is presumed to enhance all neurons responding preferentially to the attended feature. Consequently, while spatial attention enhances response of neurons whose receptive field coincides with the focus of attention, feature-based attention preferentially modulates the response of neurons across the visual field whose preferred feature matches the attended feature. Since cortical areas along the visual processing hierarchy shows tuning to multiple stimulus dimensions, it is worth investigating if these attentional effects affect all stimulus dimensions an area shows selectivity for.

Area MSTd is one of the areas along the dorsal pathway involved in motion processing. It is characterized by large receptive fields and receives majority of its inputs from area MT and shows selectivity for spiral motion (Graziano, Andersen et al. 1994) and linear motion stimuli (Saito, Yukie et al. 1986; Tanaka, Hikosaka et al. 1986; Duffy and Wurtz 1991). Multiplicative spatial attention effects have been reported from area MSTd (Treue and Martinez Trujillo 1999) with linear motion stimuli, but possible attentional effects for spiral motion stimuli has not been characterized. We recorded spatial and feature-based attentional effects for the two stimulus dimensions (spiral and linear motion stimuli) from same neurons in area MSTd and determined if these attentional effects in area MSTd exist for both of these stimulus attributes.

In this study we found comparable spatial attention effects for both spiral and linear motion stimuli, while feature-based attentional modulation was confined to spiral motion stimuli only. We further found significant correlations of firing rates with the behavior (reaction times) of the monkey restricted again to the preferred spiral motion stimuli, indicating an existence of functional specialization of MSTd neurons to spiral motion stimuli. These results suggests that, mere existence of tuning for a feature does not necessarily indicates functional involvement of the neuron in its perceptual processing.

MATERIALS AND METHODS

We recorded responses of 105 well isolated motion-selective neurons in area MSTd of visual cortex from two hemispheres of two macaque monkeys engaged in a spatial and feature-based attention task. Experiments were performed in a dimly lit room. During the experiment, a custom computer program running on an Apple Macintosh PowerPC controlled the stimulus presentation, monitored and recorded eye positions, neural and the behavioral data. Eye positions were determined using video-based eye tracking (ET49, Thomas Recording, Giessen, Germany). Monkeys sat in a custom-made primate chair viewing visual stimuli on a computer monitor (distance of 57 cm). The monitor covered 40º x 30º of visual angle at a resolution of 40 pixel/deg.

Stimuli

We used random dot patterns (RDPs) of small bright dots (density: 8 dots per degree, luminance 75 cd/m^2) plotted within a stationary circular aperture on a gray background of 35 cd/m^2. Stimuli were spiral motion space patterns considering expansion, clockwise rotation, contraction and counterclockwise rotation as neighboring stimuli with a continuum of stimuli in between these cardinal directions and linear motion stimuli. Movement of the dots was created by an appropriate displacement of each dot at the monitor refresh rate of 75Hz.

Animal preparation and neural recordings

Following initial training, monkeys were implanted with a custom made orthopedic implant preventing head movements during training and extracellular recording. A recording chamber was placed on top of a craniotomy over left (monkey N: 3.25 mm posterior/16.3 mm lateral; Crist Instruments, CILUX Recording Chamber 35º, Hagerstown, MD) or the right (monkey W: 3 mm posterior/ 15.5 mm lateral; custom-fit computer-aided milled magnetic resonance imaging (MRI) compatible chamber, via digitized monkey skull surface reconstruction, 3di, Jena, Germany) parietal lobe. Pre-surgical MRI was used to position the chambers; post-surgical MRIs verified the correct positioning and precise targeting of area MST. All surgeries were performed under general anesthesia and sterile conditions. Animal care and all experimental procedures were conducted in accordance with German laws governing animal care and approved by the animal ethics committee of the district government of Braunschweig, Lower Saxony, Germany.

For extracellular recordings we simultaneously used up to three micro-electrodes in a three-electrode twelve channel system (Mini-Matrix, Thomas Recordings, Giessen, Germany). The dura mater was penetrated with sharp guide tubes so that electrodes could be inserted into the brain. The raw signal of the electrodes was amplified (gain range 1000 - 32 000) and filtered (frequency range 40kHZ). Action potentials were online-sorted (waveform window discrimination, Sort Client, Plexon Inc., Dallas, TX) and recorded.

Receptive field (RFs) of well isolated single MSTd cells were identified by its responses to a stationary RDP stimulus manually swept across the screen. To characterize the spiral motion stimuli direction and speed of the individual cell the monkey performed a luminance task on a central positioned fixation point, while a RDP was presented within the estimated MSTd RF. Twelve spiral motion stimuli directions (in the steps of 30°) at a maximum velocity of 8 degrees per second for the dots furthest away from the center (central dots maintaining their position giving an impression of self motion) were randomly chosen in intervals of 827 ms. Responses of the individual spiral motion stimuli direction were defined as a mean firing rates in an interval of 80-800 ms after onset of a particular spiral motion stimuli direction. A spiral motion stimuli direction tuning curve was fitted online with a circular Gaussian. The spiral motion stimuli direction yielding the highest mean firing rate was referred to as ‘preferred’ direction, while the direction 180° to the preferred direction was taken as an anti-preferred direction (the direction evoking minimum response). The preferred direction was presented at eight different speeds (spaced between 0.5 and 64 deg/sec) to determine preferred speed of individual neuron. In a similar fashion preferred and anti-preferred direction and preferred speed for linear motion stimuli was also determined.

Behavioral Tasks

For the main experiment, two monkeys were trained in a spatial attention task (Figure 1). A single trial started with the presentation of a fixation point (0.2º x 0.2º) placed in the center of a computer screen positioned at the location to be fixated throughout the trial. Once the animal attained the fixation and touched the response lever the trial was initiated and after 150ms a cue RDP (4°stimulus, dot density of 20 dots / degree) was presented for 67 ms at the spatial location where monkey had to attend in the given trial. The cue period was followed by a blank period for 400ms, where the screen was completely blank except for the central fixation point, where the gaze was held. The blank period ended with onset of two random motion RDPs simultaneously for 375 ms. One RDP was placed in the RF while the other was placed at equal eccentricity to fixation point outside the RF (opposite hemi-field). The random motion stimuli were replaced by 100% coherent stimuli (spiral or linear motion stimuli). The stimulus at the cued location was referred as ‘Target’, while the other one was referred to as ‘Distractor’. The target could be either inside (attention-in condition) or outside (attention-out condition) the RF. In a random time period between 200 ms and 2000 ms after the onset of coherent motion stimuli (total possible trial length 3000 ms), there was a

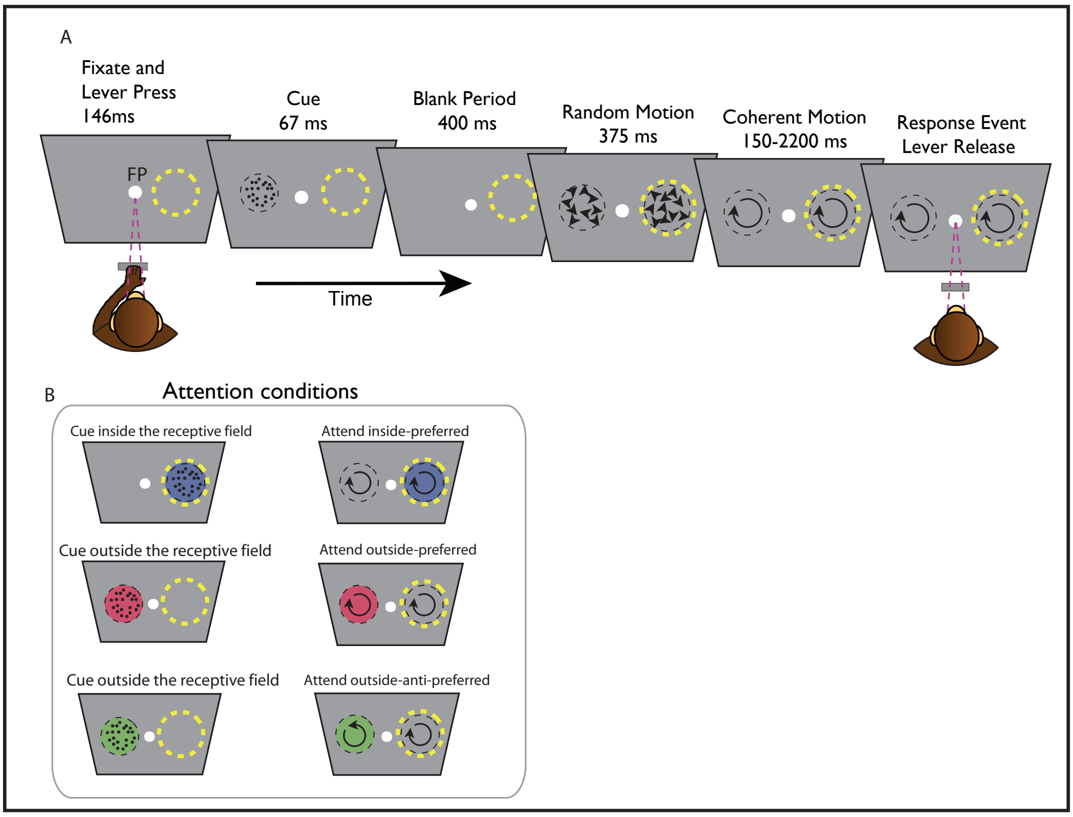

Figure 1 : Trial course

A. Trial Course : Each trial began when monkey attained fixation at the central fixation point (FP) and touched the lever. After about 146ms, a cue (static random dot pattern) was presented either inside or outside the receptive field (dashed circle). This was followed by a blank period for 400ms and then two random motion RDPs were simultaneously presented both inside and outside the receptive field for 375ms. The random motion period was followed by onset of coherent motion stimuli (spiral or linear motion stimuli) and within a time period of 200-2000ms there was a speed increment either in the target (stimulus at the cued location) or the distractor. Monkey’s task was to release the lever upon speed increment in the target and ignore the speed changes in the distractor.

B. Attentional conditions : The three attentional conditions for which response of the neurons were measured. Preferred direction was always presented inside the RF. When cue was presented inside the RF the attention was, directed to preferred direction (attend inside-preferred), when cue was presented outside the RF, attention was directed to either preferred direction (attend outside-preferred) or to anti-preferred direction (attend outside-anti-preferred).

speed increment either in the distractor or the target stimulus. The task of the monkeys was to ignore all speed changes in the distractor stimulus and release the lever upon a speed increment in the target stimulus. Upon successfully releasing the lever for a speed increment in the target stimulus, monkey was rewarded with a drop of water.

In all the trials, coherent motion stimulus (spiral or linear motion stimuli) inside the receptive field (inRF) was always the preferred direction of the neuron, while the one outside the receptive field (outRF) could either be the preferred or the anti-preferred direction. There were three attentional conditions, for which data was collected, first when attention was directed inside the RF to the preferred direction (inRF-Pref), second when attention was directed outside the RF to the preferred direction (outRF-Pref), and third when attention was directed outside the RF to the anti-preferred direction (outRF-anti-Pref).

Data Analysis

Data was analyzed offline with custom scripts using MATLAB (The Math Works, Natick, MA). For the analysis of neuronal data only correctly performed, completed trials were included.

Spike rates:

To estimate spike rates, spike density functions (SDF) were evaluated for all correctly performed, complete trials of different attentional conditions, by convolving each spike in a trial with a Gaussian function ($\sigma = 30$, equation 1). The SDFs of trials from the same attentional conditions were averaged and the firing rates were evaluated by taking mean of the averaged SDFs over a time window of 570ms starting from 270ms after the onset of coherent motion stimuli, corresponding to period of sustained activity.

$$f(x)=s+a+b\cdot e^{\left(-\frac{(x-d)^2}{2c^2}\right)} \qquad \text{............ (equation 1)}$$

Tuning Properties:

Each neuron's preferred direction and speed were assessed before starting the experiment, by fitting Gaussian function to the response of the neuron collected by presenting 12 different spiral or linear motion directions (in the steps of 30°) randomly in the RFs. To further assess the selectivity of the neuron to spiral or linear motion, directionality index was evaluated using equation 2. Directionality index (DI) gives a good measure of the selectivity of a neuron as it captures a relative difference in the firing rates between the preferred and the anti-preferred directions.

$$DI = 1-(\text{Response}_{\text{Anti-preferredDirection}}/\text{Response}_{\text{PreferredDirection}}) \quad \text{......... Equation 2}$$

We also wanted to study if there is a difference in the strength of response of a neuron to different stimulus dimensions (spiral or linear motion stimuli), for which response index (RI) was calculated (equation 3), which measures relative difference in firing rate of the preferred direction for spiral or linear motion stimuli.

$RI = 1-(\text{Spiral motion}_{\text{preferredDirection}} / \text{Linear motion}_{\text{preferredDirection}})$ ……… Equation 3

Attentional modulation:

The spatial attention (SA) was measured by comparing the responses of neurons for the inRF-Pref condition to the outRF-Pref (equation 4), where the attended feature in the two conditions was always the preferred direction and only the spatial location to which attention was directed was manipulated. To quantify feature-based attention (FBA) we compared response of a neuron for outRF-Pref condition to outRF-anti-Pref condition (equation 5), in which case the spatial attention was held constant in two condition to outside the RF, and attention was varied between two features, the preferred and the anti-preferred direction.

SA = (inRF-Pref - outRF-Pref) / (inRF-Pref + outRF-Pref) ……… Equation 4

FBA = (outRF-Pref - outRF-anti-Pref) / (outRF-Pref + outRF-anti-Pref) .. Equation 5

RESULTS

A total of 105 MSTd neurons were recorded from two awake behaving macaque monkeys, while they were engaged in spatial or feature-based attention task. Out of the total of 105 neurons, there was a sub-set of 48 neurons for which the data for attentional task was also collected with linear motion stimuli. In a separate experiment we measured tuning properties of 123 MSTd neurons to spiral motion stimuli and for a sub-population of 61 neuron, tuning curves were measured for linear motion stimuli also (Kaping, Baloni et al.). To study the tuning properties, we pooled the tuning data of 123 neurons from the previous experiment with the data of 105 neurons from the current recordings. This gave us 226 and 103 (61 neurons from the previous experiment and 42 neurons from the current project, since we did not have tuning curves for 6 neurons for LMS for the current data set) tuning curves for spiral and linear motion stimuli respectively.

For control experiment a population of 56 neurons were recorded from area MT of the same two monkeys, while they were performing spatial and feature-based attentional task with linear motion stimuli. Amongst a total of 56 neurons, for a sub-population of 33 neurons, the attentional task was also recorded for spiral motion stimuli.

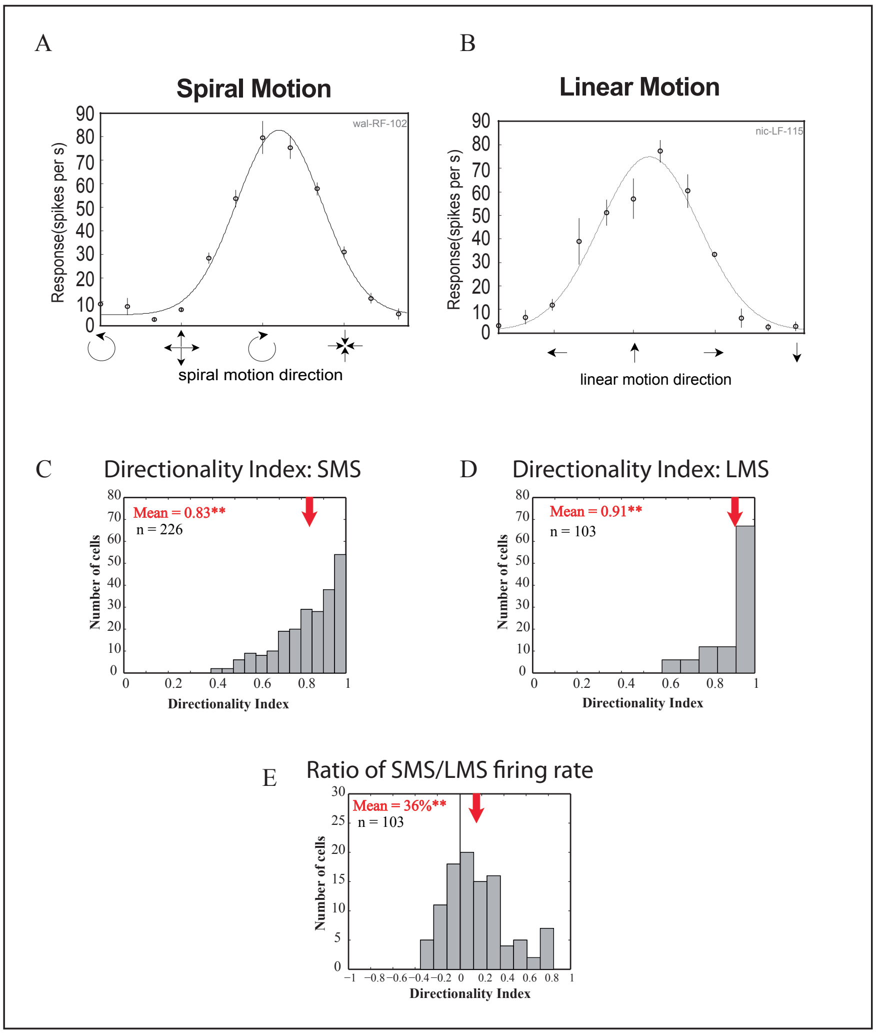

Figure 2: Tuning properties of MSTd

A and B shows example tuning curves for spiral and linear motion stimuli. The x-axis represents the spiral / linear motion directions presented and the y-axis corresponds to the response of the neuron (spikes/sec).

C and D Represents distribution of the directionality indices (equation 2 materials and method) for spiral and linear motion stimuli respectively.

E Distribution of the response index, evaluated using equation 3.

Tuning Properties

MSTd neurons show selectivity to both spiral (Graziano, Andersen et al. 1994) and linear motion stimuli (Duffy and Wurtz 1991) as shown in tuning curves of two example neurons (Figure 2A and 2B). The sole purpose to systematically measure the response quality of neurons was to provide a good measure of tuning properties to compare spatial and feature-based attentional effects against the sensory response selectivity. The resulting bell-shaped response profiles as a function of stimulus direction were plotted in Cartesian coordinates (fit with a Gaussian function) with the maximum response corresponding to the preferred direction. Repeated presentation of the set of 12 directions allowed for a discrete conformation of the preferred direction.

The selectivity of the MSTd neurons for the two stimulus types spiral and linear motion stimuli was characterized by evaluating the directionality index (equation 2). Figure 2C and 2D shows the distribution of directionality index (DI) for spiral and linear motion stimuli respectively. The mean index of 0.83 ($p \ll 0.01$, signrank test) for spiral motion and 0.91 ($p \ll 0.01$, signrank test) for linear motion stimuli, indicates that the responses of MSTd neurons to preferred direction (spiral and linear motion stimuli) is on average more than five times higher than their response to anti-preferred direction, indicating strong selectivity to both stimuli.

Although having comparable direction selectivity, there was significant difference in absolute firing rate between the spiral and linear motion stimuli tuning. We evaluated the response index (equation 3), over the preferred direction for 103 units, for which we had tuning curves for both spiral and linear motion stimuli and found that, MSTd neurons exhibit 36% higher responses to the preferred spiral motion stimulus direction (Figure 2E).

MSTd Spatial Attention

In the previous study we recorded tuning curves of 123 MSTd neurons, while monkeys were engaged in spatial attention task (Kaping, Baloni et al.). We found a multiplicative increase of response across the tuning curve, when attention was directed inside the RF as compared to outside the RF. For the preferred direction a response modulation of 30% was observed. Multiplicative spatial attention modulation across the tuning curves in MSTd has also been reported for linear motion stimuli (Treue and Maunsell 1996), with modulation of 30% for the preferred direction.

In the current data set we measured spatial attention only for the preferred spiral and linear motion directions. Figure 3A and 3B shows the population spike density function for 105 and 48 neurons recorded with spiral and linear motion stimuli respectively. The x-axis is aligned to onset of coherent motion stimuli (figure 1), and the y-axis represents normalized response, the blue curve corresponds to condition when attention was directed inside the RF, while the red curve is for when attention was outside the RF. It can be seen that the response of MSTd neurons was higher when attention was directed inside than outside the RF for both spiral and linear motion stimuli. To quantify the amount modulation, attentional indices (equation 4), were evaluated for each neuron over a 570ms time period (gray shaded area in figure 3A and 3B) starting 270ms after the onset of coherent motion. Distribution of attentional indices for spiral and linear motion stimuli are plotted in figure3C. The mean attentional modulation of 105 neurons for spiral motion stimuli (upper dark histogram) was 26% (p<<0.01, signrank test), while that of 48 neurons for linear motion stimuli (Lower light histogram) was 28% (p<<0.01, signrank test).

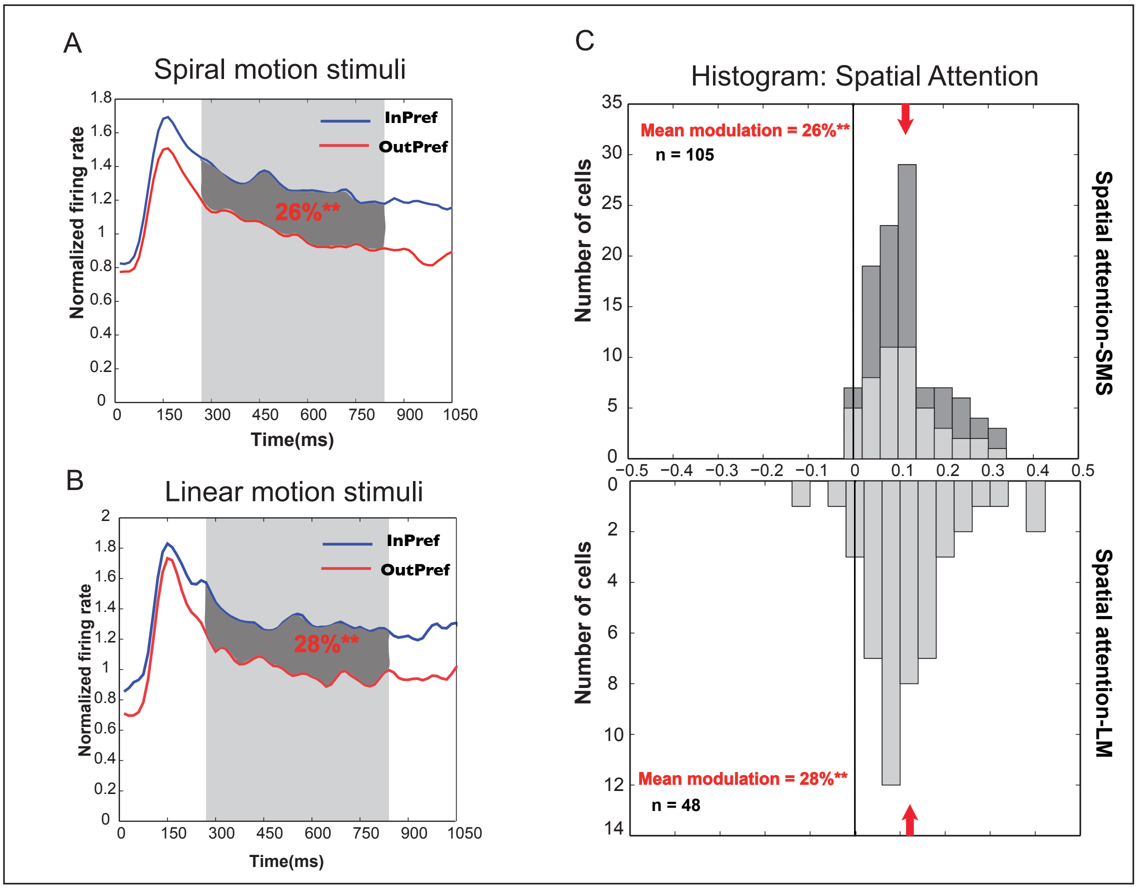

Figure 3: Spatial attention modulation in area MSTd

A. Normalized population sdfs plotted as a function of time, when attention was directed to preferred (blue curve) direction inside and outside the receptive field for spiral motion stimuli. Zero on the x-axis represents onset of coherent spiral motion onset. The gray shaded area represents the 570ms analysis period window (starting 270ms after the onset of coherent motion period), over which attentional indices were evaluated.

B. Normalized population sdfs plotted as a function of time, when attention was directed to the preferred (blue curve) direction inside and outside the receptive field for linear motion stimuli. Zero on the x-axis represents onset of coherent linear motion onset. The gray shaded area represents the exact same 570 ms analysis period window used for evaluating attentional indices for spiral motion stimuli.

C. Distribution of spatial attention indices for 105 spiral (above, dark gray histogram) and 48 linear motion stimuli (bottom, light gray histogram) neurons. The light gray region in upper histogram represents attention indices of 48 neurons for which spatial attention was measured for both spiral and linear motion stimuli.

To further compare spatial attention modulation across the two stimulus types, we performed a ranskum test between attentional indices for the same 48 neurons with linear and spiral motion stimuli. Mean attentional modulation of 48 neurons with spiral motion stimuli (upper light histogram) was 26% ($p<<0.01$, signrank test) and was not significantly different from that of attentional modulation with linear motion stimuli. We observed a reliable spatial attention modulation of 28% irrespective of stimulus type.

MSTd Feature-based Attention

Different to the results above demonstrating a location dependent enhancement of all stimuli, feature-based attention should subject to the similarity between currently attended feature and the preferences of neuron under study (Treue and Martinez Trujillo 1999; Martinez-Trujillo and Treue 2004). We tested same 105 neurons (48 neurons on both linear and spiral motion) in a feature-based attention task. Animals were required to attend only to the stimuli placed outside the neuron's receptive while ignoring stimulus inside the RF. To evaluate feature-based attentional response enhancement the attended feature (direction of spiral or linear motion) had to either match preferred or anti-preferred direction of the neuron. Population response time courses of coherent moving spiral (Figure 4A) versus linear motion stimuli (Figure 4B) behaved in the same dissimilar fashion as the single units. For spiral motion feature-based attention task units responded more strongly when animal was attending to a stimulus moving in the preferred spiral motion direction outside the receptive field (figure 4A). Surprisingly response to the linear motion feature showed no obvious effect (figure 4B). To quantify feature-based attentional increment AI (equation 5) were calculated, across the same 570ms analysis period window used for evaluating spatial attention modulation.
Distribution of feature-based attentional indices of 48 and 105 neurons for linear motion (lower histogram) and spiral motion stimuli (upper histogram) respectively are shown in figure 4C, where x-axis corresponds to attentional indices and y-axis indicates the number of neurons, vertical line at the center (corresponding to 0 in x-axis) marks point of no modulation. The distribution of AI (mean 9%, $p<<0.01$,signrank test) for spiral motion is skewed to right hand side to positive indices indicating an increase in response of MSTd neurons when preferred feature was attended. Although the response change (of roughly 9 %) for spiral motion is smaller as compared to the enhancement observed during a spatial attention task in MSTd, it is comparable with feature-based attentional enhancements previously reported in other visual areas (McAdams and Maunsell 1999; Treue and Martinez Trujillo 1999).

On the other hand, no significant population effect ($p > 0.05$, signrank test) was observed when the animal was directing its attention to linear motion stimuli (figure 4C,lower histogram). But for the same set of 48 neurons a significant increment of response (mean 10%, $p<<0.01$,signrank test) was observed when attention was directed to the preferred spiral motion feature (figure 4C, upper light shaded histogram).

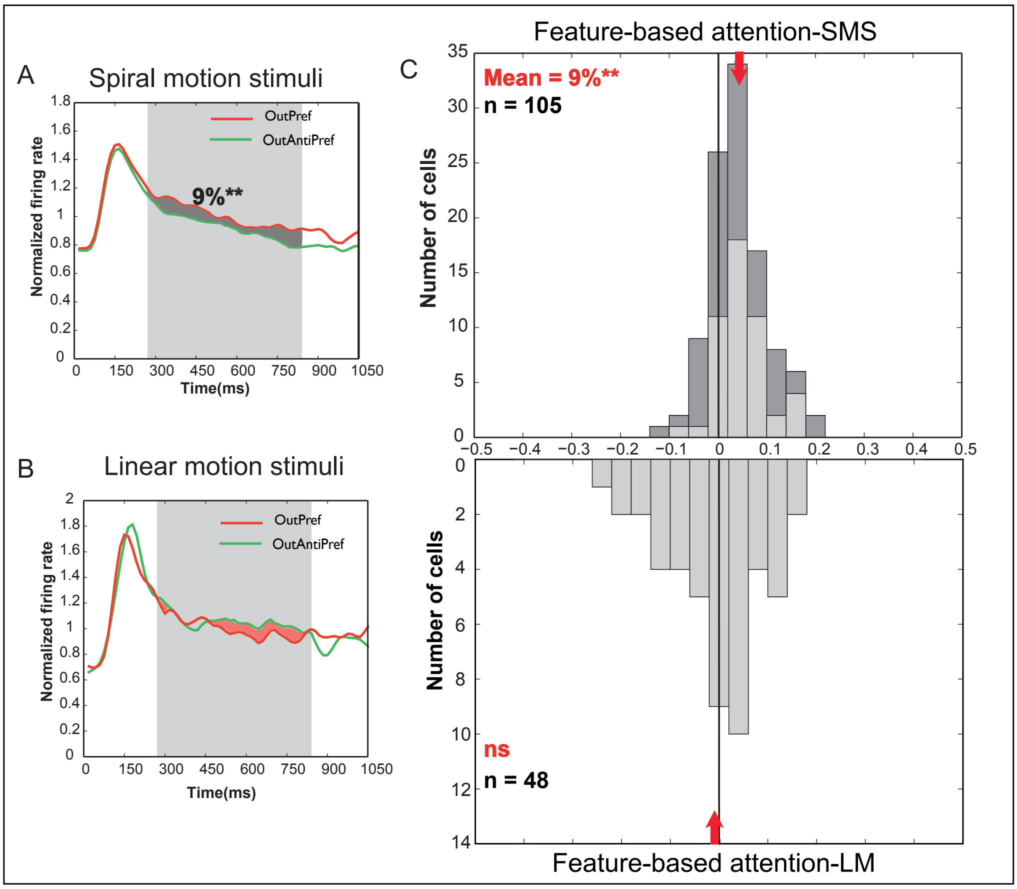

Figure 4: Feature-based attention in area MSTd

A. Normalized population spike density function plotted as a function of time, when attention was directed to the preferred (red curve) and anti-preferred direction outside the receptive field for spiral motion stimuli. Zero on the x-axis represents onset of coherent spiral motion onset. The gray shaded area represents the 570ms analysis period window (starting 270ms after the onset of coherent motion period), over which attentional indices were evaluated.

B. Normalized population sdfs plotted as a function of time, when attention was directed to he preferred (red curve) and anti-preferred direction outside the receptive field for linear motion stimuli. Zero on the x-axis represents onset of coherent linear motion stimuli onset. The gray shaded area represents the exact same 570 ms analysis period window used for evaluating attentional indices for spiral motion.

C. Distribution of spatial attention indices for 105 spiral motion stimuli (above, dark gray histogram) and 48 linear motion stimuli (bottom, light gray histogram) neurons. The light gray region in upper histogram represents attention indices for linear motion stimuli of 48 neurons (for which feature-based attention was measured for both spiral and linear motion stimuli).

Comparing feature-based attentional response modulations between spiral and linear motion trials within the same population of cells (48 neurons for which feature-based attention was measured for both spiral and linear motion stimuli) shows a significant difference (ranksum test, $p < 0.01$). Although we selected cells randomly to be recorded with both linear and spiral motion, we did not consistently find MSTd cells that showed significant linear motion spatial and feature based attention enhancements while most MSTd cells enhancing their response during the spiral motion spatial attention task also showed significant feature-based attentional enhancements.

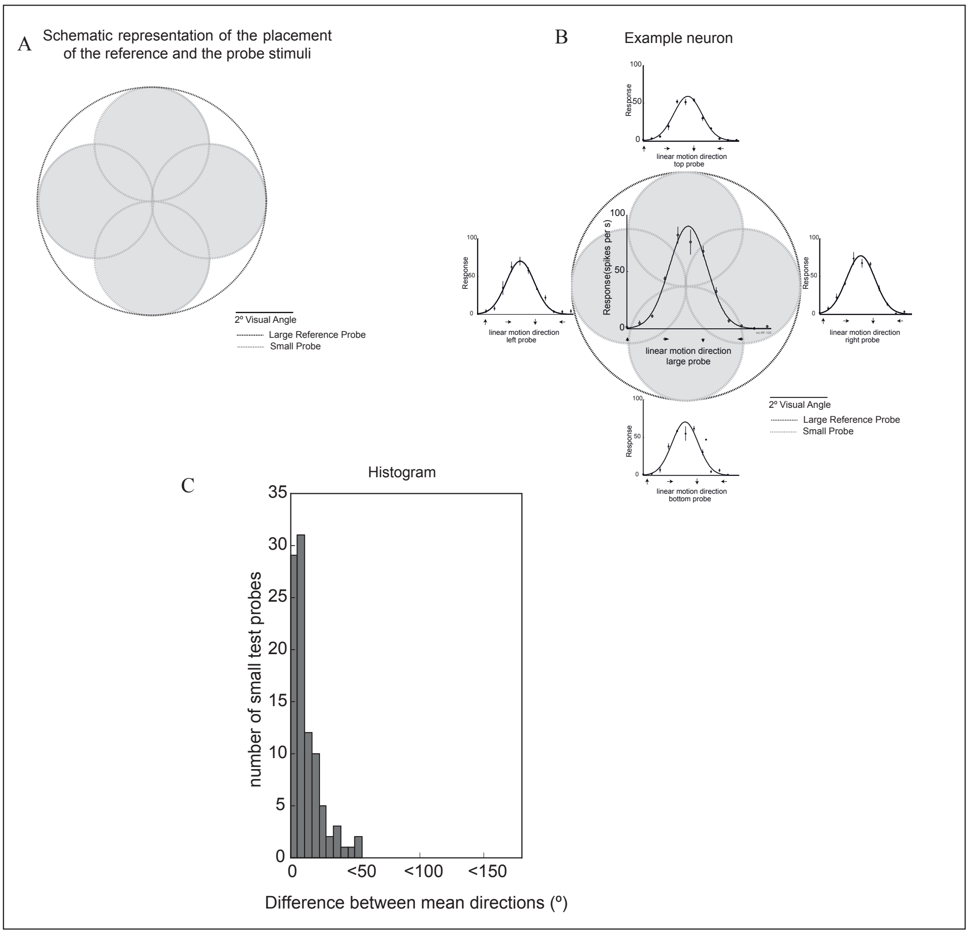

Figure 5: Position Invariance test in MSTd

A. Schematic representation of the placement of reference and probe stimuli to measure the tuning curves at 5 positions within the RF. The probe stimuli were one-fouth the size of the RF and were presented randomly at four partially overlapping positions shown in the figure, while the reference stimuli was matched to the size of the RF. Eight linear motion directions (in the steps of 45°) were presented randomly at five above shown location as probe and reference stimuli to measure the tuning curves.

B. An example MSTd neuron, with the associated tuning curves measured at five positions within the RF. The center and the four outer tuning curves represents the reference and the probe positions respectively.

C. Distribution of the difference between the preferred direction of the four probe stimuli and the reference stimuli (the preferred directions were taken from the Gaussian fits to the tuning curves).

Position Invariance

To ensure that the lack of feature-based attentional response enhancement of linear motion stimuli within MSTd is not a result of poor stimulus placement, we tested 25 neurons for position response differences in MSTd RF's to linear motion. Five linear motion stimuli tuning curves were measured for eight directions (in the step of 45°) that were randomly presented within the RF of a neuron. Four 'probe' tuning curves were recorded by presenting linear motion stimuli in an aperture of size of one-fourth the RF, in four different sub-locations (figure 5A), while the fifth 'reference' tuning curve was measured by presenting linear motion stimuli whose size was matched to the size of the RF. This allowed us to compare four probe tuning curves to the reference linear motion tuning curves obtained at five different positions within the RF.

An example is shown in Figure 5B of a MSTd cell preferring clockwise contracting spiral motion stimuli in addition to right downward linear motion. All tuning curves are for the linear motion stimuli, the central and the ones at the four cardinal positions refer to the reference and probe tuning curves respectively. To test if the tuning preference (the preferred direction) changes within the sub-locations of the RF, we evaluated the difference of the preferred directions obtained after fitting the Gaussian equations to the linear motion tuning response at each of the four sub-locations (where probe stimuli were presented) to the one obtained when the stimulus size matched the size of the RF (reference probe). Figure 5C plots the distribution of the number of probes as a function of their difference to the preferred direction obtained from the reference tuning curve. For Majority of the probe tuning curves, the difference in preferred direction to the reference tuning curve was less than 30°, indicating that the linear tuning preferences were preserved at all the positions and sizes tested. While some cells showed some form of directional displacement the overall selectivity did not change.

Feature-based attention: MT

Neurons in area MT are known to be direction selective to linear motion stimuli (Dubner and Zeki 1971; Albright 1984), and their responses are modulated by feature-based attention (Treue and Martinez Trujillo 1999). Since the monkeys were trained for a long period of time with spiral motion stimuli as compared to linear motion stimuli, to make sure that they were attending to the linear motion stimuli, as a control experiment we recorded 56 neurons in area MT with feature-based attention task.

Tuning properties:

The assessment of preferred and the anti-preferred linear motion stimuli direction for each neuron was exactly similar to the one for MSTd recordings. Besides showing selectivity to linear motion stimuli, MT neurons are also known to show selectivity to color (Seidemann, Poirson et al. 1999; Barberini, Cohen et al. 2005), orientation (Albright 1984) etc. In our data set out of total of 56 neurons that were recorded, 33 showed tuning to spiral motion stimuli also. We report existence of spiral motion stimuli selectivity also amongst the population of MT neuron. An example neuron with tuning for both linear motion stimuli and spiral motion stimuli stimuli is shown in figure 6A

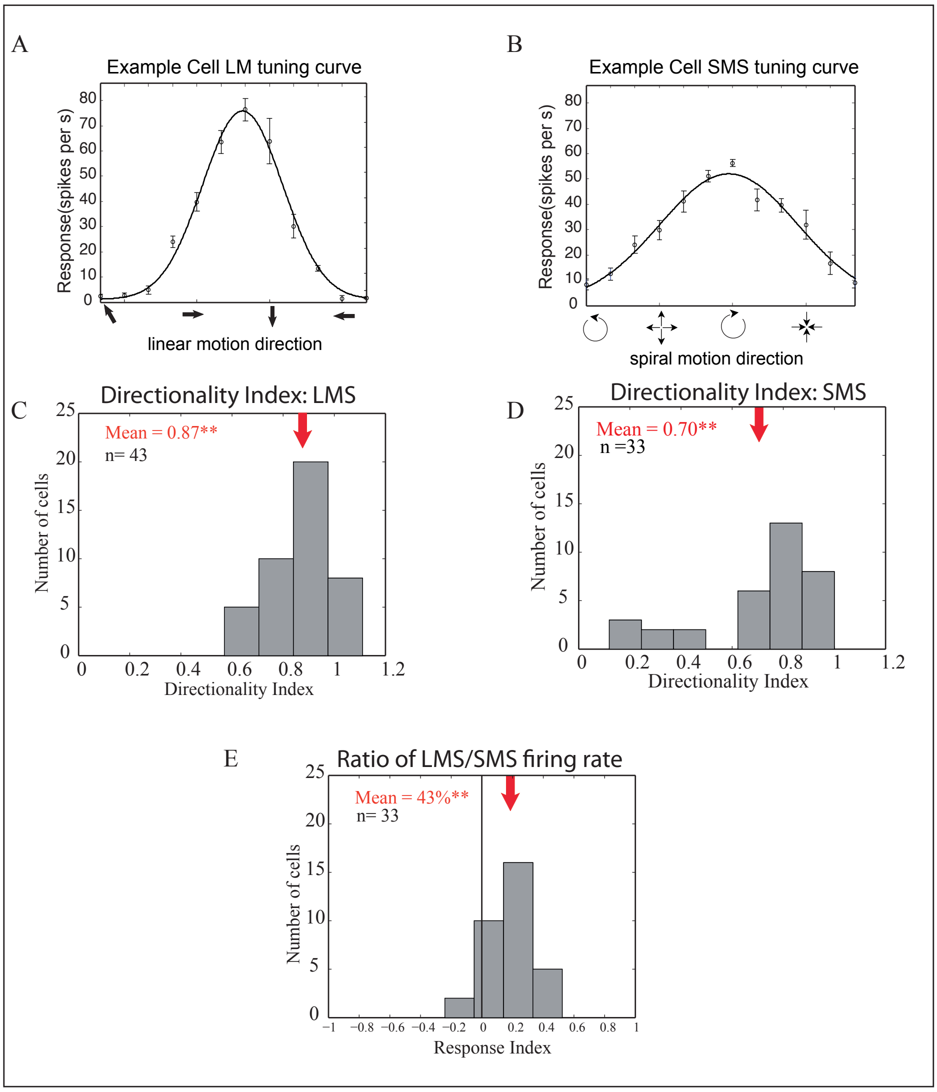

Figure 6: Tuning properties of area MT

A and B shows example tuning curves for linear and spiral motion stimuli respectively. The x-axis represents the spiral motion / linear motion directions presented and the y-axis corresponds to the response of the neuron (spikes/sec).

C and D Represents distribution of the directionality indices evaluated using equation 2 (materials and method) for linear and spiral motion stimuli respectively.

D Distribution of the response index, evaluated using equation 3.

and 6B respectively. We evaluated the directional selectivity for linear motion (n = 43) and spiral motion stimuli (n = 33) for which we had complete tuning cures and found to be 0.87 (figure 6C) and 0.70 (figure 6D) respectively. The data from directionality index indicates that the selectivity of MT neurons to spiral motion is less pronounced than that for linear motion stimuli.

Feature-based attention in MT

We then recorded feature-based attention task for 56 neurons with linear motion stimuli and a sub-population of 33 neurons with both linear motion and spiral motion stimuli. The time course of the

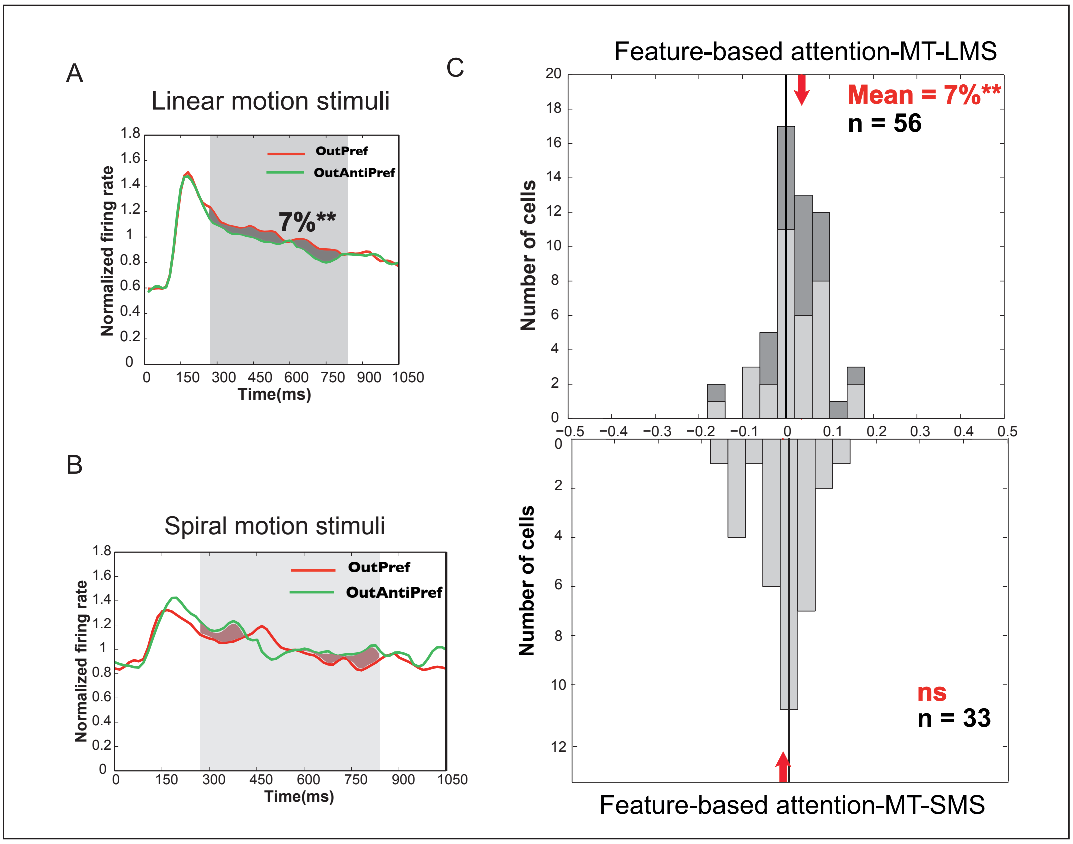

Figure 7: Feature-based attention in area MT

A. Normalized population spike density function plotted as a function of time, when attention was directed to the preferred (red curve) and anti-preferred direction outside the receptive field for linear motion. Zero on the x-axis represents onset of coherent linear motion onset. The gray shaded area represents the 570ms analysis period window (starting 270ms after the onset of coherent motion period), over which attentional indices were evaluated.

B. Normalized population sdfs plotted as a function of time, when attention was directed to he preferred (red curve) and anti-preferred direction outside the receptive field for spiral motion stimuli. Zero on the x-axis represents onset of coherent spiral motion stimuli onset. The gray shaded area represents the exact same 570 ms analysis period window used for evaluating attentional indices for linear motion.

C. Distribution of spatial attention indices for 56 linear motion (above, dark gray histogram) and 33 spiral motion stimuli (bottom, light gray histogram) neurons. The light gray region in upper histogram represents attention indices for 33 neurons (for which feature-based attention was measured for both spiral and linear motion stimuli).

trials, was exactly similar to that for the recordings from MSTd (figure 1). Figure 7A and 7B shows the population spike density function for 56 and 33 MT neurons with linear and spiral motion stimuli respectively, when attention was directed to preferred direction (red curve) and anti-preferred direction outside the RF (green curve). Responses of most of the neurons in population was enhanced, when attention was directed to preferred linear direction outside the RF, but not for the preferred spiral motion direction. Figure 7C plots the distribution of the feature-based attentional indices for linear (upper histogram) and spiral motion stimuli (lower histogram). A significant feature-based attentional modulation of 7% (p<<0.01, signrank test) was observed in area MT for linear motion but not for spiral motion stimuli. The 33 neurons, for which feature-based attention was recorded for both linear and spiral motion stimuli, had a significant 6% (p<<0.01, signrank test) modulation for linear motion but not with spiral motion stimuli.

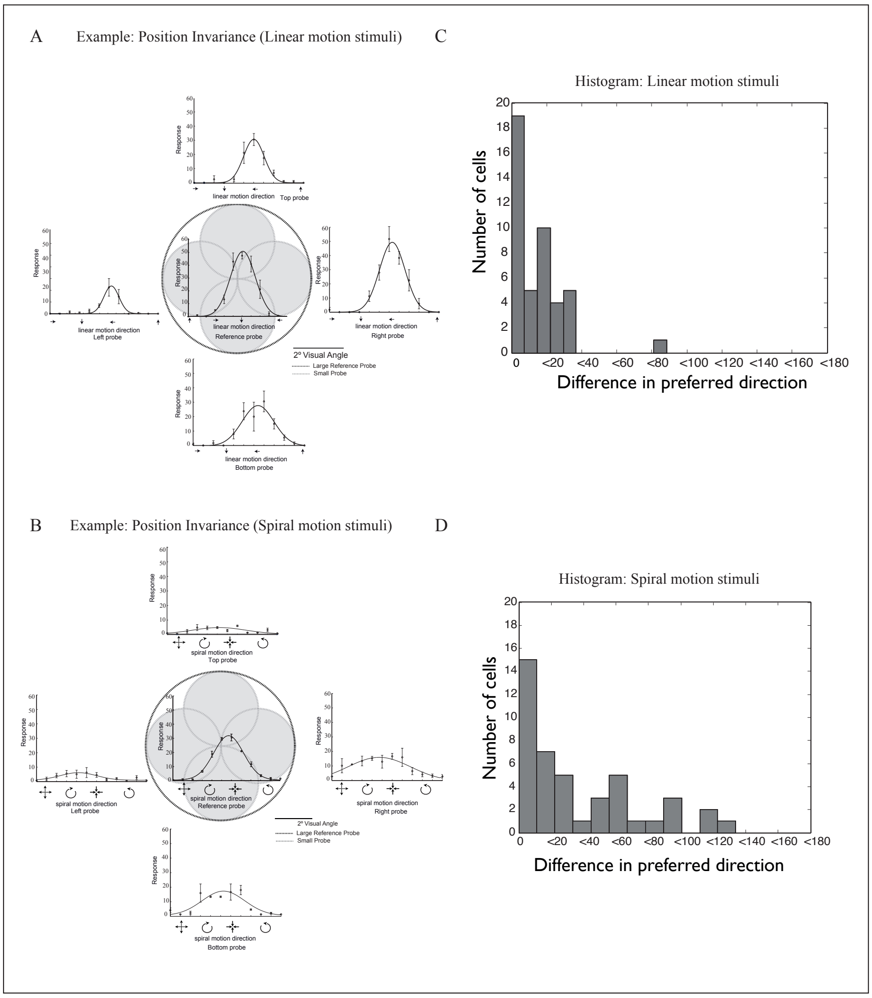

Figure 8: Position Invariance test in MT

The tuning curves measured at five sub-locations within the RF of MT neuron for linear motion (A) and spiral motion stimuli (B) from the same neuron. C and D plots the distribution of difference of the preferred direction of the reference tuning to the preferred directions from the 4 probe tuning curves for linear and spiral motion stimuli respectively.

Like MSTd, MT also showed feature-based attentional effect restricted to one of the two stimulus types tested, namely spiral motion for former and linear motion stimuli for the later. But, spatial attention was observed for both stimulus types in area MSTd (figure 3C) and MT (supplementary figure 1).

Position invariance

Like in area MSTd, we tested if the absence of feature-based attention in area MT for spiral motion stimuli maybe due to its poor placement in the RFs, by measuring probe tuning curves at four sub-locations within the RF, and comparing it to the reference tuning curve obtained by presenting stimulus of the size of the RF, like for MSTd for 20 neurons.

Figure 8A and 8C shows the position dependent tuning curves measured at five locations for linear and spiral motion stimuli respectively for an example neuron. This typical example neuron shows position invariant response and selectivity for linear but not for spiral motion stimuli. Figure 8B and 8D shows the distribution of the difference between the preferred direction from four probes and the reference tuning curves for linear and spiral motion stimuli respectively. It can be seen that the tuning is preserved across the MT RF for linear but not for spiral motion stimuli. Absence of consistent spiral tuning across MT receptive field, indicates that spiral motion tuning in MT might be an artifact.

Trial to Trial correlation of behavior and neural activity

To test whether the discrepancy between duplex tuning preferences (spiral / linear motion) and isolated spiral motion feature-based attentional enhancements in MSTd reflect a functional partition, we calculated trial-by-trial correlation of behavioral responses (reaction time) and firing rate. This measure has been shown to be a valid predictor of the task-related recruitment of particular neurons in various regions throughout visual cortex, including MT & VIP, where firing rates were correlated with reaction times in a motion detection task (Cook and Maunsell 2002) (Cook and Maunsell 2002), LIP (Janssen and Shadlen 2005), and FEF (Everling and Munoz 2000). For the 48 neurons trial-by-trial correlation of neural activity to reaction times (RT) was evaluated. Firing rates were calculated in epochs of 50ms before and 125ms after the onset of the task-relevant speed increment under three different attentional conditions: attention to preferred direction within the RF, attention to the preferred direction outside the RF and attention to the anti-preferred direction outside the RF.

In order to prevent the large variations in firing rate that characterize the transient response period from entering analysis, only trials with at least 800ms duration before speed increment onset were included. After this selection criterion was applied, 45 neurons remained for attention to the preferred direction within the RF and outside the RF, while 40 neurons remained for attention to the anti-preferred direction outside the RF.

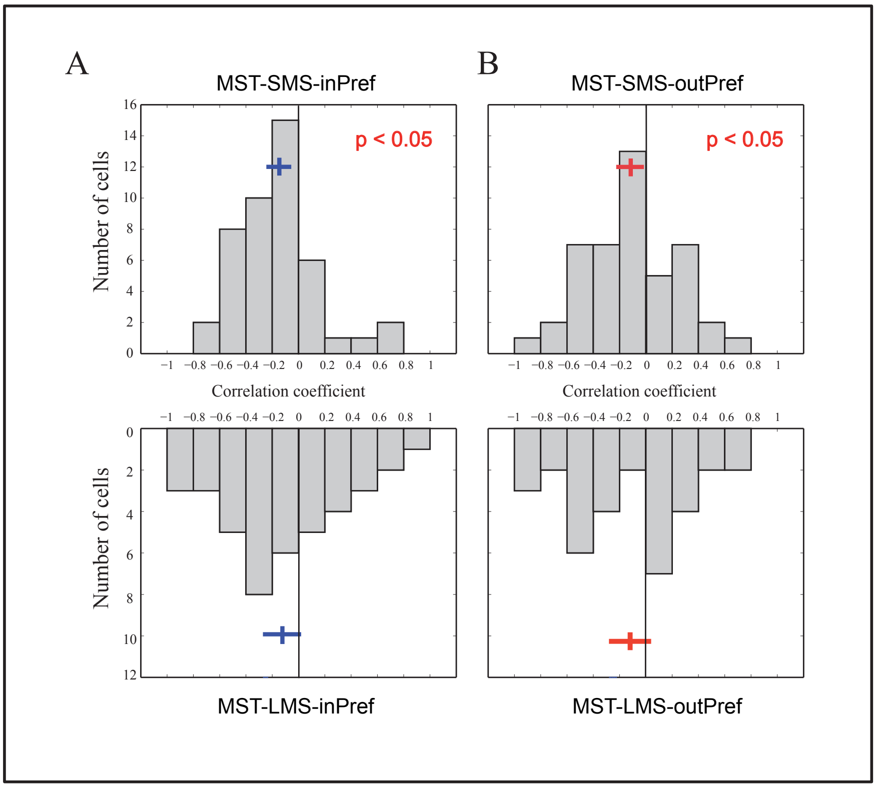

Figure 9: Correlation of firing rates with reaction times in MSTd

A: Distribution of correlation coefficients for attention to the preferred spiral (upper histogram) and linear motion stimuli (lower histogram) inside the receptive field in a time window of 50ms before and 125ms after the speed increment. Horizontal bars represent 95% confidence intervals while vertical bars correspond to the mean of the distribution.

B: Distribution of correlation coefficients for attention to the preferred spiral (upper histogram) and linear motion stimuli (lower histogram) outside the receptive field in a time window of 50ms before and 125ms after the task-relevant speed increment.

For each recording session we subtracted the mean from neural activity and reaction times. This removed the effect of between-stimulus time and absolute firing rate differences, leaving only residual changes (Janssen and Shadlen 2005). Figure 9A-B plots distribution of correlation coefficients for spiral and linear motion, respectively, for attention to the preferred direction within and outside the RF. Modest but significant negative correlations were observed when attention was directed to the preferred spiral motion stimulus inside the RF (figure 9A: upper histogram, mean correlation coefficient: -0.14, t-test, $p<0.05$) and outside the RF (figure 9B: upper histogram, mean correlation coefficient: -0.12, t-test, $p<0.05$). No significant correlations were observed for attention to the anti-preferred direction outside the RF. This is in agreement with the significant negative correlations of firing rate with RTs close to the detection time and weak correlation close to the lever release time previously reported in MT (Cook and Maunsell 2002). Importantly, no significant effect was observed in any of the attentional conditions for linear motion stimuli (figure 9A-B lower histograms). Similar negative correlations were observed in data recorded from area MT (Supplementary figure 2B).

DISCUSSION

We compared the tuning properties of two stimulus dimensions (spiral and linear motion stimuli) in area MSTd and MT. MSTd showed position invariant tuning profile for both spiral and linear motion stimuli with comparable directionality indices, but in terms of frequency of tuned neuron and the response index, the tuning properties for spiral motion stimuli outweighed than that for linear motion stimuli. In area MT also we observed tuning for both spiral and linear motion stimuli, but they were position invariant only for linear motion stimuli, moreover the tuning properties of linear motion stimuli outweighed than that for spiral motion in all measured parameters like response index, directionality index, and frequency of tuned neurons. By recording the two attentional paradigms (spatial and feature-based attention) from the same neuron we showed that spatial attention modulates responses of neurons in both areas MT and MSTd irrespective of the stimulus type. On the other hand feature-based attention is stimulus specific and is restricted to the most preferred stimulus dimension of an area (spiral motion stimuli for MSTd and linear motion stimuli for MT).

Tuning Properties:

Tuning properties of neurons for most of the areas in the visual cortex are very well defined. There is evidence for the existence of selectivity for multiple stimulus dimensions across the visual cortex e.g., area V1 shows selectivity primarily for orientation (Hubel and Wiesel 1968), but besides that there are also binocular disparity (Cumming and DeAngelis 2001), color and direction selective neurons (Sincich and Horton 2005). In the dorsal pathway, area MT neurons are primarily direction selective to linear motion (Albright 1984), but besides that a sub-population also demonstrates selectivity to disparity, orientation and color (Born and Bradley 2005). To add to that, we observed selectivity to an additional stimulus dimension in area MT, that is spiral mot. 58% (33 neurons) of the total cells recorded from area MT (56 neurons), showed tuning to spiral motion in addition to linear motion stimuli (figure 6), though not as defined as that for later, as indicated by their DI (figure 6C vs. figure 6D) and also the firing rate which was on average 43% higher for linear motion stimuli. Interestingly, the tuning for spiral motion stimuli was not position-invariant in sub-location of the RF unlike that for linear motion stimuli (figure 8), suggesting that this might be an artifact. Therefore, MT neurons are more selective for linear motion stimuli.

In area MSTd we found almost all neurons were tuned to spiral motion stimuli but a sub-population of 76% neurons (48 neurons) were tuned to linear motion stimuli also. The tuning for both linear and spiralmotion stimuli was position invariant. The DI was comparable for the two stimulus types (Figure 2) but the firing rate for spiral motion stimuli was on average 36% higher than linear motion stimuli (figure 2E), indicating that amongst the two stimulus types MSTd neurons are more selective to spiral motion stimuli.

Spatial Attention

We observed spatial attention modulation of responses of neurons, in both the areas MT and MSTd irrespective of the two tested stimulus (linear and spiral motion stimuli). Location dependent modulation of responses is a very robust phenomenon, which has been demonstrated reliably in various regions of the visual cortex (Maunsell and Cook 2002). The magnitude of attentional modulation differs between visual areas with weakest effect observed in earliest stages of the visual cortex and stronger as we go higher up in the visual processing hierarchy (Cook and Maunsell 2002). We compared the magnitude of spatial attention for the spiral and linear motion stimuli within areas MT and MSTd and also between them. We found modulation of comparable magnitude, 23% and 30% for linear and spiral motion stimuli respectively in area MT and 28% and 26% for linear and spiral motion stimuli respectively in area MSTd.

We compared sub-populations of 48 and 33 neurons from area MSTd (figure 3C, upper light shaded histogram) and MT (Supplementary figure 1C, upper light shaded histogram) respectively for attentional effects with both spiral and linear motion stimuli. There were no significant differences (paired t-tests, $p<0.05$) in the modulation strength between two stimulus dimensions either in an area or between the two areas. Our results are in contrast to the previous studies, according to which there is a general trend of increase in the strength of attentional modulation as we go higher in the visual processing hierarchy (Cook and Maunsell 2002). This increase of the attentional modulation was suggested to be due of the increasing complexity of the stimulus dimension to which an area shows selectivity e.g., area V1 for orientation stimuli (Hubel and Wiesel 1968), area MT for depth perception (DeAngelis, Cumming et al. 1998; Born and Bradley 2005), area VIP for optic flow and extra-retinal stimuli (Colby, Duhamel et al. 1993). The higher the complexity of the stimulus analyzed by an area, the higher the modulation.

But comparable attentional modulation for the two stimulus dimensions (spiral and linear motion stimuli) in both areas (MSTd and MT) demonstrates that these effects are independent of the complexity of the stimulus as suggested by previous study. As spiral motion is a component of optic flow stimuli and constitutes as more complex stimuli than linear motion stimuli. Hence, our data suggests that attentional modulation remains relatively constant not only within areas across the visual hierarchy, but also within different stimulus dimensions.

Feature-based Attention

We found feature-based attention in areas MT and MSTd dependent upon the tuning properties of the representative neurons. In area MSTd and MT feature-based attention was confined to spiral (figure 4C) and linear motion stimuli (figure 7C) respectively, that is to the stimulus type they showed better tuning for. The magnitude of this effect (spiral motion in MSTd and linear motion in MT) was comparable between the two areas and was not significantly different from each other (paired t-test, $p<0.05$).

Interestingly, there were no feature-based attentional effects in area MSTd and MT with linear and spiral motion stimuli respectively. We considered the presence of position-invariant tuning to be a criterion to validate feature-based attentional effect. This conservative approach was necessary especially for explaining the absence of feature-based attentional effects in MSTd and MT with linear and spiral motion stimuli respectively. If tuning is not position invariant then the feature-based attentional effects could largely depend upon the placement of stimuli in the receptive field of the neuron. In area MSTd we ruled out poor stimulus placement as the reason for the absence of feature-based attentional effects, as linear motion tuning was position invariant. On the contrary, in area MT the spiral motion tuning was not position invariant. Hence, the modulation effects for spiral motion stimuli in MT cannot be attributed to feature-based attention.

This paradigm allowed us to compare feature-based attentional effects for different stimulus attributes from the same set of neurons. We compared sub-populations of 48 and 33 neurons from area MSTd (figure 4C, upper light shaded histogram) and MT (figure 7C, upper light shaded histogram) respectively for attentional effects with both spiral and linear motion stimuli. There was no significant attentional modulation at the population level for the less preferred stimulus (linear motion stimuli stimuli in MSTd and spiral motion stimuli in MT). But the same population showed significant attentional modulation with the more preferred stimulus type (spiral motion stimuli in MSTd and linear motion in MT).

The presence of feature-based attentional effects in 48 MSTd neurons for spiral motion stimuli indicates that these neurons were engaged in perceptual processing, when monkey was performing the behavioral task with spiral motion stimuli. But these 48 neurons were not recruited in processing of linear motion stimuli stimuli, when monkey was performing behavioral task with linear motion stimuli. Same argument holds for presence of feature-based attentional effects in area MT with linear motion stimuli. Previous studies have indicated that correlation between firing rates and the RT could be taken as a reliable measure of engagement of a neuron in processing of a stimulus. These correlations have been shown in different parts of the visual cortex (Everling and Munoz 2000; Cook and Maunsell 2002; Janssen and Shadlen 2005). We also found modest but significant correlations of the firing rates with the reaction times in area MSTd and MT but again limited only to spiral motion stimuli (figure 9) and linear motion stimuli (Supplementary figure 2) respectively, that is to say to the more preferred stimulus. These results further provide evidence that MSTd and MT neurons are engaged in processing of spiral motion stimuli and linear motion stimuli respectively. Therefore, presence of feature-based attention can be taken as a correlate of engagement of neurons in the perceptual processing of the stimuli. And the mere existence of the tuning for a stimulus by a neuron alone does not necessarily imply its recruitment in the behavioral task.

The absence of feature-based attentional effect in MSTd with linear motion stimuli is an exception to the feature similarity gain model (Treue and Martinez Trujillo 1999). Feature similarity gain model states that feature-based attention modulates the response of neurons whose feature preference matches the attended feature. We in our experiments recorded the feature-based attention for linear motion stimuli and spiral motion stimuli in MSTd, by extracting the stimulus features (preferred direction and speed), from the tuning curves. Hence, the features for linear motion stimuli were matched to the tuning preferences of each neuron. The absence of attentional effect suggests that maybe feature-based attention modulates the response of neurons whose feature preference matches the feature preference of attended stimulus dimension.

CONCLUSION

To the best of our knowledge, this is the first study to compare the feature-based and spatial attention from the same set of neurons for different stimulus dimensions. We observed that spatial attention modulates the responses of neurons irrespective of the feature of the stimuli. On the other hand, feature-based attention is restricted not only to the attended feature but also to the stimulus dimension for which a neuron shows best selectivity e.g., spiral motion stimuli in MSTd and linear motion in MT.

Visual processing has been suggested to operate by combining top-down attentional modulations with bottom-up sensory signal in order to create an integrated saliency map that would highlight the region of interest relevant for behavioral outcome (Treue 2003). Spatial attention will contribute to this saliency map by strengthening the location of the region of interest. All neurons whose receptive fields overlap with the attended location will be recruited in processing. The feature-based attention on the other hand will add to this saliency map by modulating the response of neurons whose features are similar to the attended feature. Amongst the modulated neurons only those will be recruited in perceptual processing whose features matches the features of the attended stimulus dimension.

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Supplementary Material for

Relationship of the tuning properties with the spatial and feature-based attention attentional modulation in area MSTd of macaque visual cortex

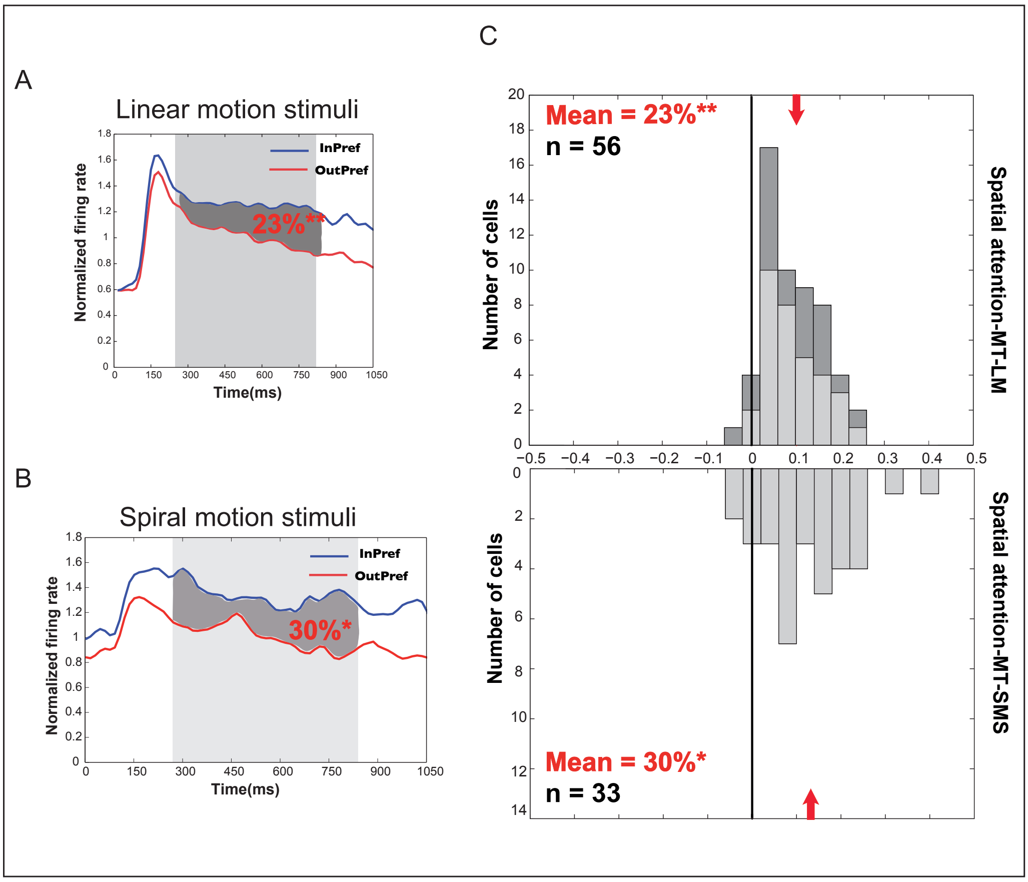
Daniel Kaping[1], Sonia Baloni[2,3], Stefan Treue[2,3]

The supplementary material provides additional information

1. Spatial attention modulation in area MT with linear and spiral motion stimuli.
2. Trail by trail correlations of firing rates with the reaction times in area MT.

Area MT: Spatial Attention modulation

Spatial attention modulations has been demonstrated by previously in area MT for linear motion stimuli. We measured responses of well isolated neurons in area MT from two macaque monkeys, while they were engaged in spatial attention task (main text, figure 1). The spatial attention was measured only for the preferred spiral motion and linear motion directions. Supplementary figure 1A and 1B shows the population spike density function for 33 and 56 neurons recorded with spiral and linear motion respectively. The x-axis is aligned to onset of coherent motion stimuli (figure 1), and the y-axis represents normalized response, the blue curve corresponds to condition when attention was directed inside the RF, while the red curve is for when attention was outside the RF. It can be seen that the response of MT neurons like neurons in area MSTd were higher when attention was directed inside than outside the RF for both spiral and linear motion. Attentional indices (equation 4), were evaluated for each neuron over a 570ms time period (gray shaded area in Supplementary figure 1A and 1B) starting 270ms after the onset of coherent motion. Distribution of attentional indices for spiral and linear motion are plotted in Supplementary figure 1C. The mean attentional modulation of 56 neurons for linear motion (upper dark histogram) was 23% ($p<<0.01$, signrank test), while that of 33 neurons for spiral motion (Lower light histogram) was 30% ($p<<0.01$, signrank test).We compared attentional modulations across the two stimulus dimension for the 33 neurons, as for these we had data for both spiral and linear motion stimuli. The mean attentional modulation of 33 neurons with the linear motion stimuli (upper light histogram) was 21% ($p<<0.01$, signrank test) and was not significantly different from that of attentional modulation with spiral motion stimuli. Just like in area MSTd, in area MT also we observed a reliable spatial attention modulation of 30% irrespective of stimulus type.



Supplementary figure 1: Spatial Attention in area MT

A. Normalized population sdfs plotted as a function of time, when attention was directed to the preferred (blue curve) direction inside and outside the receptive field for linear motion. Zero on the x-axis represents onset of coherent linear motion onset. The gray shaded area represents the 570ms analysis period window (starting 270ms after the onset of coherent motion period), over which attentional indices were evaluated.

B. Normalized population sdfs plotted as a function of time, when attention was directed to the preferred (blue curve) direction inside and outside the receptive field for spiral motion stimuli. Zero on the x-axis represents onset of coherent spiral motion onset. The gray shaded area represents the exact same 570 ms analysis period window used for evaluating attentional indices for linear motion stimuli.

C. Distribution of spatial attention indices for 56 linear motion (above, dark gray histogram) and 33 spiral motion (bottom, light gray histogram) neurons. The light gray region in upper histogram represents attention indices for linear motion of 48 neurons (for which spatial attention was measured for both spiral and linear motion).

Area MT: Trial by trial correlation of behavior and neural activity

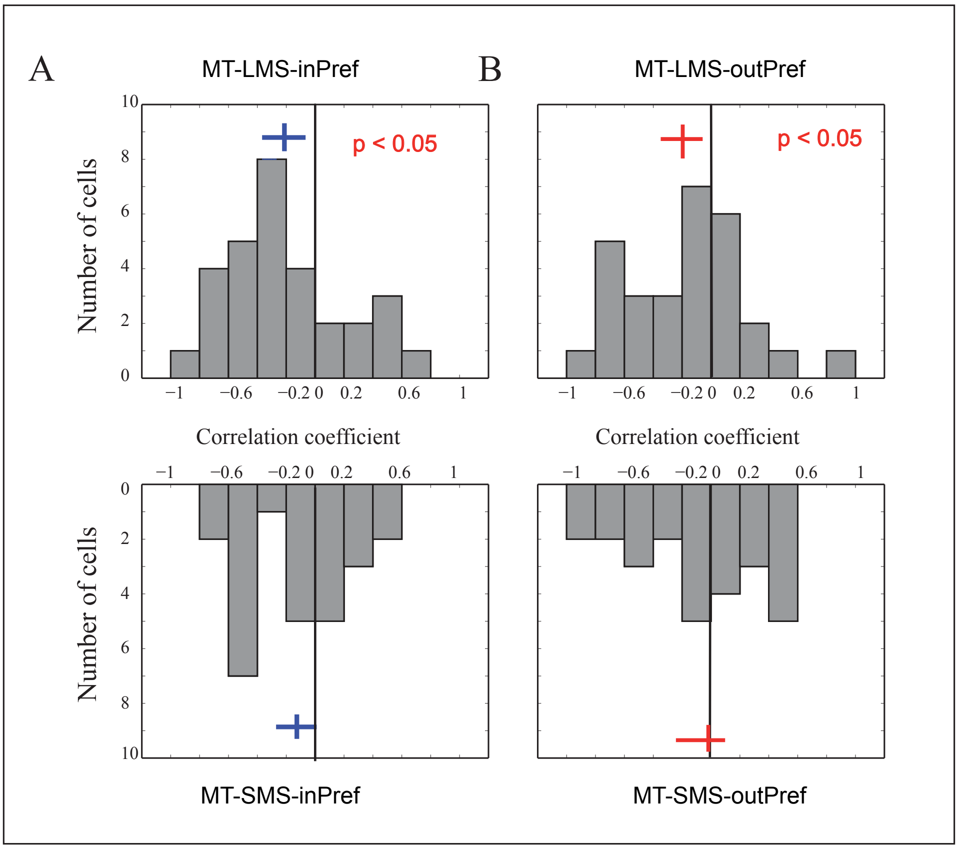
We observed modest but significant trial-by-trial correlations of the firing rate and reaction times for MSTd neurons when attention was directed inRF to the preferred spiral motion stimuli. On the other hand there were no correlation observed when attention was directed inRF to the preferred linear motion stimuli. These results provides us with a direct evidence of involvement of MSTd neurons in perceptual processing of the spiral and not linear motion stimuli.

To see if similar trend exists in area MT, we computed similar correlations, under the same three attentional conditions; attention inside the RF to the preferred spiral/linear motion stimuli, attention outside the RF to the preferred spiral/linear motion stimuli and attention outside the RF to the anti-preferred spiral/linear motion stimuli.

In order to avoid the large variation in firing rate during the transient response period, only trials that had passed 800ms before the presentation of the response event were included. With this selection criteria, we had 30 neurons for attention inside the RF and 29 neurons for attention outside the RF to preferred direction condition while, 30 neurons for attention to the anti-preferred direction outside the RF. For each recording session we subtracted the mean neural activity and mean reaction time from the data. This removed the effect of time and absolute firing rate differences between the stimulus types, leaving only the residual changes (Janssen and Shadlen 2005).

We observed negative correlation of firing rates and reaction times when attention was directed inside the RF to the preferred linear motion direction for a time epoch of 100ms before and 50ms after the response event time (Supplementary figure 2A, upper histogram, mean coefficient = -0.21, t-test, $p<0.05$). For attention outside the RF to the preferred linear motion direction there were significant negative correlation for a time epoch of 150ms before and 50ms after the response event time (Supplementary figure 2B, upper histogram, mean coefficient = -0.19, t-test, $p<0.05$). But no correlations were observed for attention outside the RF to the anti-preferred linear direction. And also no significant correlations were observed when attention was directed to spiral motion stimuli in any of the attentional conditions (Supplementary figure 2A-B, lower histogram).

These negative correlations between firing rate and reaction times in area MT, when attention was directed to preferred linear motion stimuli, can be taken as a neuronal correlate of involvement of MT neurons in perceptual processing of linear motion stimuli. Similar negative correlations were also observed in area MSTd (figure 9) but for spiral and not linear motion stimuli. If we compare the trends in area MT and MSTd, we can see that for each area; just like feature- based attentional modulations, trial-by-trial correlations of the firing rate and reaction times were also restricted to the stimulus dimension for which they show better preference (spiral motion in MSTd and linear motion stimuli in area MT).



Supplementary Figure 2 : Correlation of firing rates with reaction times in area MT

A: Distribution of correlation coefficients for attention to the preferred linear (upper histogram) and spiral motion stimuli (lower histogram) inside the receptive field in a time window of 100ms before and 50ms after the speed increment (response event time). Horizontal bar represents 95% confidence intervals while, the vertical bars corresponds to the mean of the distribution.

B: Distribution of correlation coefficients for attention to the preferred linear (upper histogram) and spiral motion stimuli (lower histogram) outside the receptive field in a time window of 150ms before and 50ms after the speed increment (response event time). Horizontal bar represents 95% confidence intervals while, the vertical bars corresponds to the mean of the distribution.

Chapter 4: Temporal Attention

In this chapter we investigate the temporal characteristics of visual motion processing by means of visual processing deficit termed as ‘attentional blink’. We found that the motion processing is degraded when the second of the two motion stimuli are presented within 450ms after the first stimulus.

Author’s contribution:

Sonia Baloni and Stefan Treue designed the experiment. Data collection and analysis was done by Janina Hueer. The manuscript was written by Sonia Baloni and was edited by Stefan Treue. All authors discussed the results and worked upon the manuscript at all stages.

Attentional blink in visual motion processing

Sonia Baloni[1,2], Janina Hueer[1], Nils Mueller[3], Stefan Treue[1,2]

[1]Cognitive Neuroscience Laboratory, German Primate Center, Goettingen, Germany

[2]Bernstein Center for Computational Neuroscience, Goettingen, Germany

ABSTRACT

Attentional blink is a visual processing deficit, where the processing of the second target is compromised severely when it is presented (amongst the distractors in a rapid serial visual presentation (RSVP)) at a close temporal proximity (200-500ms) to the first target. This is a very robust and widely studied phenomenon, demonstrated with a wide range of stationary stimulus dimensions like numbers, letters, images etc. We extended the classic attentional blink paradigm from the Raymond et al (1992) to motion domain. We found attentional blink in the motion domain also as the processing of second motion stimuli is dramatically degraded when presented within 500ms of the presentation of the first motion stimuli. But the processing of the second motion stimuli was dependent upon the direction of the first target, suggesting of some kind of interaction between the motion stimuli.

INTRODUCTION

Processing of visual information is achieved through a complex network of more than 30 cortical visual areas (Felleman and Van Essen 1991), which are functionally segregated into two major pathways namely the ventral pathway, involved in object recognition (Mishkin and Ungerleider 1982; Haxby, Grady et al. 1991; Goodale and Milner 1992) and the dorsal pathway involved in motion processing (Maunsell and Van Essen 1983; Ungerleider and Desimone 1986; Maunsell and Newsome 1987; Newsome and Pare 1988; Vaina 1994). In spite of this functional specialization of different areas in the visual cortex, it is practically impossible to process all the sensory information that enters our system, hence evolution has provided us with numerous mechanisms to filter (selection) out the relevant aspects of sensory information necessary for behavioral outcome through various cognitive abilities one of which is attention (Moran and Desimone 1985).

Attention optimizes processing by selecting the most relevant of the multiple stimuli, but performance suffers when attention and processing resources need to be divided or distributed in space and time. Attentional blink is one of the phenomena, which demonstrate the limitations of attentional resources in visual processing in the temporal domain (Broadbent and Broadbent 1987; Weichselgartner and Sperling 1987; Raymond, Shapiro et al. 1992; Chun and Potter 1995).

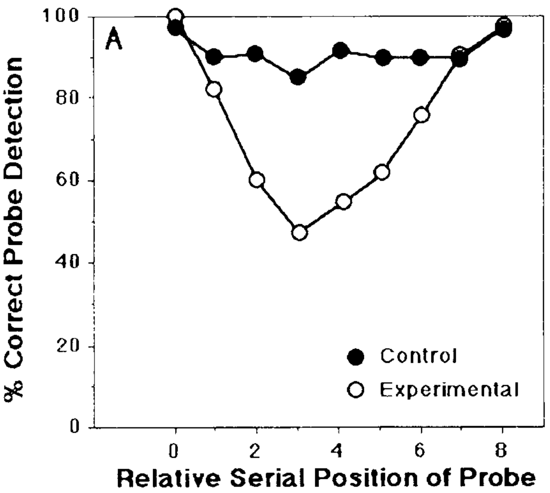


Figure 1: Attentional blink, Raymond.et.al,1992

The graph is plots the performance of correct detection of the probe (y-axis) as a function of the relative position (x-axis) at which the probe was presented with respect to the target. Filled circles and the open circles correspond to the performance in the control and experimental conditions respectively.

Attentional blink is a post-target processing deficit, where if two relevant stimuli are presented in close temporal proximity, then the processing of the second stimulus is severely degraded when it is presented within a time window of 200ms - 500ms, after the first stimulus (Broadbent and Broadbent 1987; Weichselgartner and Sperling 1987; Raymond, Shapiro et al. 1992; Chun and Potter 1995). This shortcoming in visual processing was first demonstrated by Broadbent & Broadbent (1987) & Weichselgartner & Sperling, 1987. But in these two studies it was not clear if this deficit was a lapse of information processing or an inability to retrieve the otherwise processed stimuli from memory. Raymond et al (1992) demonstrated for the first time that this post-target processing deficit is attentional and therefore called it an 'Attentional Blink'.

Figure 1 shows Attentional Blink results from Raymond et al (1992) study, where the two curves represent the performance for the processing of the second (referred to as probe) of the two relevant stimuli presented at different relative serial positions in a rapid visual serial presentation of letter stimuli. In the control condition (filled circles), when the subjects were supposed to ignore the first stimulus (referred to as target) and only process the probe, the performance was high at all serial positions. But, in the experimental condition (open circles) when the subjects were supposed to process both the target and the probe, the performance was degraded at relative serial positions 2-5 (corresponding to the time period of 180ms-450ms) as compared to that of the control conditions. This inability to process target for a defined time interval was explained by competition amongst the two stimuli for the attentional resources due to their close temporal proximity. Since attentional resources were engaged in processing the first target stimuli, they were unavailable for processing the second stimuli leading to the processing deficit.

The attentional blink can be characterized by two basic features (figure 1), first being the time period for which this effect prevails that is from 200ms – 500ms (relative serial positions 2-5 in figure 1) after the presentation of the first target and second the lag-1 sparing effect (Chun and Potter 1995), which is the absence of the post-target processing deficit when the second target immediately follows the first target (at lag-1). But the lag-1 sparing is not a robust feature; as according to the literature for almost half of the attention blink studies this effect did not prevail (Duncan, Martens et al. 1997; Jolicoeur 1998; Visser, Bischof et al. 1999) and this lead to formulation of an addition conservative criterion to access lag-1 sparing effect. The classical criteria defined lag-1 sparing effect to be present if the performance of the detection of the second target did not differ significantly between the control and the experimental conditions (Chun and Potter 1995). In a more conservative terms lag-1 effect was said to be present if the level of performance at Lag-1 exceeded the lowest level of performance by more than 5% in absolute terms (Visser, Bischof et al. 1999).

The attentional blink paradigm has been extensively studied with a range of stimuli like letters (Raymond, Shapiro et al. 1992; Shapiro, Raymond et al. 1994; Luck, Vogel et al. 1996; Husain, Shapiro et al. 1997; Potter, Chun et al. 1998), digits (Weichselgartner and Sperling 1987; Potter, Chun et al. 1998; Di Lollo, Kawahara et al. 2005) etc, which are stationary stimuli & are more likely to be processed along the ventral pathway (Mishkin, Ungerleider et al. 1983) but there has not been much exploration in motion domain, which also happens to be an important part of visual processing, stressed by the fact that an area of visual cortex (dorsal pathway) is involved in motion processing (Maunsell and Van Essen 1983; Albright 1984; Albright, Desimone et al. 1984; Ungerleider and Desimone 1986; Newsome and Pare 1988; Wurtz, Yamasaki et al. 1990; Vaina 1994).

Our aim was to test the classical attentional blink paradigm with motion stimuli, to study if temporal processing of motion stimuli follows the same characteristics as stationary stimuli qualitatively & quantitatively?

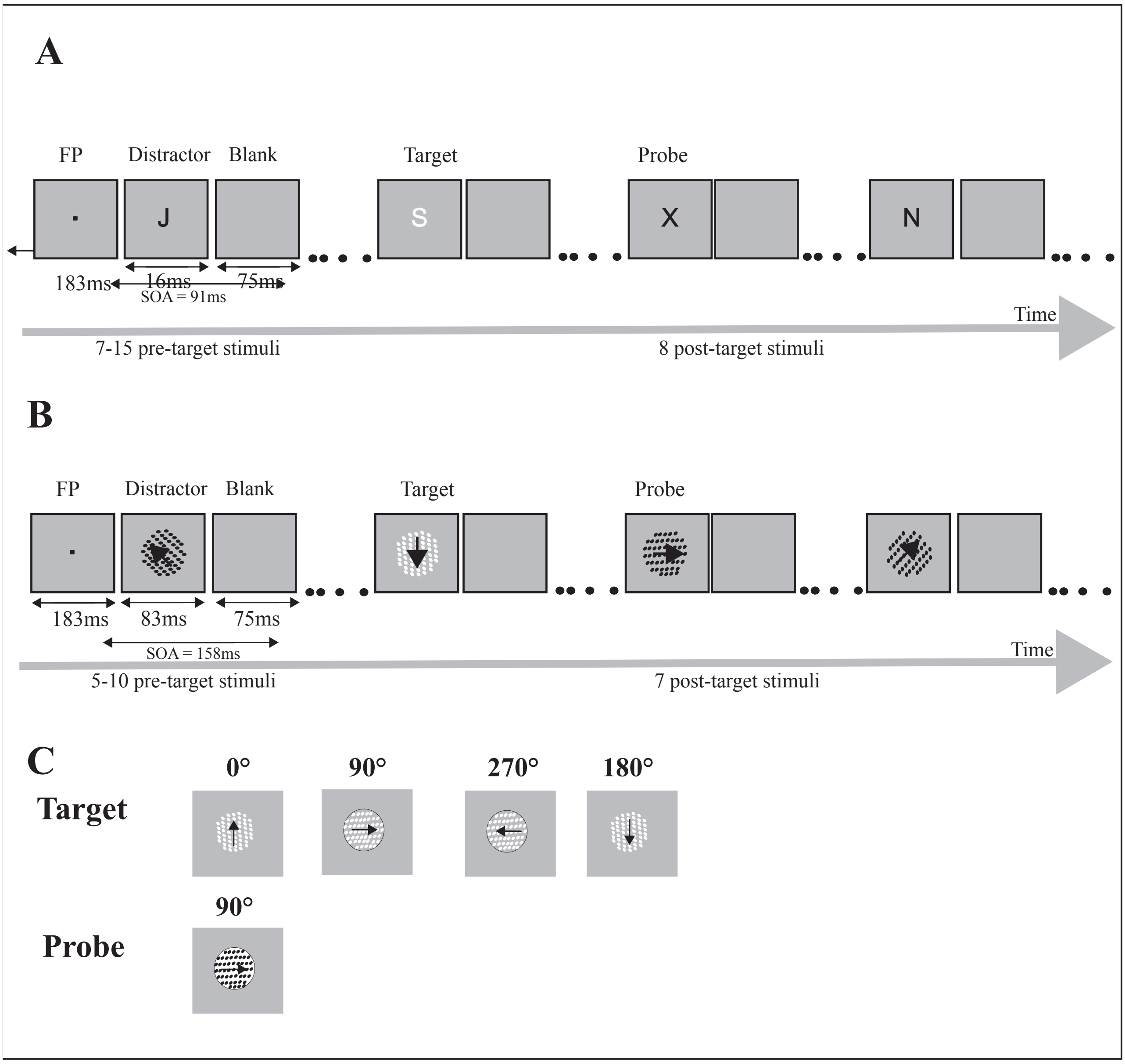


Figure 2: Trial course

A). Trial course for experiment 1: Each trial started with a onset of fixation point for 183ms & was followed by RSVP of letter stimuli, where the letters were presented for 16.6ms and were interspersed with blank frame for 75ms, giving a SOA of 91ms between consecutive letter stimuli. A RSVP sequence had two test stimuli, namely ‘Target’ & the ‘Probe’. The ‘Target’ was the only white colored letter in otherwise stream of black letters, & could be any of the 26 English alphabets, randomly presented in 8-16 positions in a trial & was always followed by 8 letter stimuli. The ‘probe’ was a black colored letter ‘X’, which was presented in only 50% of total number of trials in an experiment, randomly at 8 different SOAs after ‘Target’ presentation. All the letters apart from the ‘Target’ & the ‘Probe’ were referred to as distractors.

B). Trial course for experiment 2: Each trial started with a onset of fixation point for 183ms, followed by RSVP of random dot pattern (RDP), where RDP was presented for 83ms followed by blank frame for 75ms, giving a SOA of 158ms. The target was a white RDP which was in a trial randomly assigned one of the four direction (C), while the probe was always 90° right hand moving RDP (C). The target was randomly presented in positions 5-10 in a RSVP sequence, but was always followed by 7 RDPs. The probe was presented in 50% of total number of trials at 6 different randomly chosen positions after the target. The distractor RDPs were chosen randomly from a range of directions between 0°-45° or 135°-359°.

MATERIALS AND METHODS

All stimuli were generated in an Apple MacPro computer with MWorks (Version 0.5dev), an open source project developed by David Cox (Rowland institute at Harvard, Cambridge) and were presented on a 22” LCD-Monitor (Samsung SyncMaster 2233RZ), at a resolution of 1680 x 1050 pixel with a refresh rate of 120Hz. The monitor was placed at a distance of 57 cm from the subjects, who were seated in a semi-dark room with their head stabilized using a chin rest. The response for each trial was registered with the help of a Gamepad (Logitech Precision). The data analysis was done using Matlab (MathWorks, Inc.).

Experimental sessions:

Each experimental session lasted on average 1.5hrs and consisted of a training session followed by the main experiment. The training session had

two single task experiments and the subjects were trained until they either attained a stable criterion performance (75% hit rate) or for a maximum of 180 trials. If the subjects were not able to attain, the criterion performance until the maximum of 180 trials, they were excluded from the study.

The main experimental session consisted of two experiments, one a dual task the other a single task control experiment. The order of these two experiments was balanced amongst the subjects.

Experiment 1:

This experiment was conducted in order to replicate the Raymond et al, (1992), experiment of attentional blink with letter stimuli, in order to set a baseline, as this paradigm is well established.

Subjects:

15 healthy subjects (8 females and 4 males) with normal or corrected to normal vision, within the age group of 21-29 years, participated in the study. In all the experiments two subjects out of the total number of subjects, were graduate students from the lab, while the other were invited from the lab’s subject database. 5 subjects were excluded from the study, as they were not able to attain the criterion performance in training session.

Trial course:

Each trial (Figure 2A) started with the appearance of a white (23.3cd/m^2) fixation point of size 0.2° x 0.2° for 183.3ms at the center of a gray square of size 12.5° x 16.3° and luminance 2.9cd/m^2, which itself was placed at the center of the monitor, with a black background of luminance 0.1cd/m^2. The fixation point was replaced by an RSVP of letters from the English alphabet in Arial font subtending an angle of 0.82°, where each letter was presented for 16ms followed by blank frames for 75ms, thereby giving a stimulus onset asynchrony (SOA) of 91ms.

All the letters in a trial were black (0.1cd/m^2) in color except for one white letter (23.3cd/m^2) referred to as the target, which was similar in size and font to the black color letters except for the fact it was white in color. Amongst the black letters letter 'X' was assigned as probe and rest all were distractors. Hence, the target could be any one of the 26 English alphabets, while distractors could be any of the 25 letters in the English alphabet except for the letter 'X'. No letter was repeated in a trial. The probe was presented in 50% of the total number of trials.

Within a trial the target was randomly presented at positions 8-16 and was always followed by 8 distractor letters, hence the maximum number of letters that could be presented in a trial varied between 16-24. The probe was never presented before the target, but could appear either as target or at 8 subsequent positions (stimulus onset asynchrony - SOA) after the target. For the dual-task experiment subjects were instructed to report the white letter (target) in the RSVP stream and then detect the presence or absence of the letter 'X' (probe), while for the single task control experiment, the subjects were supposed to ignore the target and report the presence or absence of the probe.

Experiment 2:

Subjects:

12 healthy subjects (8 females and 4 males), within the age group of 21-29 years, participated in the study. The aim of this experiment was to extend the basic framework of Raymond et al, (1992) experiment of the attentional blink with letters for the motion stimulus. 4 subjects were excluded from the study, as they were not able to attain the criterion performance in training session.

This experiment has a subtle difference with respect to the standard attentional blink paradigm (Raymond, Shapiro et al. 1992). Firstly, the time of presentation of the motion stimuli which was 83ms as compared to the 15ms presentation of the letter stimuli in the standard task. We choose 83ms as time for motion stimuli presentation as 80ms-100ms is suggested to be the time required for direction discrimination (McKee and Welch 1985; De Bruyn and Orban 1988).

Trial course:

The experiment started, with the onset of a fixation point (similar to the experiment 1) at the center of gray square of size 12.5° x 16.3° and luminance 9.15cd/m^2, which itself was placed at the center of the monitor (Figure 2B). The fixation point was replaced by RSVP of motion stimuli, a random dot pattern (RDP), with 250 black dots of 0.1cd/m^2 luminance and a radius 0.2°, presented within a circular aperture of 4°, moving at a speed of 25°/s. Each RDP was presented for 83ms followed by blank frames for 75ms, thereby giving a stimulus onset asynchrony (SOA) of 158ms.

All RDPs in the RSVP sequence consisted of black dots except for the target RDP, which had white dots (23.3cd/m^2) instead of black, but otherwise identical to the black motion stimuli in terms of dot size, speed, aperture size and number of dots. All black RDPs were distractors except for the one moving in direction 90° towards right hand, which was marked as probe (Figure2C) and was presented in only 50% of total trials.

The target (Figure 2C) RDP could be any of the four directions 0° (upper direction), 90° (right hand direction), 180°(downward direction), or 270°(left hand direction). For each trial one of the four target direction was chosen randomly. Within a trial, the target was randomly presented at one of the five positions from 5 to 10 in the RSVP sequence, and was always followed by maximum of 7 stimuli, hence the total number of stimuli in a trial varied between 12-17. The probe was presented in half of the trials, never before the target, but could either be the target or at one of the 5 randomly chosen positions (stimulus onset asynchrony - SOA) after the target. The target and the probe were interspersed with distractors (black RDP), which were chosen randomly from the direction range of 0°-45° or 135° -359°, to make sure that the subjects does not confuse them with the probe (90° right hand moving stimulus).

For the dual-task experiment subjects were instructed to report the direction of the white RDP (target) in the RSVP stream and then report the presence or absence of the 90° right hand moving RDP (probe), while for the single task control experiment, the subjects were supposed to ignore the target and detect the presence or absence RDP moving in 90° right hand side direction.

Experiment 3:

9 healthy subjects (4 females and 5 males), within the age group of 25-30 years, participated in the study. This experiment was designed to attain shorter SOAs than for experiment 2 (158ms). 5 subjects were excluded from the study, as they were not able to attain the criterion performance in training session.

Trial course:

This experiment was similar to experiment 2, the only difference being the duration of the blank frames, which was 75ms in experiment 2 and was shortened to 33ms in order to attain shorter SOA, which now was 117ms. The instructions for the dual task and the single task control experiment were exactly the same as for experiment 2.

Analysis:

For all three experiments the performance for correct detection of the probe from the dual task experiments was compared to that of the single task control experiment (Figure 3), where the x-axis represents the SOA (ms), at which the probe was presented with respect to the target, 0 marks the position where the probe was presented as a target and the y-axis represents percentage correct response. The basis for this analysis was to compare how the performance of detection of the probe (control experiment) was affected when it was preceded by an additional attention task, detection and discrimination of the target (dual task). Only those trials from the dual task experiments were included, where there was correct identification of the target.

Results & Discussion:

Experiment 1:

The average performance for identification of targets in dual task experiments for 15 subjects was 85%. Figure 3A plots the performance of correct detection of the probe for the control experiment (closed circle) and the dual task experiments (open circles) for the letter task. The average performance for detection of the probe for the control experiment is on average 85% and above for all SOAs, but the performance drops across 100ms -500ms in the dual task experiment, and then reverts back to the same performance level of the control experiment from 550ms onwards.

A two variable ANOVA (condition vs SOA), showed a significant effect of the condition (single task, dual task), $F(1,126)=142.58$, $p<0.01$, a significant of the SOA, $F(8,126)=14.96$, $p<0.01$ and a significant effect of interaction of condition and SOA, $F(8,126)=13.96$, $p<0.01$.

A post hoc analysis of a paired t- test with Bonferroni correction showed a significant difference in performance of single task from dual task from 90ms – 500ms ($p<0.05$). For the dual task experiment, there was a significantly higher performance at SOA-1 (90ms) as compared to SOA-3 (180ms) (paired t-test, $p<0.05$), the lowest point in the curve, indicating presence of lag-1 sparing effect (Visser, Bischof et al. 1999; Visser, Zuvic et al. 1999)).

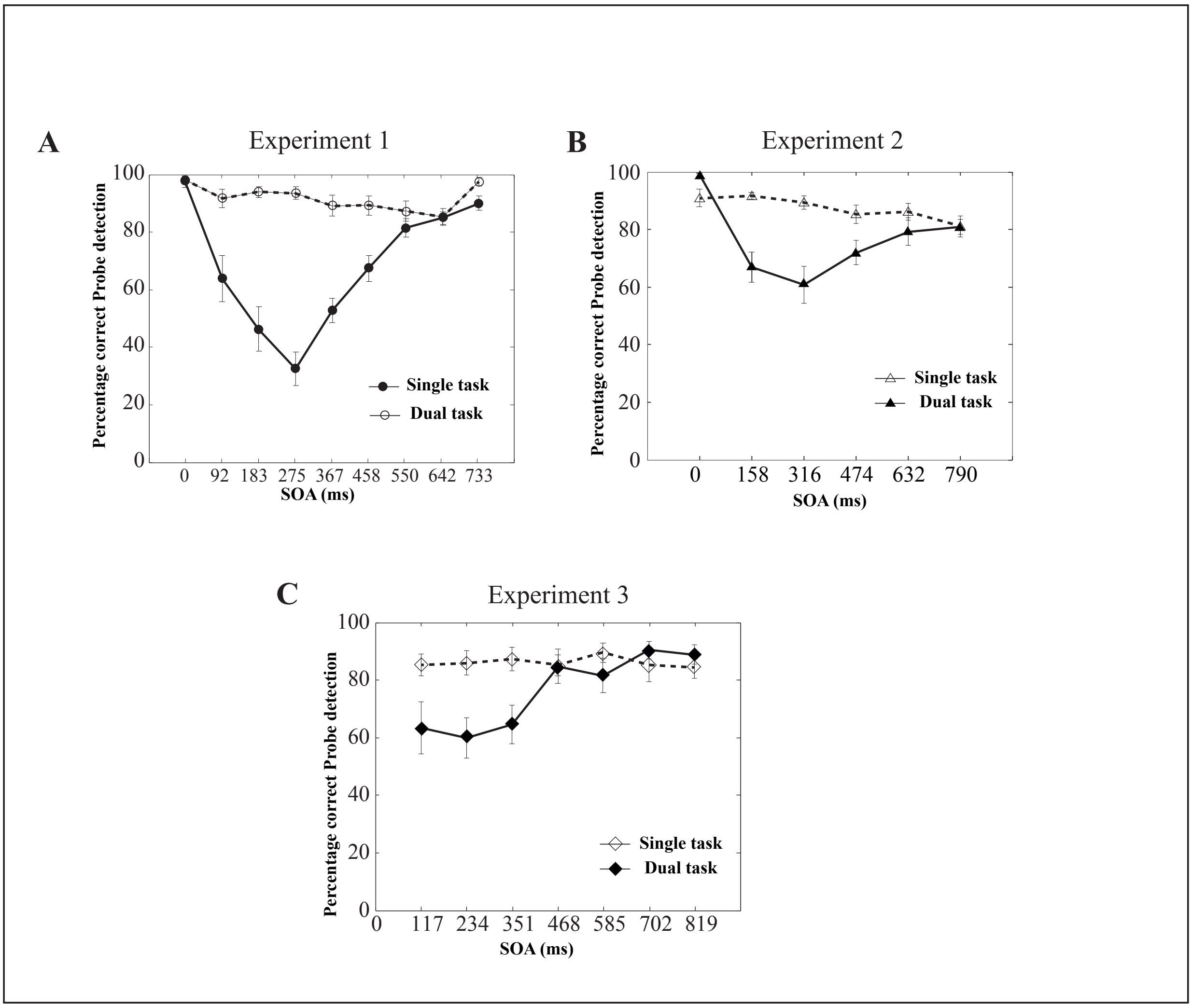


Figure 3: Plot for the mean performance of for the correct detection of the probe for dual and single task for experiments 1(A), experiment 2 (B) and experiment 3(C). X-axis represents, the stimulus onset asynchrony (SOA) in milliseconds and the y-axis represents percentage of correct detection of the 'Probe'. Error bar represents standard error of the mean.

Hence, we could replicate the attentional blink paradigm, originally designed by Raymond et al (1992), with two signature features, firstly the presence of post-target processing deficit across a time range of 180-500ms, and secondly the presence of lag-1 sparing effect.

Experiment 2:

Figure 3B shows that the average performance for the detection of the probe for both dual task (open triangle) and single task control experiment (filled triangles). The performance for the single task is on an average 85% and above at all SOA, but the performance drops across 158ms – 317ms in the dual task experiment, and then reverts back to the same performance level of the control experiment from 475ms onwards, which is about 100ms earlier than in experiment 1 (figure 3A).

A two variable ANOVA (condition vs SOA), showed a significant effect of the condition (single task, dual task), F(1,66)=26.61, p<0.01, a significant effect of the SOA, F(5,66)=6.84, p<0.01 and a significant effect of interaction of condition and lag, F (5,66)=7.36, p<0.01.

A post hoc analysis of paired a t- test with Bonferroni correction showed significant difference in performance of single task from dual task at SOA 158ms & 317ms (p<0.05), though for later SOA, there was no significant difference between the two experiments. Further, the performance at SOA-1 (160ms) for dual task experiment was not significantly different from that of SOA-2 (300ms), the lowest point in the curve, though at these two SOAs the performance for the dual task significantly differed from that of the single task, indicating the absence of lag-1 sparing effect.

Comparing the present results with Raymond et al (1992), attentional blink paradigm, we observed a post-target processing deficit over a time range of 158ms – 317ms, which was about 100ms shorter than that, observed in experiment 1, and absence of lag-1 sparing effect.

Many studies have also shown absence of lag-1 effect (Duncan, Martens et al. 1997; Jolicoeur 1998; Visser, Bischof et al. 1999), which was in most of the cases attributed either to change in dimension (audio & visual), or to switch in attentional location (Visser, Bischof et al. 1999; Visser, Zuvic et al. 1999). The absence of lag-1 effect in our experiment cannot be contributed by any of the above-defined factors as in a trial; we always had attention directed in same the dimension that is motion domain and at the same spatial location.

On the other hand, the studies that have reported the lag-1 sparing effect, in most of the cases have the probe at lag-1 being presented within 100ms after the presentation of the target. It has been shown that lag-1 sparing effect was dependent on the presentation of the probe in a time window of 100ms after target presentation (Potter, Staub et al. 2002; Nieuwenstein, Chun et al. 2005; Bowman and Wyble 2007). In our experiment, the SOA was 158ms, about 60ms more than the required time window of 100ms. Hence, we wanted to study if the absence of lag-1 effect in our data was due to this longer SOA or not, which lead us to the next experiment, where we tried to narrow down this SOA to 117ms, so as to be as close as possible to the 100ms time range.

Experiment 3:

The average performance for the detection of the probe for the control experiment (Figure 3C) is on an average 85% and above at all SOA, but the performance drops across 117ms – 350ms in dual task experiment (which is again about 100ms shorter than that for experiment 1), and then reverts back to the same performance level of the control experiment from 467ms onwards. Hence, the time course of attentional blink is the same as in experiment 2, even with shorter SOAs.

A two variable ANOVA (condition vs SOA), showed a significant effect of the condition (single task, dual task), F(1,56)=12.33, $p<0.01$, a significant effect of the SOA, F(6,56)=3.01, $p<0.01$ and a significant effect of interaction of condition and lag, F (6,56)=3.29, $p<0.01$.

A post hoc analysis of paired a t- test with Bonferroni correction showed a significant difference in performance of single task from dual task at SOA 233ms & 350ms ($p<0.05$. There was also no lag-1 effect as the performance at 117ms (SOA-1) was not more than 5% higher than that at the lowest point in the curve (233ms).

Hence even after reducing the time scale between the target and the probe at the first SOA, close to the 100ms range, we did not observe lag-1 sparing effect.

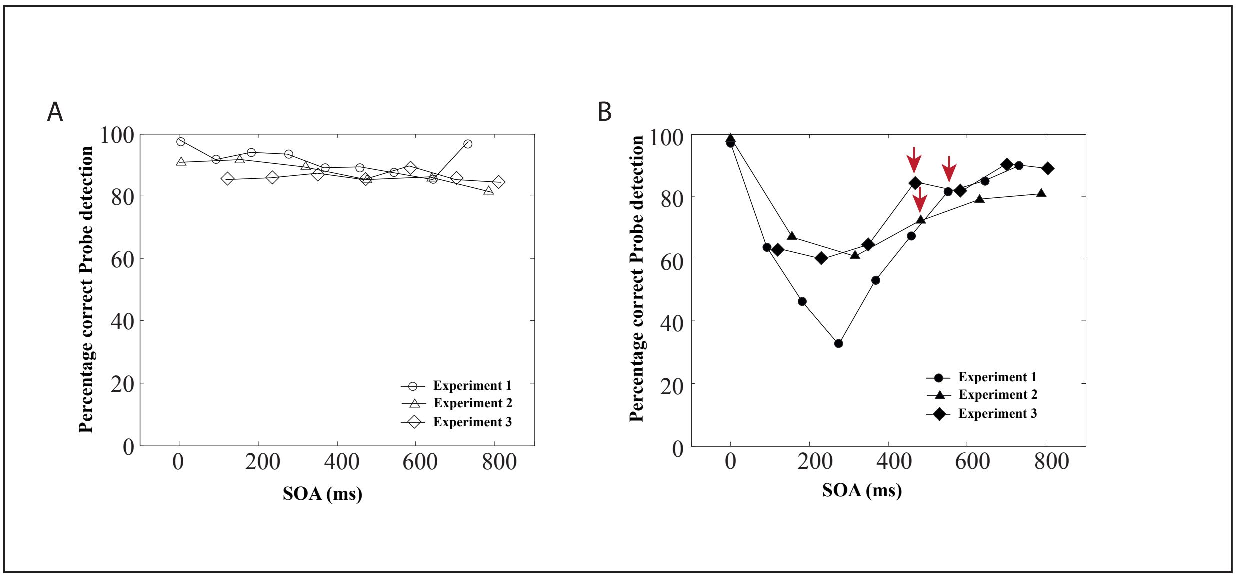


Figure 4: Average performance for correct probe detection across all three experiments for the single task (A) & the dual task (B). X-axis represents the SOA in ms, while the Y-axis represents the performance in percentage. The arrow in (B) represents the time point at which the performance of the dual task for each of the experiments 1, 2 & 3 reverted to match the single task performance.

Discussion:

Attentional blink is a post-target processing deficit, which demonstrates the limits of visual processing in the temporal domain. Almost all of the studies have been restricted to stationary stimuli like letters, digits, and computer symbols, while there is no research in the motion domain, provided us with the motivation to study the attentional blink paradigm with motion stimuli.

We first replicated the classic attentional blink paradigm with letter stimuli (Raymond, Shapiro et al. 1992) and found standard attentional blink features. The post-target processing deficit was within a time range of 100ms- 500ms and there was also a lag-1 sparing effect. We next, extended this paradigm to motion stimuli, with some modification in terms of the presentation time of the motion stimuli (80ms as compared to the 16ms presentation time for the letter task), giving us a SOA of 158ms for the motion task as compared to the SOA of 92ms for the letter task.

With motion stimuli, we also found a post-target processing deficit of the probe within a time period of 150ms-300ms, but we did not find a lag-1 sparing effect. We speculated the absence of lag-1 sparing effect to be due to the longer SOA (158ms) as compared to the 100ms SOA for the standard AB task, which is shown to be critical for Lag-1 sparing effect (Chun and Potter 1995). So, we designed another experiment with shorter SOA of 117ms (experiment 3), for which we got a post-target processing deficit within the same time range (117ms – 350ms), but still no lag-1 effect.

Figure 4 shows the performance for correct detection of the probe, in the single tasks (Figure4A) & dual tasks (Figure4B), from all the three experiments. The performance for the single task does not differ between the three experiments across all lags (Figure4A), but there are two notable points for the dual task across the three experiments. Firstly, the post target processing deficit for experiments 2 and 3 (the motion tasks), lasts approximately for the same time period, that is 300ms (experiment 2) and 350ms (experiment 3), but for letter task (experiment 1) this deficit lasts until 480ms (figure 4B), which is about 150ms longer than for the motion tasks. The red arrows in figure 4B corresponds to the SOAs at which the performance for the dual task for each experiment reverted back to the order of the performance in the single task control experiments. Secondly, the absence of lag-1 sparing effect in motion task (experiments 2 & 3, figure 8B).

Post-target processing deficit:

Post-target processing deficit is the inability to process the probe when it is presented within a time range of 200ms -500ms (Raymond, Shapiro et al. 1992; Chun and Potter 1995). Outside this critical time range the probe is processed reliably. Many models have been proposed to explain this deficit (Broadbent and Broadbent 1987; Raymond, Shapiro et al. 1992; Chun and Potter 1995). In our experiments we also found this post-target processing deficit, but for about 150ms shorter timescale than those reported for other attentional blink studies with stationary stimuli.

One very obvious difference is the nature of stimuli used. We have used motion stimuli, which are processed along the dorsal pathway (Maunsell and Van Essen 1983; Maunsell and Newsome 1987; Newsome and Pare 1988), in contrast to the stimuli used by other studies like letters, words, digits etc., which are more likely to be processed along the ventral pathway (Mishkin and Ungerleider 1982; Haxby, Grady et al. 1991; Goodale and Milner 1992).

There are psychophysical studies, which have shown that the processing time for motion stimuli direction discrimination is within 80ms-100ms (McKee and Welch 1985; De Bruyn and Orban 1988) and for letter or word stimuli identification, is within 100ms (Gathercole and Broadbent 1984). Hence, the processing time for both motion and stationary stimuli is more or less the same. So, the post-target processing deficit for shorter time scale observed in motion domain might be due to an interaction of probe and target.

Snowden & Braddick, 1989 proposed two alternative mechanisms for motion stimuli processing, that is either by engaging neurons with longer latenies or by 'cooperative interaction' of units tuned to similar directions and having similar spans and delays. Raymond & Isaak, 1998, showed that coherence thresholds for second motion stimuli were elevated when it was preceded by motion stimuli moving in similar direction, but were lowered when preceded by motion stimuli in the opposite direction, thereby supporting the 'cooperative interaction' theory (Snowden and Braddick 1989).

To verify if the shorter time scale for the attentional blink in our data was due to interaction between target and probe directions, we did a post-hoc analysis, where we segregated the performance of correct detection of the probe for dual task, depending on the target direction which could be any of the four directions 0° (upper direction), 90° (right hand direction), 180°(downward direction), or 270°(left hand direction) (figure 3b). Trials with 90° (right hand direction) as target were excluded from the analysis since these trials did not had the probe direction, as in these trials probe was presented as the target.

The performance for correct probe detection for the dual task was segregated on the basis of the target direction for experiment 2 and experiment 3 is plotted in figure 5 A-C and figure 5 D-F respectively. In both motion task experiments (figure 5A and 5B), significant post-target processing deficit (paired t-test, $p<0.05$) was observed when the target directions were orthogonal to the probe direction (0° & 180°) but not when it was opposite to the probe direction (270°), indicating the existence of a possible interaction between target and probe directions. Though for experiment 3, the performance for the single and dual task did not differ significantly (paired t-test, $p<0.05$), at lag 1 and 2, which could be due to less number of subjects.

A three variable ANOVA (condition vs Target direction vs SOA), was conducted on the data set from experiment 2 and experiment 3. For experiment 2, there was a significant effect of the condition (dual task, single task), $F(1,88)=75.43$, $p<0.05$, direction (0°, 180°, 270°), $F(2,88)=5.19$, $p<0.01$. The results also showed significant condition vs SOA interaction, $F(4,88)=3.74$, $p<0.01$ and condition vs direction interaction, $F(2,88)=5.19$, $p<0.01$. For experiment 3, there was a significant

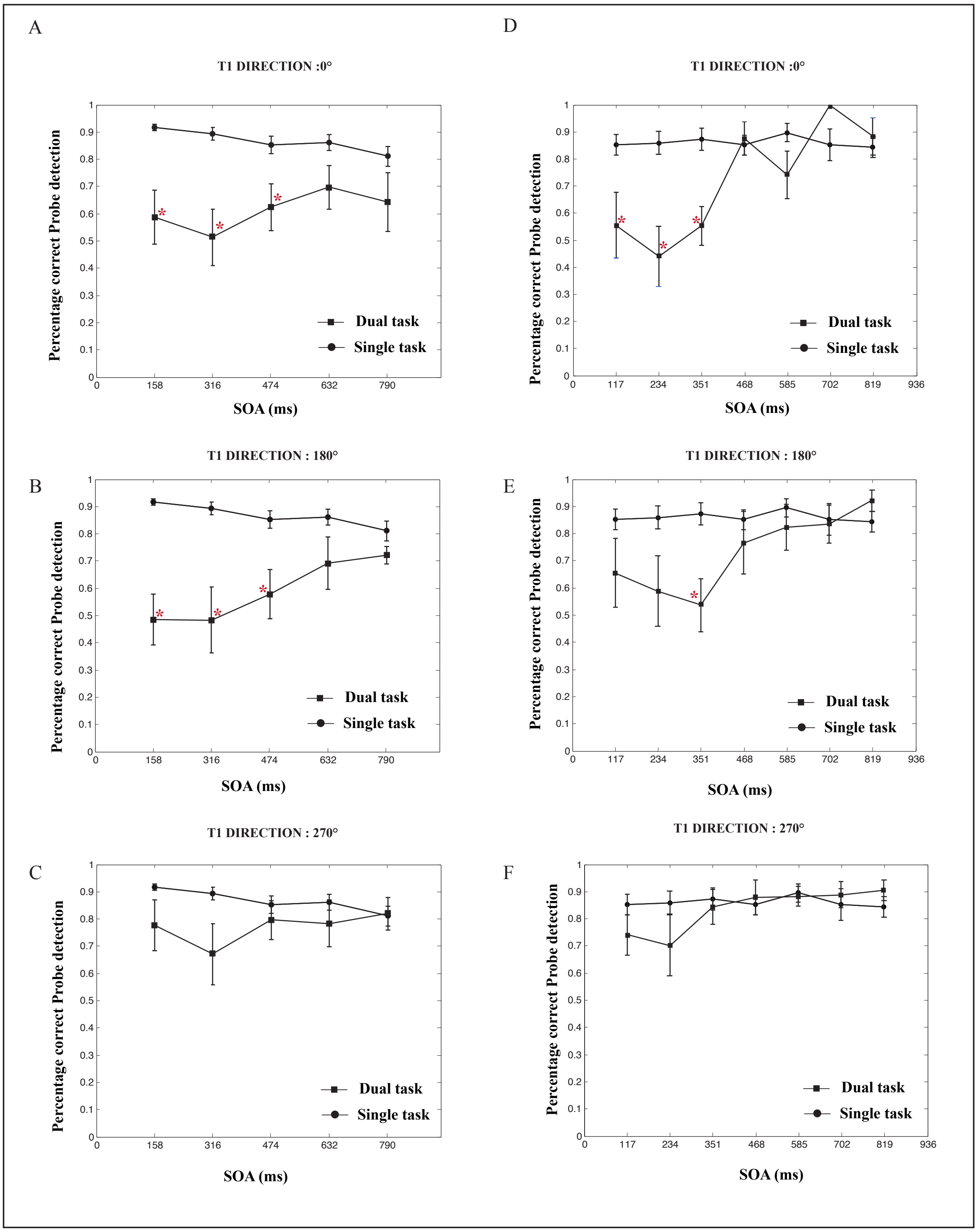


Figure 9: Performance for correct detection of probe for dual & single task in experiments 2 (A-C) & 3 (D-F), segregated on the basis of ‘target’ direction. The lags for which, the performance of single & dual task differ significantly from each other (paired t-test, $p<0.05$) is marked with (*).

effect of the condition (dual task, single task), $F(1,108)=23.02$, $p<0.05$, direction (0°, 180°, 270°), $F(2, 108)=3.10$, $p<0.05$ & SOA, $F(6, 108)=6.05$, $p<0.01$. The results also showed significant condition vs SOA interaction, $F(6, 108)=6.66$, $p<0.01$ & condition vs direction interaction, $F(2, 108)=3.10$, $p<0.05$.

These results taken together, demonstrates a target dependent processing of the probe, indicating a possible interaction between the two. These results are in agreement with the study by Iyer et al., 2011, who showed that the interaction amongst the motion stimuli could be either facilitatory or suppressive and is dependent on the time lag between them. In their experiments, they presented RSVP of motion stimuli and asked the subjects to press a key whenever an upward motion was presented and reported that the detection of the upward motion was facilitated when the preceding stimuli was moving in the opposite direction and was suppressed when the preceding stimuli moved in the same direction. These suppressive interactions persisted for the time lag of 80-278ms between two motion stimuli, which is similar to the post target processing time period that we observed in our data.

Lag-1 effect

In attentional blink experiments, it has been observed that generally the probe is detected reliably when it is presented immediately after the target within a time window of 100ms (Raymond, Shapiro et al. 1992; Chun and Potter 1995; Potter, Staub et al. 2002; Nieuwenstein, Chun et al. 2005; Bowman and Wyble 2007). This detection performance is comparable and reliable for both dual task (where the probe is processed after processing the target) and for the single task where only probe is processed and the target is ignored and is referred to as lag-1 sparing effect. It has been shown that for this effect to prevail, it is imperative that the probe appears within 100ms after the presentation of the target (Potter, Staub et al. 2002; Nieuwenstein, Chun et al. 2005; Bowman and Wyble 2007).

There are two alternative hypotheses to explain the lag-1 sparing effect, the first one being the 'attentional gate hypothesis', which proposes existence of a 'gate – like ' ballistic processing mechanism which opens when T1 gains access into the system and remains open for about 150ms -200ms and if T2 gain access into the processing within this time window, then it is processed along with T1, as both T1 and T2 are integrated into a single perceptual 'episode' (Chun and Potter 1995), the second one being the competition model (Potter, Staub et al. 2002). Hommel and Akyürek, 2005, provided evidence, that above mentioned alternative hypotheses are not mutually exclusive, rather the 'attentional gate hypothesis' is a special case of competitive model. If two targets T1 and T2 come in close temporal proximity, then they compete for the attentional resources, and if one is more salient than the other, then the salient stimuli gains competitive advantage, while if both stimuli are of equal strength, then they are processed in conjunction as a single perceptual 'episode'. This is also supported by neurophysiological studies (Kessler, Schmitz et al. 2005).

Since motion stimuli are integrated across time, it could be a possibility that when two motion stimuli (target and the probe), come in close temporal proximity, they interact during this integration or competitive epoch, leading to suppression of the probe, when the preceding stimulus is either in same direction or in orthogonal directions, and facilitation of probe, when the preceding stimulus is in the opposite stimuli (Raymond and Isaak 1998; Raymond, O'Donnell et al. 1998; Iyer, Freeman et al. 2011). Which is also the case we found in our results that there was no post-target processing deficit in any of the lags, when the probe was preceded by target stimuli moving in the opposite direction (figure5C).

Hence our results suggests that the absence of lag-1 sparing might not be due to the fact that the probe is not presented within 100ms after the target, but could be explained by interaction amongst the direction tuned neurons which are being engaged in processing the motion stimuli in RSVP.

The absence and presence of a lag dependent post-target processing deficit of the probe in experiments 2 and 3, when preceded by target stimuli in opposite direction and orthogonal directions respectively, suggests that when two motion stimuli comes in close temporal succession they compete for attentional resources, since motion stimuli are shown to be processed by ‘cooperative integration’ of similar tuned neurons (Snowden and Braddick 1989), it leads to interaction amongst these neuronal population tuned to different directions leading to either suppression or facilitation of the processing of the target stimuli.

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SUMMARY

The three projects documented in this thesis investigated the role of three forms of attention in visual processing. Spatial, feature-based and temporal attention. The spatial and feature-based attentional characteristics were studied by conducting extracellular recordings from neurons of area MT and MSTd of macaque visual cortex. While the role of temporal attention was studied in a human psychophysics project.

In the physiology projects we first defined the tuning characteristics of neurons from area MT and MSTd for two stimulus dimensions, namely spiral motion stimuli (SMS) and linear motion stimuli (LMS) on the basis of directionality index, the relative frequency of tuned versus untuned neurons, and the individual cells responses to the two forms of stimuli. We found that MT and MSTd showed differential tuning to LMS and SMS. Area MSTd demonstrated better selectivity for SMS as compared to LMS. Conversely, area MT was better tuned to LMS than SMS.

Further, we compared spatial and feature-based attentional modulation in area MT and MSTd across SMS and LMS. We found that spatial attention modulates the responses of neurons in both the areas irrespective of the feature dimension defining the attended stimuli. On the other hand feature-based attention was restricted to the stimulus dimension for which an area showed better selectivity, that is SMS for MSTd and LMS for MT. We also observed that the correlation of firing rates with reaction times was restricted to an area's preferred stimulus dimension. The presence of a significant negative correlation of firing rate with reaction time in area MSTd when attention was directed to its preferred dimension (SMS), indicated that these neurons were involved in perceptual processing of SMS. Similarly, the presence of a significant negative correlation of firing rates with the reaction times in area MT when attention was directed to LMS, provides evidence that MT neurons were involved in perceptual processing of LMS.

Taken together, these results show that neurons across the visual cortex are tuned to a range of stimulus dimensions. This multiple stimulus selectivity is thought to be utilized to develop a saliency map (by interaction of bottom-up and top-down processes), which marks the behaviorally relevant aspects of visual space. These behaviorally relevant aspects of the visual space are then preferentially processed throughout the visual hierarchy, and our results suggests that a given area contributes to visual perception by flexibly processing only the stimulus dimension for which it shows best selectivity as a function of stimulus relevance.

Finally in human subjects we investigated the temporal characteristics of visual motion processing, using the 'attentional blink' paradigm. Attentional blink is a widely studied phenomenon, but almost

all studies to the date have been are restricted to stationary stimuli. We here extended this paradigm to motion stimuli. We found the presence of an attentional blink in the motion domain, in that the detection of second of the two target (motion) stimuli was severely degraded when it was presented within 450ms of the first target (motion) stimulus. However, our results were slightly different from the experiments with the stationary stimuli. First, there was an absence of the lag-1 sparing effect typically found with stationary stimuli and second, the time interval over which the attentional blink was observed was about 100ms shorter than typically reported for stationary stimuli. Post-hoc analysis showed that these effects in the motion domain were dependent upon the direction of motion of the first target. Our data showed that when the first target moved in the opposite direction to the second target, there was no attentional blink, but when the first target moved in an orthogonal direction to the second target, there was an attentional blink. These results are in agreement to previous studies showing that the processing of motion stimuli is facilitated when it is preceded by a stimulus moving in opposite directions, while processing of motion stimuli is suppressed when it is preceded by a stimulus moving in an orthogonal direction.

Taken together the results of this thesis provides an important contribution to our understanding of the role of attention in visual motion processing. It will be interesting to extend this study in other visual cortical areas and measure spatial and feature-based attention from same set of neurons across different stimulus dimension.

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Curriculum Vitae: Sonia Baloni

Education:

Since 2007	Graduate student, German Primate Center, Goettingen, Germany Advisor: Prof. Dr. Stefan Treue
2005-2007	Project assistant, National Brain Research Center, Haryana, India Advisor: Dr. Narender.K.Dhingra
2002-2005	M.Sc. Bioinformatics, Allahabad University, India
1999-2002	Bachelor's in Zoology, Delhi University, India

Courses and workshops:

September 2007	Bernstein Center For Computational Neuroscience (BCCN), Göttingen, Fall Course on Computational Neuroscience.
November 2007	EUPRIM-NET course on 'Positive Reinforcement Training with Primates'. Goettingen
January 2009	G-Node winter course in neural data analysis, Munich.
November 2009	BCCN course work 'Analysis and Models in Neurophysiology', Freiburg

Conference contributions

September 2009	Bernstein Conference on Computational Neuroscience (BCCN) Göttingen, Germany Poster: Multiplicative changes in area MST neuron's responses in primate visual cortex by spatial attention.
March 2010	Primate Neurobiology meeting, Tuebingen, Germany Poster: ' Spatial and feature-based attention in area MST of macaque visual cortex.'

November 2010	Society for Neuroscience (SFN), SanDiego, USA Poster: Magnitude of spatial but not feature-based attentional modulation in MSTd cells of Macaque visual cortex depends on a cell’s preferred spiral motion direction.’
March 2011	Primate Neurobiology meeting, Goettingen, Germany Poster: ‘ Spatial and feature-based attentional modulations in area MT and MST of macaque visual cortex.’
March 2011	Goettingen Neurobiology meeting, Goettingen, Germany Poster: ‘ Spatial and feature-based attentional modulations in area MT and MST of macaque visual cortex.’
November 2011	Society for Neuroscience, Washington D.C, USA Poster: ‘A quantitative comparison of attentional effects in areas MT and MSTd of macaque visual cortex.’

Publications:

2008	Intravitreal Injection of Flourochrome-Conjugated Peanut Agglutinin Results in Specific and Reversible Labeling of Mammalian Cones In Vivo. Krinshnamoorthy,V. et al. (2008) Investigative opthalmology and visual science 49(6).

Personal Details:

Date of birth: 4th September 1980

Place of birth: New Delhi, India