The role of attention and adaptation in shaping cortical representations and the perception of abrupt changes in the visual environment

D I S S E R T A T I O N
for the award of the degree
"Doctor rerum naturalium"
of the Georg-August-Universität Göttingen

within the doctoral program *Theoretical and Computational Neuroscience*
of the Georg-August University School of Science (GAUSS)

submitted by
Vahid Mehrpour

from Zanjan, Iran
Göttingen 2017

Thesis Committee

- Prof. Dr. Stefan Treue
  Cognitive Neuroscience Laboratory, German Primate Center (DPZ)

- Prof. Dr. Alexander Gail
  Sensorimotor Group, German Primate Center (DPZ)

- Prof. Dr. Fred Wolf
  Theoretical Neurophysics Group, Max Planck Institute for Dynamics and Self-Organization (MPIDS)

Members of the Examination Board

- Referee: Prof. Dr. Stefan Treue
  Cognitive Neuroscience Laboratory, German Primate Center (DPZ)

- 2nd Referee: Prof. Dr. Florentin Wörgötter
  Department of Computational Neuroscience, Third Institute of Physics – Biophysics

Further members of the Examination Board

- Prof. Dr. Alexander Gail
  Sensorimotor Group, German Primate Center (DPZ)

- Prof. Dr. Fred Wolf
  Theoretical Neurophysics Group, Max Planck Institute for Dynamics and Self-Organization (MPIDS)

- Prof. Dr. Hansjörg Scherberger
  Research Group Neurobiology, German Primate Center (DPZ)

- Prof. Dr. Martin Göpfert
  Department of Cellular Neurobiology, Schwann-Schleiden Research Centre

Date of oral examination: February 28, 2017

ACKNOWLEDGEMENT

My exciting journey to a doctoral degree in Neuroscience would not have been possible without the support and guidance of many people.

First and foremost I wish to express my deep gratitude to an excellent scientist and teacher, my great supervisor, Professor Stefan Treue, director of the German Primate Center (DPZ). Stefan gave me the opportunity to do my doctoral studies under his supervision in his outstanding laboratory and has been supportive since I joined his team in 2010. His constant support, encouragement, and knowledgeable advice have been always my ultimate solution to overcome any obstacle on the road to my scientific goals. His leadership, his vision, and his acute attention made my Ph.D. an unforgettable and life-changing period.

I owe Professor Julio Martinez-Trujillo a debt of gratitude not only for sharing with me the electrophysiological data he had recorded but also for his invaluable and insightful discussions about my doctoral project.

I would like to give special thanks to the members of my thesis committee, Professor Alexander Gail, and Professor Fred Wolf, for their more than great advice, comments, and suggestions on my doctoral study through all these years.

I would like to express my sincere gratitude to Professor Florentin Wörgötter, Professor Hansjörg Scherberger, and Professor Martin Göpfert, who kindly agreed to serve on the examination board of my doctoral thesis.

Many thanks to Beatrix Glaser for her untiring support and help in handling the administrative work. I also thank Ralf Brockhausen, the IT expert in our lab, for sorting out the computer problems and troubleshooting. I greatly

appreciate Sonia Baloni, Sina Plümer, and Leonore Burchardt, who have taught me monkey training and monkey electrophysiology.

I am grateful to my friends for our friendship, fruitful discussions, offering me advice, and supporting me throughout my Ph.D.

Very special thanks to my beloved mother and father, who raised me with love of science, dedicated themselves to me, always emotionally supported me, believed in me, and inspired me to follow my dreams. I warmly thank and appreciate my hero, my darling brother, Hamed for all his love, encouragement, and precious help in every step of my journey. Words cannot express how much I love them.

My heartfelt thanks to Maryam for her unwavering love and support. She always stood by me, encouraged me in difficult moments and rejoiced in my success. She has been my motivation and inspiration to keep moving forward. Her unconditional love, dedication, and support worth more than the few words mentioned here.

I dedicate this thesis to the memory of my grandmother and my uncle, who passed away during my doctoral studies. I also dedicate this thesis to my beloved family for their love and unending support.

Vahid Mehrpour
Göttingen, January 2017

I dedicate this thesis to the memory of my grandmother and my uncle and to my family for their constant support and love

"We need above all to know about changes; no one wants or needs to be reminded 16 hours a day that his shoes are on."

– David Hubel

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1 ABSTRACT

The visual system receives a wealth of visual information about objects with changing features in time. Attention is a mechanism allowing us to prioritize the processing of relevant information at the expense of other information. Most physiological research efforts have focused on the cortical processing of stimulus properties, which remain unchanged in time and its attentional modulation. Instead, this study systematically investigates the neuronal representation of change events and addresses, for the first time, how attention affects this representation. I did this in the context of visual motion processing in a well-studied visual motion area, MT that contains a high proportion of direction-selective cells with responses enhanced by attention.

In this thesis, electrophysiological recordings from area MT in two monkeys performing a motion direction change detection task were analyzed. While the monkeys maintained their gaze on a fixation point, a static random dot pattern (RDP) was displayed either inside or outside the receptive field (RF) of the neuron under study, cueing an upcoming target location. Subsequently, two RDPs moving in one of 12 directions were simultaneously presented inside and outside the RF. At a random time after motion onset, the direction of target or distractor changed by 25°. The animals were rewarded for detecting a target direction change and ignoring similar changes in distractor.

The data show that MT population response to motion (prior to direction change) is precise and attention enhances MT responses. Population responses around the direction change event indicate that distractor and target direction changes of 25° have MT representation of 31° and 39°, respectively. My finding

demonstrates that a change in motion direction has an overestimated representation in MT and that this overestimation is almost twice as high for attended vs. unattended stimuli.

Further analysis of the data shows that these observations cannot be simply explained by classical models of adaptation (fatigue-based models), but rather they might be accounted for by a modern normalization model of adaptation.

Although the design of the electrophysiological task was not suitable to identify the source of adaptation in this study, several lines of evidence suggest that the effects induced by adaptation are mostly generated locally in MT.

I conducted a human psychophysical study to examine the perception of direction change in a task, which was very similar to that of monkey electrophysiology. The results indicate that perceived direction change in human subjects was also overestimated by about 7°. The results of a second psychophysical experiment support the idea that there is a causal link between the overestimation of represented direction change in MT and the overestimation of perceived direction change.

Overall, This thesis demonstrates that: (1) although MT representation of motion is precise, a change in motion direction is overestimated in MT, (2) visual attention not only modulates neuronal responses, but also further exaggerates the direction change overestimation in MT, (3) changes in neuronal responses following the unattended and attended direction changes can be understood in the framework of motion adaptation (prior to the direction change) and its attentional modulation. These changes cannot be explained by fatigue models of adaptation. In contrast, a normalization model of adaptation might capture the response changes induced by the direction change, (4) perception of direction change is overestimated, and that this is causally linked to the overestimation of represented direction change in MT.

2 INTRODUCTION

We live in the mental world our brains create for us. The human brain is perhaps the most complex organized structure we know of in the universe. It contains about 120 billion neurons (Herculano-Houzel, 2009) with 21–26 billion in the outermost layer of the brain, the cerebral cortex (Pelvig et al., 2008). This complex organ does everything that makes us human, from seeing a landscape to learning a language, forming and retrieving a memory, thinking, and expression of emotion. The cerebral cortex is an arrangement of six layers of neurons, which processes the information it receives from different sensory organs to provide an internal representation of the outside world and ultimately, to produce perception and behavior.

Much of our knowledge of the world comes to us through vision. As much as 50% of primate cortex - visual cortex - is devoted to processing visual information (Felleman & Van Essen, 1991; Van Essen et al., 1992). Both parallel and serial (hierarchical) processing of visual information is recruited in the visual system. Parallel processing enables the visual system to segregate the information about different attributes of the visual scene (e.g. color, face, and motion) into different independent channels (pathways). In each pathway, hierarchical processing of visual signals makes it possible to have selective responses to features with increasing complexity along the pathway. For instance, cells in the first visual cortical area respond selectively to simple features of the visual scene like edges, whereas neurons in high cortical areas integrate the output of lower areas and exhibit selective responses to complex visual attributes like faces or visual motion patterns (optic flow) (Nassi & Callaway, 2009).

Due to the high cost of brain activity (Lennie, 2003), the visual system cannot process all the visual information available to the retina (Duncan & Humphreys, 1989). Top-down attention is a process which enables us to select a subset of the visual signals (relevant information) for further processing at the expense of the rest (irrelevant information) (Maunsell & Treue, 2006; Seidemann & Newsome, 1999; Treue, 2003). This indicates that hierarchical processing of visual information is bidirectional: feedforward flow of sensory information (bottom-up signals) is affected by feedback signals (top-down signals) (Hochstein & Ahissar, 2002).

Motion is an important feature of objects and therefore, processing and perception of the information about visual motion and its change are crucial. The middle temporal visual area (MT) plays a key role in processing the visual information about motion (Maunsell & Van Essen, 1983c; Mikami et al., 1986a, 1986b; Newsome et al., 1986) and its neuronal activity is linked to motion perception (Bosking & Maunsell, 2011; Britten et al., 1996; Dodd et al., 2001a; Galashan et al., 2013; Newsome & Paré, 1988; Newsome et al., 1989; Nichols & Newsome, 2002; Price & Born, 2010, 2013; Salzman et al., 1990; Zihl et al., 1983).

Although many studies have examined perception and encoding of visual motion, little is known about the neuronal representation and perception of a change in motion direction. There is a large body of research investigating the influence of attention on motion processing in MT and motion perception. To my knowledge, there is no published study concerned with the effect of attention on the representation of change event. The research presented here instead focuses on understanding the neural representation of a change in motion direction, how it is perceived, and how attention affects the representation.

I begin with a review of different visual areas involved in the processing of visual motion information. This includes a comprehensive look at the fundamentals of early visual processing, primary visual cortex (V1), and area MT. I also provide an overview of the link between MT activity and motion perception. Neuronal and behavioral effects associated with attention are treated next. I discuss how attention influences signal processing in visual cortex and

how behavior is affected by attention. A section is devoted to describing a phenomenon called adaptation, the dependence of behavior and neuronal activity on sensory history. This section deals with neuronal and perceptual effects of adaptation, the time course of adaptation, and its source in the visual area MT. I also discuss attentional modulation of perceptual aftereffects induced by adaptation.

2.1 Early visual processing

The striking capability of seeing objects begins at the back of our eyes, the retina. The retina is a laminated tissue of about 200 micrometers thick, with six types of cells. These cells make the visual system capable of converting the energy of photons into electrical signals through a process known as phototransduction (Purves et al., 2001). Retinal cells parse the information of the image on the retina into three parallel streams: magnocellular, parvocellular, and koniocellular pathways:

- The magnocellular (M) pathway arises from parasol retinal ganglion cells (RGCs) with large diameter axons and conveys information about visual motion (Blasdel & Lund, 1983; Conley & Fitzpatrick, 1989; Hendrickson et al., 1978; Hubel & Wiesel, 1972; Leventhal et al., 1981).

- The parvocellular (P) pathway originates from midget ganglion cells, which have small-diameter axons and carries the information of color and shape (Leventhal et al., 1981; Rodieck et al., 1985; Schiller & Malpeli, 1978).

- The koniocellular (K) pathway projects from bistratified ganglion cells (smallest diameter axons) and has an influence on the information processing in M and P pathways (Callaway, 1998; Conley & Fitzpatrick, 1989).

The axons originating from RGCs exit the retina from the optic disc. The axons travel through the optic nerve, the optic chiasm, and the optic tract to target the lateral geniculate nucleus of the thalamus (LGN). The axons of RGCs located in both nasal and temporal halves of the retina (nasal and temporal hemiretinae) form the optic nerve. In optic chiasm, the axons of nasal hemiretinae decussate to the opposite optic tracts. Each optic tract, therefore, transmits the visual information of the contralateral half of the visual field to the LGN.

The LGN is a laminar structure with 6 main layers (three layers for each of the two eyes - every other layer receives its inputs from one eye), which acts as a relay station in visual processing (Bisazza et al., 1998). The neuronal response

properties in the LGN are very similar to those of the RGCs they are connected to (Kaplan & Shapley, 1984; B. B. Lee et al., 1983). The LGN contains three major classes of neurons with monocular inputs: magnocellular (M), parvocellular (P), and koniocellular (K). As the names suggest these cells are located in the magnocellular, parvocellular, and koniocellular pathways, respectively. The magnocellular cells are mainly found in the two most ventral layers of the LGN (magnocellular or M-layers) and receive input from about 10% of the total population that project to the LGN (Dacey, 2000), whereas parvocellular cells are located in the outer four layers (parvocellular or P-layers) (Conley & Fitzpatrick, 1989; Leventhal et al., 1981) with a share of 70% of the total projections to the LGN (Dacey, 2000). The koniocellular cells are ventral to each magnocellular and parvocellular layers and, therefore, there exists six thin koniocellular or K-layers (Casagrande & Kaas, 1994; Hendry & Reid, 2000). The K-layers receive about 8% of the total population of cells that project to the LGN (Dacey, 2000).

The receptive fields (RF)[1] of M and P cells have a center-surround concentric organization. M cells have relatively large RFs, which lack chromatic RF organization. The RFs of P cells are, however, small and show color selective center and surround (color opponent RF) (Dacey & Packer, 2003; Schiller & Malpeli, 1978).

2.2 Processing of visual information in V1

The primary visual cortex (V1, striate cortex, Brodmann area 17) is the first cortical area, which receives about 90% of the RGC projections through the LGN and disseminates the visual information to other brain areas for further processing (Tong, 2003). V1 is, like other cortical areas, a laminar structure of neurons with six distinct layers: 1, 2/3, 4, 5, and 6, unlike other cortical areas, however, layer 2/3 and 4 are subdivided. Layer 4 comprises 4 sub-layers: 4A, 4B, 4Cα, and 4Cß. As illustrated in Figure 1, M cells of the LGN send a large portion of their axons to layer 4Cα and a small portion to the layer 6 of V1. P cells of the LGN project mainly to layer 4Cß and to a lesser extent to layers 4A and 6 of V1.

[1] The receptive field of a neuron is an area in the retina from which the neuron's firing could be influenced by a proper visual stimulus (Hubel & Wiesel, 1959).

The koniocellular layer of the LGN afferent to layer 1 and cytochrome oxidase (CO) blobs of layer 2/3 in V1 (Callaway, 1998; Nassi & Callaway, 2009).

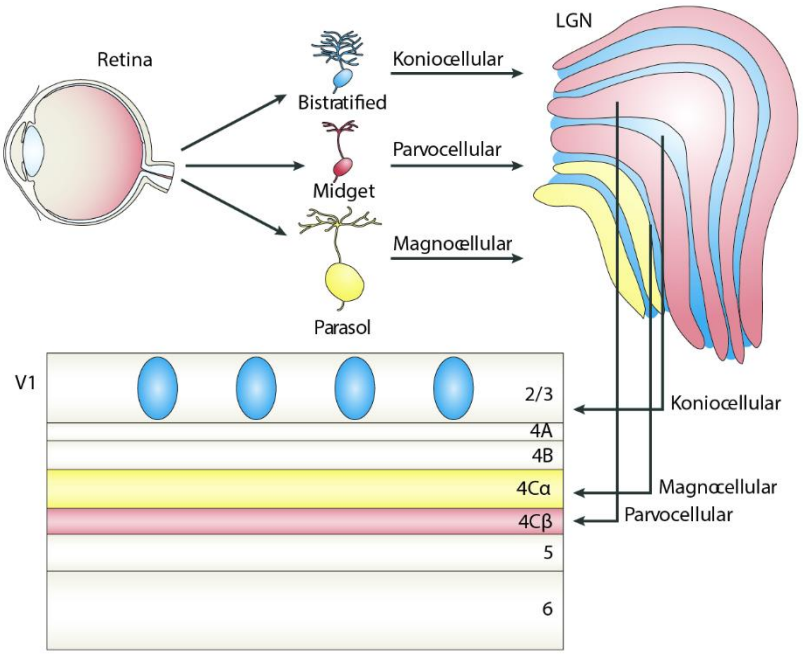

Figure 1 | Parallel pathways from the retina to V1: Magnocellular (M), parvocellular (P), and koniocellular (K) pathways originate from parasol, midget, and bistratified RGCs, respectively (indicated by yellow, red, and blue). M, P, and K pathways project to M, P, and K layers of the LGN (each eye projects to three of six layers of the LGN in an alternating fashion (Livingstone & Hubel, 1988)). Connections between the LGN and different layers of V1: M layers send a large portion of their axons to layer 4Cα, P layers mainly project to 4Cβ, and K layers project to layer 1 and CO blobs of layer 2/3. The figure is adapted from Nassi & Callaway, 2009.

Earlier studies by Livingstone and Hubel proposed that the early parallel pathways entered into the input layers of V1 maintain segregation in this cortical area (Livingstone & Hubel, 1988). They suggested that these distinctly segregated pathways form the basis for visual information streams in extrastriate cortex. In this scheme layer 4Cα transmits information from the magnocellular pathway to layer 4B of V1, layer 4Cß conveys information from the parvocellular pathway to the CO blobs and interblobs of layer 2/3 (Figure 2, left). More recent studies, however, suggest that the early parallel pathways converge in V1. Layer 4C projects to CO blobs and interblobs in layer 2/3, where CO blobs also receive direct inputs from the koniocellular layer of the LGN. Layer 4B of V1 receives axons from both layers 4Cα and 4Cß (Figure 2, right). The integration of input information in V1 occurs in a systematic and organized fashion such that V1 output forms segregated but interacting streams of visual information in the extrastriate cortex, namely ventral and dorsal streams (Nassi & Callaway, 2009).

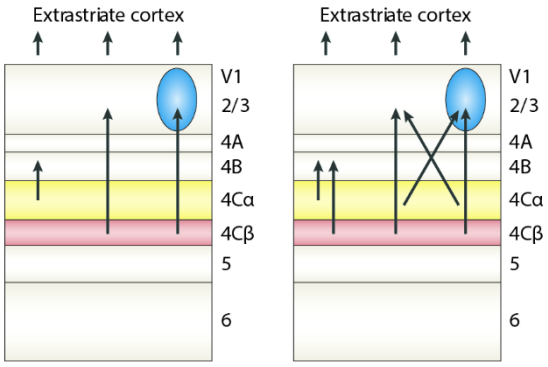

Figure 2 | Cortical processing strategies in V1: (Left) Early models of visual information processing in V1 proposed that parallel pathways inputs into V1 retain segregation in V1. Magnocellular (yellow) and parvocellular (red) inputs to the layers 4Cα and 4Cβ of V1 are projected to the layer 4B, and layer 2/3, respectively and from there to other extrastriate cortical areas. (Right) Recent models suggest that parallel inputs converge in V1 and form segregated, but interacting streams in extrastriate cortex. The figure is adapted from Nassi & Callaway, 2009.

The dorsal pathway includes areas in parietal extrastriate cortex such as middle temporal area (V5 or MT), medial superior temporal area (MST), the fundus of the superior temporal area (FST), the superior temporal polysensory area (STP), the ventral intraparietal area (VIP), the lateral intraparietal area (LIP), and visual area 7A. The ventral pathway consists of areas in the temporal extrastriate cortex, for instance, visual area 4 (V4), and inferior temporal cortex (IT). There is strong evidence that the dorsal stream is specialized for navigation and visually guided actions, whereas the ventral stream is devoted to the processing object identities (Milner & Goodale, 2008).

Primary visual cortex is the first visual cortical area where information from two eyes converges at the level of single cells. V1 neurons have complex response characteristics compared with those in the LGN. They show selective responses for orientation, direction, spatial frequency, and have response preference for one eye over the other (ocular dominance) (Barlow et al., 1967; Cumming, 2002; De Valois et al., 1979; Hubel & Wiesel, 1962, 1968). V1 cells have small RFs to provide a detailed representation of the visual scene (Hubel & Wiesel, 1962, 1968; Tong, 2003).

A traditional classification of V1 cells based on the complexity of their RFs divides them into two distinct classes: ‘simple’ and ‘complex’ cells. Simple cells have RFs with the side-to-side arrangement of inhibitory and excitatory regions segregated by straight-lines. Visual stimulation of excitatory region by light

increases the activity of the cell, whereas stimulation of inhibitory region suppresses its firing. The response of the simple cell, therefore, depends on the location of a stimulus (oriented edge or stripe) within the RF (phase-sensitive). Complex cells also have excitatory and inhibitory subdivisions, but they are coextensive in space. This means that the response of a complex cell to a stimulus (oriented edge or stripe) is independent of the stimulation location in the RF, phase-insensitive (Figure 3) (Wolfe et al., 2009).

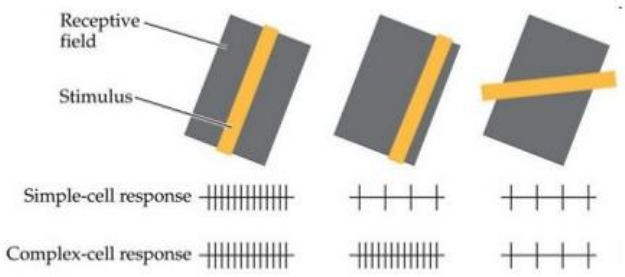

Figure 3 | Phase-sensitive and phase-insensitive responses of simple and complex V1 cells: although both simple cell and complex cell respond preferentially to a stripe with the same orientation, simple cell's response depends on the location of stripe inside the RF, whereas the response of the complex cell is independent of stripe's location. The figure is adapted from Wolfe et al, 2009 (p. 65).

One of the principles of cortical functional organization is columnar organization. It was discovered by Hubel and Wiesel (Hubel & Wiesel, 1968, 1974, 1977) in primary visual cortex following the discovery by Mountcastle (Mountcastle, 1957) in the first somatic sensory area of the cat's cerebral cortex. According to columnar organization of V1, cells in a column perpendicular to the cortex have overlapping RFs and similar physiological properties (e.g. preferred orientation (Hubel & Wiesel, 1977), ocular preference (Hubel & Wiesel, 1977), preferred color (Michael, 1981), preferred direction (Payne et al., 1981; Shmuel & Grinvald, 1996; Weliky et al., 1996), preferred spatial frequency (Shoham et al., 1997; Tolhurst & Thompson, 1982; Tootell et al., 1981)). However, properties of V1 cells tangent to the cortex change in a systematic and continuous fashion (Figure 4).

2.3 Processing of visual information in MT – General properties

Two different groups discovered the middle temporal visual area (MT, or V5) in the owl monkey (Allman & Kaas, 1971) and rhesus monkey (Dubner & Zeki, 1971) around the same time in 1971. MT was described as a visual cortical area

containing a preponderance of neurons with selective responses to motion directions (Baker et al., 1981; Felleman & Kaas, 1984; Maunsell & Van Essen, 1983a, 1983b; Van Essen et al., 1981; Zeki, 1974, 1980), which plays an important role in the initiation of slow, smooth-pursuit eye movements (Lisberger et al., 1987). Area MT receives inputs from various cortical and subcortical areas including LGN, V1, V2, V3, and etc. and projects to downstream of MT in the dorsal pathway, such as MST and VIP (Figure 5) (Maunsell & Van Essen, 1983c).

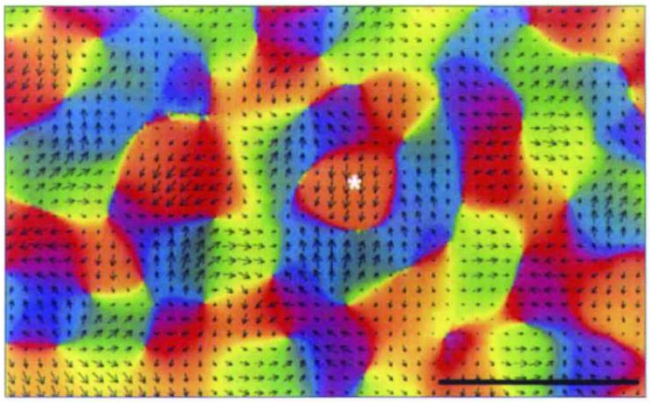

Figure 4 | Organization of direction preferences in a region of ferret V1 using optical imaging: direction preferences are color-coded. The direction of arrows overlaid on the color map indicates the preferred directions of cells and length of arrows shows the magnitude of direction selectivity. The figure is adapted from Weliky et al., 1996.

MT inputs are dominated by direct projections originating from direction selective (Movshon & Newsome, 1996), speed tuned (Orban et al., 1986) neurons in V1, which show preferences for binocular disparity (Prince et al., 2000). As much as 90% of V1 projections to MT originate from the layer 4B (Maunsell & Van Essen, 1983c; Shipp & Zeki, 1989; Tigges et al., 1981). The cells in the layer 4B of V1 sending axons to MT have distinct characteristics. These cells are large and have dense dendritic trees located close to the bottom of the layer (Nassi & Callaway, 2009). It has been shown that V1 inactivation (Girard et al., 1992) or its removal (Rodman et al., 1989) impairs both responsiveness, and to less extent, direction-selectivity of MT neurons. Connections between the superior colliculus (SC) and MT and callosal connections are thought to account for the MT residual direction-selective responses after inactivation or removal of V1(Born & Bradley, 2005; Girard et al., 1992; Movshon & Newsome, 1996; Rodman et al., 1990).

Several studies showed columnar organization of direction selectivity (Albright et al., 1984; Dubner & Zeki, 1971; Geesaman et al., 1997), binocular

disparity[2] (DeAngelis & Newsome, 1999), and to some extent, speed preference (Liu & Newsome, 2003) in area MT of macaque monkeys. MT cells are reported to be tuned for not only motion direction but also motion speed and binocular disparity (Baker et al., 1981; Felleman & Kaas, 1984; Maunsell & Van Essen, 1983a). Several reports, however, indicated that stimulus shape (Albright, 1984) and color (Zeki, 1983) do not have noticeable effects on MT responses. By functional binocular alignment, a recent research by Czuba et al. (Czuba et al., 2014) rule out the contributions of static disparity tuning to the 3D motion tuning and proposes that MT cells encode the information of 3D motion.

Moving along the dorsal hierarchy, the receptive fields become larger, e.g. an MT cell with RF centered at 10° eccentricities may have a receptive field size of 10° diameter, whereas the RF of V1 neuron centered at the same location may be around 1° diameter (Andersen, 1997; Born & Bradley, 2005). About half of the MT cells have RFs with center-surround antagonism, which means that a moving stimulus located in the center region of the RF (classical RF, or stimulation field) maximally drives the cell and following the invading of stimulus into the surrounding region (suppressive field) responses become suppressed (Allman et al., 1985; Born, 2000; Bradley & Andersen, 1998; DeAngelis & Uka, 2003; Raiguel et al., 1995; Tanaka et al., 1986). The highest suppression occurs when the stimuli in the center and surround regions have the same direction and disparity, meaning that the driven response of the neuron depends on the saliency of the stimulus in the center relative to the surround stimulus (Bradley & Andersen, 1998). The other half of the MT neurons have receptive fields with reinforcing surrounds, meaning that they optimally respond to wide-field motion (Born, 2000).

[2] Difference between the image location of a visual stimulus on the two retinae, which plays an important role in stereoscopic depth perception

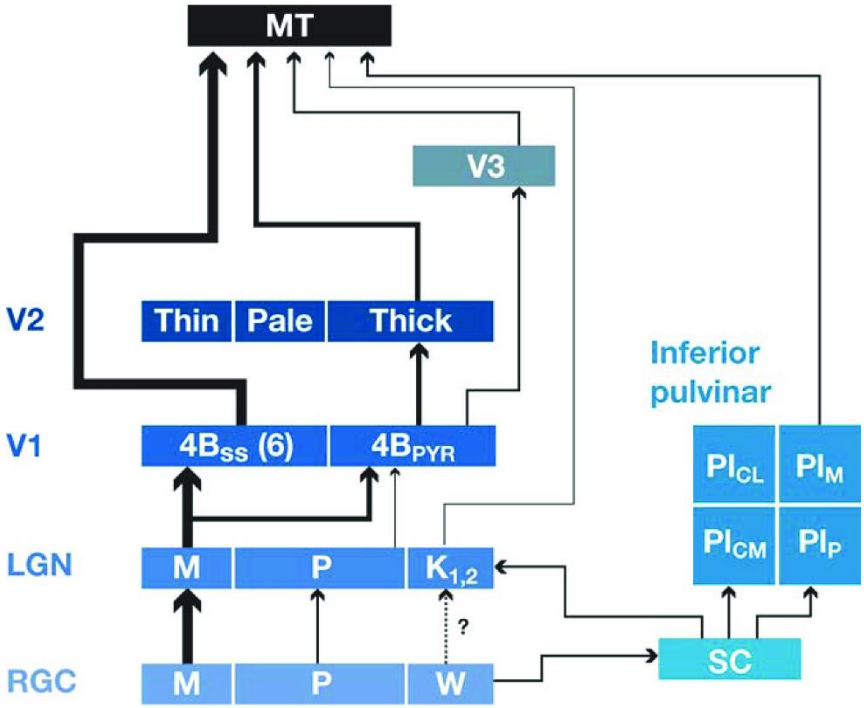

Figure 5 | Major inputs into area MT: thickness of arrow is roughly proportional to the magnitude of the inputs. Thickest arrows indicate direct cortical pathways. The figure is adapted from Born & Bradley, 2005.

Responses of cells in area MT are affected by several nonretinal sources, such as attention, smooth pursuit eye movements, and saccadic eye movements (extraretinal effects). In early studies of attentional effects on MT responses, Treue & Maunsell (Treue & Maunsell, 1996) and Seidemann & Newsome (Seidemann & Newsome, 1999) showed that attention enhances the responses of MT cells to the stimulus inside the RF. Smooth pursuit eye movements are the movements of the eye enabling us to track the moving of visual targets. These eye movements allow us to have a stabilized image of the moving objects on or near the fovea (Ono, 2015). It has been shown that responses of MT cells play a critical role in initiating the pursuit eye movements. Newsome et al. (DeAngelis et al., 1998; Parker & Newsome, 1998) have indicated that pursuit eye movements are initiated following the discharge of a subset of direction-selective MT cells, pursuit cells. The discharge of pursuit cells is reduced once the eye velocity reaches the target. These cells have foveal RFs and their responses are modulated by pursuit eye movements. Saccadic suppression is a phenomenon where the perception of image motion on the retina is dependent on its origin: the image motion induced by saccade (rapid gaze shift) is not perceived while the image motion induced by an external stimulus is perceived. Thiele and colleagues

(Thiele et al., 2002) reported a subset of direction-selective MT cells, 'saccadic suppressive cells', with responses silenced during saccadic image motion whereas responded well to an identical external image motion. They proposed that existence of saccadic suppressive cells accounts for the saccadic suppression. (A more recent study demonstrates that V1 cells also exhibit different responses to identical retinal motion depending it is internally or externally generated (Troncoso et al., 2015).)

2.4 Processing of visual information in MT – Link with motion perception

MT cells play a critical role in visual motion perception (Britten et al., 1992, 1996; Dodd et al., 2001a; Newsome et al., 1989). Simultaneous recording of psychophysical and physiological data from MT cells in monkeys performing motion direction discrimination task[3] revealed that the activity of a small subset of direction-selective MT cells might account for the psychophysical judgments of the animals. In such an experiment, comparison between neurometric function (constructed based on signal detection theory and using the distributions of MT cell responses to preferred and anti-preferred directions) and psychometric function (measured while the animals performing the task) demonstrated that the sensitivity of most MT cells was equal or higher than that of the monkeys (Newsome et al., 1989). In another experiment, Britten and colleagues (Britten et al., 1996) showed a correlation between trial-to-trial variability in the neuron's response and the psychophysical judgment of monkeys executing motion direction discrimination task: in a given trial the decision of monkey to choose in favor of the preferred direction correlates with the response of neuron to the preferred direction. Dodd and colleagues (Dodd et al., 2001a) designed an experiment to address a similar question: how trial-to-trial response variability of disparity-selective MT cells is linked to the depth perception. In line with the results of the experiment conducted by Britten and colleagues (Britten et al., 1996), they found that neuronal response and disparity judgment are correlated.

[3] Motion direction discrimination task: while the animal keeps its gaze on a fixation point, a random dot pattern appears in the receptive field of the neuron under study for a short period of time. Motion direction and coherence level of the random dot pattern (proportion of dots moving in a specific direction whereas others in random directions) varies from trial to trial. The monkey's task is to report the perceived motion direction.

Bosking & Maunsell (Bosking & Maunsell, 2011) probed the relationship between the activity of MT cells and behavior in a direction detection task. They showed that correlation between detection of motion and neuronal activity depends on the motion direction used in the task relative to the neuron's preferred direction. The correlation is strong when they are aligned, disappears in directions 90^{o} away from the preferred direction, and becomes negative in directions close to the anti-preferred direction.

To explore the causal link between the activity of direction-selective MT cells and the perceived motion direction, Salzman and colleagues (Salzman et al., 1990) micro-stimulated columns of MT cells while the monkeys were performing direction discrimination task. They compared the psychometric function computed based on electrically stimulated trials with that based on only visually stimulated trials. Their results indicate that microstimulation biased the monkeys' decision in favor of the preferred direction of the MT column electrically stimulated. They also reported that the variation in the activity of speed tuned MT cells and fluctuations in the perceptual judgment of speed in a two alternative forced choice speed discrimination task are correlated. They showed that microstimulating cluster of MT cells with homogenous speed tuning profile biased the animal's judgment toward the preferred speed of the electrically stimulated cells. The results of this study revealed the causal link between the activities of speed tuned MT cells and the perception of speed. Another study conducted in the same lab (Nichols & Newsome, 2002) showed that microstimulation of direction columns in MT influenced veridical judgments of perceived motion direction even when the visual stimulation was powerful.

Lesion studies in humans and animals have revealed that MT damage produces dramatic deficits and even loss of motion perception. A case study by Zihl (Zihl et al., 1983) reported a 43-year-old patient, who had a bilateral posterior brain damage. The patient's perception of any type of visual motion was abolished, for example: "when I'm looking at the car first, it seems far away. But then, when I want to cross the road, suddenly the car is very near." In a monkey study, Newsome & Paré (Newsome & Paré, 1988) produced lesions by injecting the neurotoxin, ibotenic acid, into area MT. They measured pre- and post-lesion

thresholds in direction discrimination and orientation discrimination tasks in each of several spatial locations contralateral and ipsilateral to the recording/lesion site. They found that chemical lesions of MT substantially elevated the direction discrimination threshold in contralateral side, whereas that of the ipsilateral side was unaffected. The results also indicate that the lesion had a little influence on the contrast discrimination threshold in the contralateral side and no effect on the contrast discrimination threshold in the ipsilateral side. This supports the notion that MT has a critical role in the perception of visual motion.

2.5 Visual attention – Psychophysics

Visual attention is the process of selecting a tiny portion of the visual information provided by the eyes for a prioritized cortical processing. Behavioral impacts of visual attention include a wide variety of effects ranging from faster reaction times (Carrasco & McElree, 2001; Carrasco & Yeshurun, 1998; Carrasco et al., 2004; Morgan et al., 1998; Nakayama & Mackeben, 1989; Posner, 1980; Posner et al., 1978, 1980), increased spatial resolution (Carrasco et al., 2002; Yeshurun & Carrasco, 1998, 1999, 2000), enhanced contrast sensitivity (Cameron et al., 2002; Carrasco et al., 2000; Foley & Schwarz, 1998; D. K. Lee et al., 1997, 1999; Lu & Dosher, 1998; J. A. Solomon et al., 1997) to change of stimulus appearance (Carrasco et al., 2004).

The effects of attention on behavioral performance has been extensively studied in many different human psychophysical experiments. Posner and colleagues (Posner, 1980; Posner et al., 1978, 1980) designed an experiment in which human subjects were instructed to use cues with different validities to report the detection of the target stimulus (shown in either visual hemifield) while fixating on a central light spot. In a given trial, the cue was one of two symbols: [+], the stimulus was likely to be displayed in either hemifield with the same probability (cue of 50 % validity, neutral trials). The second symbol, an arrow heading to the left or right hemifield, was 80% valid cue, meaning that in 80% of the time stimulus was shown in the hemifield cued by the arrowhead (valid cue trials). In the remaining 20% of trials, the target appeared in the

opposite hemifield (invalid cue trials). This task makes it possible to compare the behavioral performance (reaction time in this experiment) across various attentional conditions (graded attention). Their results indicated that valid cue trials had the shortest and invalid cue trials the longest reaction times with neutral trials having reaction times between them. Attention, therefore, reduced the reaction time for the detection of visual signals in their experiment.

It has been reported that directing attention to the location of an upcoming target improves performance (reaction time and accuracy) in both feature and conjunction visual search tasks[4] (Carrasco & McElree, 2001; Carrasco & Yeshurun, 1998; Carrasco et al., 2004; Morgan et al., 1998; Nakayama & Mackeben, 1989). Subjects searched red vertical bar (target) among the red tilted bars (distractors) in feature search task, while they searched it in a pattern of blue vertical and red tilted bars in conjunction search task. In a given trial they employed one of two different cues to achieve different attentional conditions. Appearing one type of cue, neutral cue, in the center of display indicated that target could be either present or absent in the upcoming visual stimulus and if present, it could be in any location in the array. The validity of the second cue was 5:18, meaning that the probability the target was shown in that trial at the cued location was 5/18. In the remaining cued trials the target was either absent or was displayed in a different location than the cue (Carrasco & Yeshurun, 1998). Carrasco & Yeshurun found that, in both tasks, manipulating attention with a valid cue made the detection of target faster and more accurate compared with a neutral or invalid cue.

It has been also demonstrated that another behavioral signature of attention is to increase the spatial resolution of the target regardless of its impact on performance (improving or impairing) (Carrasco et al., 2002; Yeshurun & Carrasco, 1998, 1999, 2000). For example, the results of a study by Yeshurun & Carrasco (Yeshurun & Carrasco, 1998) demonstrate that the effect of attention

[4] Visual search task: While keeping eye gaze on a fixation point, the subjects have to report whether or not the target was among the distractor items in the displayed array (yes-no task). In 2 alternative forced choice task (2AFC) two arrays of items were presented in two successive intervals, one containing the target. The subject's task is to report which interval had the target (Carrasco & Yeshurun, 1998; Morgan et al., 1998).

on subjects' performance in texture segregation task[5] depends on the eccentricity of the target. For peripheral locations, attention improved the performance (reaction time and accuracy), whereas attention impairs the performance for more foveal targets. This effect could be explained in the framework that associates attention with an increase in spatial resolution.

It has been reported that the deployment of attention also enhances contrast sensitivity (Cameron et al., 2002; Carrasco et al., 2000; Foley & Schwarz, 1998; D. K. Lee et al., 1997, 1999; Lu & Dosher, 1998; J. A. Solomon et al., 1997). In studies conducted in Carrasco's lab (Cameron et al., 2002; Carrasco et al., 2000) various tasks were used to assess the contrast sensitivity function (sensitivity, the reciprocal of the threshold[6], versus spatial frequency) at different locations. Two types of neutral and peripheral cues were used to explore how attention influences the contrast sensitivity across different spatial frequencies of the stimulus (Gabor gratings). The neutral cue shown in the middle of the screen did not convey any information, while the peripheral cue was 100% valid indicating the location of an upcoming target among 8 possible locations evenly spaced at the same eccentricity from the fixation point. Their results show that attention enhances the contrast sensitivity across different spatial frequencies.

Carrasco et al. (Carrasco et al., 2004) demonstrated that attention not only affects the contrast sensitivity but also changes the perceived contrast (stimulus appearance). In an orientation discrimination task, two stimuli (Gabor gratings) were presented on opposite sides of a central fixation point. One stimulus had always a fixed contrast near threshold (standard stimulus) while the contrast of the other stimulus was variable across trials (test stimulus). They used different cues prior to the presentation of the stimuli: neutral and peripheral. Neutral cue was a spot in the same location as the fixation point, and the peripheral cue was a spot positioned randomly at the location of standard or test stimuli. Both types

[5] Texture segregation task: A stimulus consisting of an array of small tilted bars, background texture and a small target patch composed of bars perpendicular to the background texture, target texture (present randomly in a fraction of trials) is employed in this task. The target texture is embedded at different locations in trials. Subject is required to report whether or not the target texture was present in each trial. It has been shown that performance of subjects (reaction time and accuracy) is diminished in high spatial resolution of the texture.

[6] Threshold contrast is the contrast required to see the target reliably (Pelli & Bex, 2013), for instance 80% on a given orientation discrimination task (Cameron et al., 2002).

of cues were displayed for a short period of time and did not carry any information about contrast or orientation (subjects were informed about this). The subjects' task was to indicate whether the orientation of the stimulus with a high contrast was tilted to the left or right (two-by-two alternative forced choice procedure). They compared the point of subjective equalities (PSEs)[7] of the psychometric functions, i.e. probability the contrast of test stimulus is higher than the standard stimulus versus contrast of the test stimulus, associated with test cued and standard cued with the PSE of the neutral psychometric function. They found that peripheral cue to the test stimulus shifted the PSE measured when the neutral cue was used to smaller values, whereas cueing the standard stimulus elevated the PSE. This indicates that attention can improve the apparent contrast of the stimulus. They also showed that discrimination performance was improved in the cued location, meaning that attentional modulation of contrast improves discrimination performance.

2.6 Visual attention – Physiology

Behavioral signatures of attention are thought to be related to the changes in neural responses caused by the attention. Neural correlates of attention encompass changes in spike rate (Desimone & Duncan, 1995; Martinez-Trujillo & Treue, 2004; McAdams & Maunsell, 1999; Reynolds & Chelazzi, 2004; Treue, 2001; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996), spike rate variability (Cohen & Maunsell, 2009; Herrero et al., 2013; Mitchell et al., 2007, 2009; Niebergall et al., 2011; Zénon & Krauzlis, 2012), receptive field size (Anton-Erxleben et al., 2009; Womelsdorf et al., 2006, 2008), response latency (Galashan et al., 2013; Sundberg et al., 2012), and spike count (noise) correlation between pairs of neurons (Cohen & Maunsell, 2009; Herrero et al., 2013; Mitchell et al., 2009; Zénon & Krauzlis, 2012).

Measurements of attention impact on neuronal responses in monkeys revealed that shifting of attention toward the neuron's receptive field makes the responses stronger compared with the neuron's responses when attention is away

[7] Point of subjective equality (PSE): Any of the points along a stimulus dimension at which a variable stimulus is judged by an observer to be equal to a standard stimulus.("point of subjective equality," 2008)

from the receptive field (Desimone & Duncan, 1995; Martinez-Trujillo & Treue, 2004; McAdams & Maunsell, 1999; Reynolds & Chelazzi, 2004; Treue, 2001; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996). Treue & Maunsell examined how attention modulates the responses of MT cells to visual motion (Treue & Maunsell, 1996). They compared the responses of individual MT neurons to unattended and attended stimuli (a dot moving in the preferred direction of the neuron) inside the receptive field while the monkeys performed a speed change detection task[8]. They reported a median attentional enhancement of MT responses of 19%.

The influence of attention on neuronal responses depends on mainly on two factors: (1) difficulty of the attentional task, (2) the area in the visual hierarchy (Maunsell, 2015). The dependency of the attentional modulation on the task becomes clear when the effects of attention are compared in a particular visual area between two different attentional tasks. For example, an attention study by Seidemann and colleagues (Seidemann & Newsome, 1999) reported that the median attentional modulation of MT responses in their experiment (motion direction discrimination task) was 8.7%, notably smaller than that of reported by Treue & Maunsell (Treue & Maunsell, 1996). The difference between the results was ascribed to differences between the tasks used in the two studies. As suggested by Treue & Maunsell (Treue & Maunsell, 1996) more demanding the task is, the stronger attentional modulation would be.

Modulation of neuronal responses associated with attention varies between areas in the visual hierarchy. It has been shown that attentional modulation measured while the subject performed a particular task (same difficulty) increases in magnitude when progressing along the visual hierarchy. Maunsell & Cook (Maunsell & Cook, 2002) made a comparison between average attentional modulation in different visual cortical areas while a monkey performed a given attentional task (Figure 6). As depicted in Figure 6 attentional modulation in the

[8] Motion change detection task: While the animal has kept its eye gaze on the fixation point, a cue appears on the screen instructing the animal to the location of an upcoming target. After that, two stimuli are (simultaneously) displayed, one inside and the other outside the receptive field of the neuron under study. At random times changes in the motion (usually speed, direction, or color) occur. The monkey is required to detect the target change while ignoring similar changes in distractor to get reward. Comparing between responses to target and distractor stimulus inside the receptive field allows measuring the attentional modulation of the neuron.

early stage of visual processing is weak, whereas it becomes stronger at later stages.

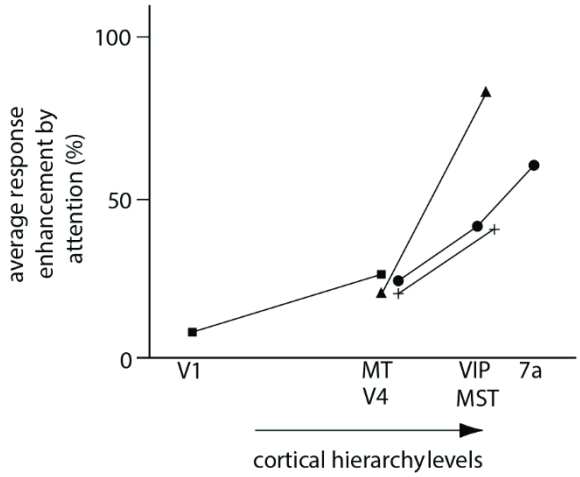

Figure 6 | Attentional modulation in visual cortical areas: average attentional modulation as a function of the level of cortical processing. Each marker type indicates results based on a study in which attentional modulation of two or more cortical areas were measured in the same subjects (rhesus monkeys) while they performed a given task: squares, McAdams & Maunsell, 1999, match-to-sample task, feature-based attention ; crosses, Treue & Maunsell, 1999, speed change detection task, spatial attention; circles, Ferrera et al., 1994, match-to-sample task, feature-based attention; triangles, Cook & Maunsell, 2002, motion detection task, spatial attention. The figure is adapted from Maunsell & Cook, 2002.

Another proven effect of attention on the responses at the level of single cells is to reduce the spiking rate variability (Cohen & Maunsell, 2009; Herrero et al., 2013; Mitchell et al., 2007, 2009; Niebergall et al., 2011; Zénon & Krauzlis, 2012). Niebergall et al. (Niebergall et al., 2011) computed the Fano factor in an experiment where the monkeys performed two different attentional tasks while keeping eye gaze on the fixation point. In the first task, monkeys were instructed to attend to the fixation point to be able to detect a change in the fixation point luminance while two moving random dot patterns were displayed on the screen (attend fixation). In the second task, however, the animals had to attend to the two moving random dot patterns to report a speed change, which occurred randomly (same probability) in either random dot pattern (tracking). They showed that Fano factor[9] of MT cells in the tracking task was less than attend fixation task, indicating that attention decreases spike count variability in MT.

It has been suggested that attention can influence the neuronal receptive field profile. Womelsdorf and colleagues (Womelsdorf et al., 2006) conducted an

[9] Responses of a neuron to repeated presentations of the same stimulus vary from trial to trial. Fano factor (the ratio of variance to the mean of spike count) is a commonly used quantity to measure this spike count variability.

experiment to test this hypothesis by cueing the monkeys to attend to different locations within and outside the receptive field of MT neurons being recorded. In their experiment, they carefully mapped the receptive field at high resolution by successive brief presentations of a probe stimulus (a small patch of random dot pattern moving in the preferred direction of the neuron under study) across the neuron's receptive field. The animals directed attention to one of two stimuli inside the receptive field or another stimulus outside the receptive field (moving in anti-preferred direction). The results show that attention shifts the hotspot (mass center) of the MT receptive fields toward the attended location by an average about 30% of the distance between two possible attended locations inside the receptive fields. By comparing receptive fields when the monkey directed its attention to the stimulus inside the receptive field versus outside the receptive field, they found attention also slightly made the receptive field shrink around the attended location.

Attention also could impact on the latency of neuronal responses (Galashan et al., 2013; Sundberg et al., 2012). A recent study by Galashan and colleagues (Galashan et al., 2013) investigated this in area MT of monkeys performing the speed change detection task and correlated it with improved behavioral performance (shorter reaction times) in attended condition. They reported that an instantaneous increase in the speed of stimulus (drifting Gabor gratings) induced a strong, transient response in the MT cells, which was modulated by attention. Furthermore, they showed that attention reduced the latency of the transient response to the speed change. Although they did not find any correlation between the behavioral reaction time and the amplitude of responses elicited by speed change, their results show that the reaction time covaries with the latency of the MT responses to the change. The latter might explain the faster reaction times in attended versus unattended condition.

Attention is dominantly associated with changes in the spike count correlation[10] (Cohen & Maunsell, 2009; Maunsell, 2015; Mitchell et al., 2009;

[10] Spike count correlation: A form of correlation, which measures co-fluctuations between trial-to-trial responses of a pair of neurons. It has been reported that the spike count correlation is a small, positive number in many cortical areas (Cohen & Kohn, 2011).

Zénon & Krauzlis, 2012). It has been shown that directing attention toward the stimulus inside the receptive fields of simultaneously recorded neurons reduces spike count (noise) correlation in different cortical areas from V1 to V4 and MT (Cohen & Maunsell, 2009; Herrero et al., 2013; Mitchell et al., 2009; Zénon & Krauzlis, 2012). For example, Zénon & Krauzlis (Zénon & Krauzlis, 2012) showed that attention reduced noise correlation between pairs of MT (and MST) cells in monkeys executing motion change detection task. This reduction in noise correlation could account for the improved population representation of a stimulus in attended compared with unattended condition (Cohen & Maunsell, 2009; Maunsell, 2015).

Although it has been thought that a common mechanism lies behind the different correlates of attention (spike rate, spike rate variability, receptive field, response latency, and spike count correlation between pairs of neurons), a new study provided a piece of evidence suggesting multiple mechanisms may be involved in the changes associated with attention (Maunsell, 2015; Ruff & Cohen, 2014). Ruff & Cohen (Ruff & Cohen, 2014) have demonstrated that attention could either increase or decrease spike count correlation of neurons in area V4 of monkeys while they performed a discrimination task. Attentional modulation of neuronal responses was, however, the same for both groups of neurons. This finding contrasts with previous studies that attention always reduces spike count correlation and enhances firing rate through a single neuronal mechanism. The results of this study indicate that attentional modulation of spike count correlation could be different across neuronal populations with the same response modulation associated with attention and therefore, the different mechanism might underlie the changes associated with attention (Ruff & Cohen, 2014).

2.7 Visual adaptation – Psychophysics

Adaptation is an umbrella term used to describe a large variety of phenomena that are contingent upon sensory experience and range from tens of milliseconds to minutes. Adaptation adjusts neuronal responses and perception depending on the temporal and spatial context the stimulus is embedded. It optimizes the consumption of cortical activity and improves sensory coding of the events around

us (Clifford et al., 2007; Price & Prescott, 2012; Schwartz et al., 2007). Perceptual effects of visual adaptation have been recognized across a diverse set of visual attributes for many years. These include impairing absolute sensitivity while improving relative sensitivity. For example, in a phenomenon called direction aftereffect, impairment of absolute sensitivity leads to overestimation of a test direction (biased judgments). Relative sensitivity improvement, however, results in a decrease of discrimination and detection thresholds for the directions close to the adapting direction (Clifford & Langley, 1996; Clifford et al., 2001; Dahmen et al., 2010; Phinney et al., 1997; Price & Prescott, 2012).

A psychophysical study by Blakemore and Campbell (Blakemore & Campbell, 1969) reported two aftereffects induced by prolonged exposure to a high-contrast grating pattern of a given orientation and spatial frequency (adapting stimulus, inducing stimulus, or adapter). Contrast adaptation is the elevation of contrast detection threshold (decrease of perceived contrast) of the subsequently viewed stimulus (test stimulus) with the similar orientation and spatial frequency. The second aftereffect is the shift of the apparent frequency of test stimulus with the same orientation. The orientation, spatial frequency-specific aftereffects were thought to be mediated by fatigue of neurons selective for orientation and spatial frequency (Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971; Blakemore et al., 1970; Klein et al., 1974) in primary visual cortex (Duong & Freeman, 2007).

Another visual illusion caused by adaptation is tilt aftereffect (TAE): prolonged inspection of a pattern of lines (adapter) causes a subsequently presented pattern to appear more tilted from the adapter than it physically is (Clifford, 2002; Gibson & Radner, 1937). It has been shown that TAE is constant for adapting periods between 20 and 1000 ms (Sekuler & Littlejohn, 1974). Direction aftereffect (DAE) is the analog of TAE when applied to the unidirectional moving adapter (Clifford, 2002; Levinson & Sekuler, 1976; R. Patterson & Becker, 1996; Schrater & Simoncelli, 1998).

Perception is not only affected by the temporal context of the stimulus but also by its spatial context. For example, it has been reported that the acute angle

between two transparent moving stimuli is overestimated, a phenomenon referred as to direction repulsion (Marshak & Sekuler, 1979).

The motion aftereffect (MAE) is another visual illusion ascribed to visual motion adaptation. Viewing a moving pattern (e.g. a waterfall) for a prolonged period of time (30 or so) causes the subsequent viewed stationary stimulus (e.g. river bank) appears to move in a direction opposite to the direction of inducing stimulus (waterfall illusion) (Anstis et al., 1998). The complete interocular transfer[11] of MAE suggests that this perceptual effect is a result of a distorted response pattern in the cortex rather than retina or LGN (Nishida et al., 1994).

It has been shown that adaptation is not a slow process, but rather it could occur on different timescales. A study by Glasser (Glasser et al., 2011) has investigated the perceptual effect of short-term (rapid) adaptation and its neuronal correlate. They designed a human psychophysical experiment in which subjects were presented with gratings moving to the right or left (adapting stimulus). The duration of exposure was set in a way that the direction discrimination of the adapting stimulus was at chance level (67 ms). The adapting stimulus was followed by the presentation of a stationary grating pattern (test stimulus). The subjects were required to indicate the perceived direction of the test stimulus. The psychophysical results of the study demonstrate that the subjects reported apparent motion of the test stimulus in a direction opposite to the adapting direction (MAE) despite the fact that they did not perceive the adapting direction. To assess the shortest adaptation required to elicit MAE, they altered the duration of exposure to adapting stimulus. They found that rapid motion adaptation as brief as 25 ms is able to produce perceivable MAE, which means that MAE is produced every time motion is sensed.

[11] Interocular transfer: visual neurons fall into three classes: (1) neurons responding solely to stimulus presented to one eye, such as neurons in retina and the LGN, (2) neurons responding to stimulation of both eyes, (3) neurons responding to the stimulus in either left or right eye. The two latter classes are found in the layers 4B and 4C of V1 and downstream neurons from V1. Based on this, interocular transfer of adaptation indicates where adaption occurs by measuring the extent adaptation is transferred when inducing stimulus is viewed with one eye compared with both eyes (for a review see Anstis et al., 1998).

2.8 Visual adaptation – Physiology

Visual experience (adaptation) perturbs the activity pattern across diverse neuronal populations. This perturbation underlies the perceptual effects following the adaptation (Anstis et al., 1998; Huk et al., 2001). It has been shown that prolonged visual stimulation of the (classical) receptive field of direction-selective cells in rabbit's retina, cat's V1, and monkey's MT with their preferred direction reduces the responsivity of the cells to the subsequent preferred direction. On the contrary, anti-preferred direction prolonged adaptation of the receptive field has facilitory or no effect on the responses to the preferred direction (BARLOW & HILL, 1963; Foley & Schwarz, 1998; Giaschi et al., 1993; Hammond et al., 1985, 1986, 1988; Kohn & Movshon, 2004; Marlin et al., 1988; Petersen et al., 1985; Vautin & Berkley, 1977).

In an old study, Barlow & Hill (BARLOW & HILL, 1963) reported that stimulation of motion sensitive RGCs in rabbits with a moving pattern reduced neuronal activity over the time course of 15-20 s. The activity of the adapted neuron was below the spontaneous activity following the stop of moving stimulus. They proposed that this effect might explain the perceptual MAE.

Another motion adaptation study in MT (Petersen et al., 1985) reported the effects of 20 s adaptations to preferred and anti-preferred directions on the responses to the preferred direction. The test stimulus was shown after a delay period of 5 s, and the adapter and test stimuli used were a moving random dot pattern and a moving bar, respectively. The results of this study indicated that adaptation to preferred direction reduced responses to the preferred direction, while the responses were facilitated following anti-preferred direction adaptation. This result explicitly contradicts the reduced responsivity following the adaptation, predicted by fatigue models of adaptation.

Kohn and Movshon studied the effect of prolonged motion adaptation on the direction tuning of MT neurons (Kohn & Movshon, 2004). Using an adapt-test paradigm they compared direction tunings prior and following a prolonged adaptation of 40 s (top-up: 5 s) to a sine-wave gratings pattern moving in

different directions relative to the preferred direction. They showed that responsivity of MT neurons changed least for test stimuli similar to the adapter and was maximally reduced for nearby directions. Adaptation to a direction on the flank of the tuning, therefore, produced an attractive shift toward the adapting direction, whereas preferred direction adaptation narrowed direction tuning. They employed a simple population coding model (labeled-line model) to demonstrate how physiological effects of motion adaptation in MT can underlie perceptual direction aftereffect (DAE). It has been suggested that the effects of prolonged adaptation to gratings in MT are inherited from V1, because: (1) adapting a subregion of MT receptive field to gratings altered the contrast sensitivity at that location without affecting other locations inside the receptive field (Kohn & Movshon, 2003), (2) adaptation with small gratings reduces MT responses more than adaptation with large stimuli (C. A. Patterson, Duijnhouwer, et al., 2014).

Kohn and Movshon investigated how prolonged motion adaptation in MT influences both response and contrast gain (Kohn & Movshon, 2003). Following a prolonged adaptation (40 s duration; 5 s top-up) to a full contrast sinusoidal gratings drifting in the preferred direction, they measured the responses of MT cells to varying contrasts of a test stimulus (1 s duration). They compared the responses to different contrasts following the adaptation with those prior to the adapting stimulus. The results indicate that neuronal response reduction following prolonged adaptation was not primarily a result of changes in response gain (fatigue), but rather a substantial change in contrast gain (allowing the cells to shift their operating range of contrast). They also measured the spatial specificity of contrast gain change by dividing the receptive field of MT cells into two segregated subregions, corresponding to a distinct population of V1 neurons. They showed that although adaptation in one subregion altered the contrast gain for the test stimulus in the same location, it did not influence the contrast gain in the other subregion. Based on the spatial specificity of adaptation within the receptive field and the fact that adaptation affects the contrast gain of V1 neurons in a similar way, they suggested that contrast gain change in MT is not a locally generated effect, but rather is inherited from V1.

Adaptation is not restricted to prolonged exposure and can occur in a wide time range from tens of milliseconds to minutes (Lisberger & Movshon, 1999; Müller et al., 1999; Price & Born, 2013; Priebe & Lisberger, 2002; Priebe et al., 2002). It has been shown that different visual areas respond to abrupt changes in specific attributes of the stimulus with a transient-sustained pattern (Priebe et al., 2002). For example, contrast change can produce such a pattern in the responses of cells in retina (RGCs) (Kaplan et al., 1983; Victor, 1987), LGN (Saul & Humphrey, 1990), and V1 (Kulikowski et al., 1979; Müller et al., 1999; Nelson, 1991; Tolhurst et al., 1980). The rapid change in the response, quick transition from transient level (unadapted response) to sustained level (unadapted response), is a form of adaptation referred to as short-term or rapid adaptation. A velocity step (e.g. when a stimulus starts moving, or it changes speed or direction) also induces a transient change in MT response, which decays quickly (20-80 ms) to a sustained rate. The rapid response change following a velocity step is the signature of short-term adaptation in MT (direction-selective V1 cells lack this) (Priebe et al., 2002; Traschütz et al., 2015).

In a study about the source of short-term motion adaptation in MT, Priebe and colleagues (Priebe et al., 2002) used a simple condition-test paradigm. In this experiment, a conditioning stimulus, either a stationary or moving random dot pattern, was followed by a test random dot pattern moving in the preferred direction and speed of the neuron under study (they showed that a duration of exposure to conditioning and test stimuli of 64 ms was sufficient for their investigations). Their study had several important findings: (1) a velocity step caused a transient-sustained pattern in the response, (2) input-specific mechanisms (synaptic fatigue), such as fatigue already present at the level of V1 neurons or short-term depression of transmitter release from the terminals of presynaptic V1 cells cannot describe the short-term adaptation effects. In a condition-test paradigm, they presented small conditioning and test stimuli in the spatially segregated locations inside the receptive field, such that they activated different populations of V1 cells. The results indicate that short-term adaptation in MT transfers between locations. Moreover, they demonstrated that short-term adaption was absent in the responses of direction-selective V1 cells to

velocity step in their configuration (using random dot pattern). This implies that adaptation is not a result of synaptic fatigue, (3) Simple fatigue of MT cells (spike-rate adaptation) cannot account for short-term motion adaptation in MT. They showed that there is no correlation between the spike count during transient phase (starting from response onset) and that during the subsequent brief time window. Their results also revealed that the initial part of sustained response in trials without transient component is not in any way greater than that in trials with transient component, (4) Short-term motion adaptation in MT occurs within this brain area and is its intrinsic circuit property (Price & Born, 2013; Priebe et al., 2002; Traschütz et al., 2015). It has been reported that the amplitude of the transient response (unadapted response) following change events plays an important role in the sensation and perception of theses brief events (Britten et al., 1996; Celebrini et al., 1993; Cook & Maunsell, 2002b; Galashan et al., 2013; Ghose & Harrison, 2009; Herrington & Assad, 2009; Macknik & Livingstone, 1998; Mechler et al., 1998; Pack & Born, 2001; Price & Born, 2010; Raiguel et al., 1999a; Smith et al., 2011; Traschütz et al., 2015). The amplitude of the MT transient response following a change in the stimulus speed depends not only on the post-change speed but also the stimulus speed prior to the change (Price & Born, 2013; Priebe & Lisberger, 2002; Traschütz et al., 2015).

To examine the neurophysiological correlates of MAE produced by brief motion exposure, Glasser and colleagues (Glasser et al., 2011) recorded from neurons in area MT of alert monkeys while brief moving gratings pattern (adapting stimulus) followed by a stationary gratings pattern were presented inside the receptive field of the neurons. Physiological results indicate that although responses to preferred direction were larger than those to anti-preferred direction during adapting period, the responses to the subsequently presented stationary pattern preceded by anti-preferred direction were larger than those adapted to the preferred direction. They proposed that this direction-selective response to the stationary pattern accounts for the perceptual MAE induced by brief motion exposure. They also suggested that short-term motion adaptation in MT in their experiment stemmed from adaptation in early visual areas (like V1) because (1) MAE following rapid motion adaptation was not completely

transferred from one eye to the other (incomplete interocular transfer), (2) increasing stimulus size improved both perceptual MAE and direction selective responses to the stationary pattern despite the reduction of direction selective responses during rapid adaptation (the latter can be explained by the activation of the inhibitory region of the receptive field (suppressive field) by large stimuli). In other words, direction-selective responses to stationary pattern preceded by rapid adaptation do not depend on MT motion processing, (3) motion perception is not required to produce MAE, (4) and the magnitude of MAE following rapid adaptation depends on the motion of elements of the test stimulus and not the resultant motion of test stimulus.

A study by Price & Born investigates how adaptation to different reference (adapting) speeds with a duration of 550-5000 ms affects speed tuning of MT cells (Price & Born, 2013). They recorded from monkeys while they executed a speed change discrimination task. A random dot pattern moving in the preferred direction of the neuron with one of two reference speeds was shown inside the neuron's receptive field. After a random interval (550-5000 ms), the stimulus speed abruptly changed to a test speed (the ratio of test to reference speed was 0.5-1.5). The animal was rewarded for correctly reporting whether the stimulus speed was increased or decreased by making a saccade to one of two choice targets within a time window 150-750 ms after speed change. The electrophysiological results showed that: (1) the speed change induced a transient change in the response. The amplitude of the transient response was dependent on the preceding stimulus (reference speed), (2) post-change speed tunings (computed using the responses averaged over the time window 50-150 ms after speed change) corresponding to adaptation with two different reference speeds were shifted. Since they did not sample data from full range of the speed tuning curve, the observed shift could be thought as a lateral shift of preferred speed, vertical gain change, or both, (3) spiking rate, spike count variability, or tuning curve did not change over the time course of adaptation between 550 and 5000 ms. Shift of speed tunings, therefore, might depend on the change in the first 550 ms of adaptation, (4) correlation between the ratio of transient to sustained responses following motion onset and shift of post-change speed tuning ($r=0.37$)

suggested that rapid (short-term) adaptation and shift of speed tuning following the speed change have a common origin: the intracortical circuit within MT. They also examined the time course of performance improvement in a human speed change discrimination task (very similar to the monkey task). They showed that improvement reaches a plateau for durations > 350 ms after motion onset, consistent with their electrophysiology finding.

Kar & Krekelberg (Kar & Krekelberg, 2016) studied how different levels of adaptation impact the direction tuning of MT cells. They compared the direction tuning curves following 300 ms adaptation to a 100% coherently moving random dot pattern (strong adapter) with those after adaptation to a 0% moving random dot pattern (weak adapter) of the same duration. Motion directions (test stimuli) used to determine the post-adaptation tuning, were presented for 300 ms. A blank period of 300 ms separated adapting and test periods, meaning that the results of this study reflect adaptation effects which last beyond 300 ms. Comparison between the tuning curves following weak and strong adaptations rules out the components that are inherited from other areas and are not coherent motion specific mechanism (for instance, contrast adaptation, which could be inherited from V1). The results of the study indicate that adaptation reduced both the amplitude and bandwidth of tuning curves. Suppression and sharpening effects were strongest when the adapter moved in the preferred direction of the cell and become weaker as adapter direction deviated from the preferred direction (stimulus-specific adaptation). They also reported response enhancement following adaptation in many cells (particularly, when the direction of test stimulus was opposite to the adapting direction). The response enhancement following adaptation was attributed to the network adapted by the stimulus. For example, the adapter might stimulate the suppressive surrounds of the receptive fields of the neurons surrounding the neuron being recorded, which leads to disinhibition of the neuron and its post-adaptation response enhancement.

An adaption study by Patterson et al. (C. A. Patterson, Duijnhouwer, et al., 2014; C. A. Patterson, Wissig, et al., 2014) found that both V1 and MT recruit distinct strategies to adapt on different timescales. They reported that

physiological effects of adaptation to drifting gratings were similar in V1 and MT under matched stimulus conditions, while the effects were strongly dependent on adaptation duration and the size of adapting stimulus. Small gratings (1.3^{o} diameter) produced a repulsive shift away from the adapter (in the flank of tuning) and strongly reduced responsivity. Adaptation duration strengthens both effects (duration scaling[12]). Although brief exposure (400 ms) to a large grating (7.4^{o} diameter) induced a repulsive shift of preference away from the adapter, tuning was attracted toward the adapting direction following the prolonged adaptation (40 s). Both brief and prolonged adaptation to large gratings slightly decreased the responsivity. They suggested that weakening of surround suppression following the prolonged adaptation to large gratings might underlie the attractive shift and weak response reduction of post-adaptation tuning curves (surround suppression followed by brief adaptation to large gratings is weak). In contrast, adaptation to small gratings causes stimulus-specific suppression of neural response, which could explain the strong loss of responsiveness and repulsive shift of tuning following the adaptation.

A number of neural mechanisms have been proposed to parallel the perceptual effects of adaptation. A classical adaptation model, simple fatigue model (Georgeson, 2004; Sekuler & Pantle, 1967; S. G. Solomon & Kohn, 2014), postulates that visual stimulation fatigues neurons over the stimulus exposure period by elevating action potential threshold. The fatigue associated with adaptation causes a decrease in the neuronal response to subsequently presented stimuli. The degree of fatigue (and thereby, its effects) mainly depends on two factors: (1) adaptation duration, longer the adaptation is, stronger the adaptation-induced effects are, (2) adapter-driven response, adaptation-induced effects are more pronounced if adapter matches the preference of neuron, whereas they become weak as the adaptor differs from the neuron's preference. This simple model is able to explain the perceptual effects of prolonged adaptation. According to the simple fatigue model response reduction following the adaptation is independent of the characteristics of the test stimulus (S. G.

[12] Duration scaling: physiological and perceptual effects induced by brief stimulus exposure become stronger as adaptation duration increases (C. A. Patterson et al., 2013).

Solomon & Kohn, 2014). It has been shown, however, that adaptation effects are contingent on the test stimulus (adaptation effects are stimulus-specific) (Dragoi et al., 2002; Jin et al., 2005; Kohn & Movshon, 2004; Müller et al., 1999; C. A. Patterson et al., 2013; Petersen et al., 1985; Price & Born, 2013). The synaptic fatigue (stimulus-specific fatigue) model takes this into account by assuming that synaptic inputs from neurons with preferences similar to the adapter are reduced during adaptation (because these afferents are either fatigued or neurotransmitter release from their terminals are depressed) (Abbot et al., 1997; Manookin & Demb, 2006; S. G. Solomon & Kohn, 2014). Although the stimulus-specific fatigue model explains stimulus-specific response reduction following the prolonged adaptation to stimuli tailored to match the classical receptive field, it fails to capture facilitory effects of adaptation observed using some adaptation protocols (response enhancement following the adaptation) (C. A. Patterson et al., 2013; Petersen et al., 1985; S. G. Solomon & Kohn, 2014; Webb et al., 2005; Wissig & Kohn, 2012). A modern plausible description of adaptation based on normalization models overcomes the limitations of the fatigue models. The normalization model of adaptation assumes that adaptation influences both excitatory and inhibitory signals of the receptive field[13] in a stimulus-specific way. Adaptation of classical receptive field reduces excitatory signals and results in a responsivity decrease, which becomes prominent as adaptation duration lengthens, whereas suppressive field adaptation weakens suppression and leads to response facilitation. The resultant effect of adaptation, therefore, depends on the extent to which adaptation alters these two signals (C. A. Patterson et al., 2013; S. G. Solomon & Kohn, 2014).

2.9 Combined effects of visual attention and visual adaptation

Attention and adaptation are two mechanisms recruited by the brain to optimize the energy consumption of the cortex to provide an efficient representation of the sensory information. I briefly reviewed how physiological effects of attention

[13] Receptive fields are composed of two distinct mechanisms, a classical receptive field (CRF, or stimulation field), which describes neuron's selectivity in terms of spatial position and preference, and a suppressive field, which characterizes the spatial positions and features contributing to the suppression of neuronal responsivity. Stimulation of CRF has facilitatory effect (enhances neuronal response), while suppressive field stimulation suppresses the responses (Reynolds & Heeger, 2009; S. G. Solomon & Kohn, 2014).

might underlie the improved perceived stimulus appearance (which mainly results in improved psychophysical performance) in attended location, and how neural adaptation parallels the enhanced perception of change events. Here I present studies on how attention alters adaptation-induced effects. This comprises several psychophysical studies, as there are, to my knowledge, no electrophysiological reports as yet of attention effects on neural adaptation.

Many human fMRI and human psychophysical studies have investigated how attention influences perceptual and physiological effects of motion adaptation (Alais & Blake, 1999; Berman & Colby, 2002; Blaser & Shepard, 2009; Chaudhuri, 1990; Huk et al., 2001; Lankheet & Verstraten, 1995; Rees et al., 1997; Rezec et al., 2004; Seiffert et al., 2003; Taya et al., 2009). Most of these studies have employed similar approaches, which probe the effect of attention on the perceptual and physiological MAE induced by prolonged exposure to a moving pattern (Berman & Colby, 2002; Blaser & Shepard, 2009; Chaudhuri, 1990; Huk et al., 2001; Rees et al., 1997; Rezec et al., 2004; Seiffert et al., 2003; Taya et al., 2009).

A psychophysical study by Chaudhuri (Chaudhuri, 1990) was the first to report attention modulates the MAE following prolonged motion adaptation. He compared the duration of MAE (as a measure of MAE strength) when an adapter was unattended (less-attended) versus it was passively viewed (more-attended). The adapter was a unidirectional moving texture pattern shown for 30 s in the background of a display. In the less-attended condition, subjects were required to perform an alphanumerical discrimination task[14] in a small window on the screen during the time course of adaptation. In the more-attended condition, using the same configuration as the previous task, subjects passively viewed the window without performing the discrimination task. The results showed that the MAE was weaker in less-attended condition (subjects were performing the discrimination task in a small window) compared with more-attended condition

[14] Alphanumerical discrimination task: subjects were required to report appearing numerical characters within a small window. Alphabetical and numerical characters were shown randomly with a frequency of 4 Hz. The probability of a numeral appearing was 1/8.

(passive viewing the window). This suggests that the perceptual effects of adaptation might be susceptible to attention mechanism.

A follow-up human fMRI/psychophysical study by Berman & Colby (Berman & Colby, 2002) measured the duration of MAE[15] in two different tasks: (1) subjects passively viewed an expanding concentric pattern for a prolonged period of time in the absence of any attentional demand, (2) subjects were performing attentional tasks (either a visual task (alphanumerical discrimination task) in the fixation point or an auditory task) while being visually adapted to the identical expanding pattern with the same duration. The results showed that duration of MAE in the latter task was significantly shorter as compared to the first task. This suggests that shifting attention away from adapting stimulus reduces its physiological and perceptual effects.

In a psychophysical study, Alais and Blake (Alais & Blake, 1999) showed that shifting attention toward an adapting stimulus strengthens the effects it induces. Subjects viewed a stimulus consisting of two superimposed moving random dot patterns for a prolonged timescale (32 s). One pattern, 'adapting dots', was a 100% coherent motion while the other, 'attending dots', was a moving pattern at 0% coherence level with a brief (1 s duration), weak coherent motion bursts. The coherent motion bursts were displayed 8 times at random time points during the adaptation period. In 'active attention' trials subjects were required to detect the coherent bursts moving in a cued direction. In 'passive attention' trials, however, subjects passively viewed the same stimulus as the 'active attention' trials (no need to detect weak signals). At the end of each trial, subjects reported the MAE direction. They found that the deviation of MAE direction (relative to MAE direction expected from adaptation with 'adapting dots') in active attention trials was substantially larger than that in passive attention trials. As adaptation with two superimposed random dot patterns moving in two different directions produces MAE in a single direction, which is the vector sum of MAEs induced separately by each of random dot patterns (Lankheet & Verstraten,

[15] MAE duration was measured physiologically as the time the post-adaptation increased activity of MT+ returned to its pre-adaptation baseline (decay time). Perceptual MAE duration was the time post-adaptation aftereffect stopped.

1995; Riggs & Day, 1980; Verstraten et al., 1994), their study suggested that attending to one adapting stimulus strengthens the effects it evokes.

Lankheet and colleagues (Lankheet & Verstraten, 1995) investigated the interaction between attention and adaptation mechanisms in motion processing using an experimental design, which employed another approach to measuring the MAE. After adaptation with a moving adapting stimulus (1.26 – 10 s duration), subjects were required to report the perceived direction of a test stimulus shown for 1 s after a blank period of 500 ms following the adaptation (left-right discrimination task). Test stimulus was a dynamic random dot pattern consisting of unidirectional moving dots and twinkling noise. Due to the fact that physical motion cannot be distinguished from apparent motion in a dynamic random dot pattern (Hiris & Blake, 1992), they varied the coherence level of the test stimulus in a way that perceptual MAE was canceled (this yielded the point of subjective equality, PSE). In this design, PSE reflected the strength of MAE with zero corresponding to the absence of MAE (unbiased observer). They measured PSEs without any preceding stimulus and following exposure to two types of adapting stimulus: a 100% coherent moving random dot pattern, and two superimposed random dot patterns moving in opposite directions (it has been shown that the MAE evoked by this adapter has a single direction. This direction is opposite to the vector sum of the directions of adapter components (Riggs & Day, 1980; Verstraten et al., 1994)). Subjects performed the latter experiment while attending to one of moving random dot patterns. They showed that PSE in the task without adapter was the least and it was the largest following adaptation to a unidirectional adapter. Viewing superimposed patterns while attending to one of the patterns elevated PSE to about 70-75% of the PSE following adaptation to the unidirectional pattern. This indicated that attention modulates effects induced by adaptation.

2.10 Key points

The main goal of this study was to investigate the neuronal representation and perception of abrupt changes in the visual environment and to examine how attention affects this representation. I addressed these issues in the context of

processing of information about visual motion and its direction change in area MT as a large body of previous physiological work have documented that: (1) MT plays a critical role in the processing and perception of visual motion, (2) attention enhances MT responses to moving stimuli, (3) physiological effects of motion adaptation in MT are well-studied. It has been shown that these effects depend on the exposure time, stimulus size, and perhaps the pattern of inducing stimulus (adapter). On the other hand, previous psychophysical studies investigated both perceptual effects of visual motion adaptation and attentional modulation of these effects. It has been demonstrated that attention modulates the effects induced by motion adaptation.

3 MATERIALS AND METHODS

3.1 Monkey electrophysiological study

The electrophysiological data were collected by Julio C. Martinez-Trujillo in Cognitive Neuroscience Laboratory, Department of Neurology, University of Tübingen and other aspects of this data have been published previously (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999).

3.1.1 Experimental procedures

Data were collected from two male rhesus macaques. After initial training of monkeys, they underwent a surgery under anesthesia to implant a headpost, a scleral eye coil, and a recording chamber. Animal procedures complied with the NIH Guide for Care and Use of Laboratory Animals and were approved by the local animal care committee.

A custom-written computer program running on an Apple Macintosh PowerPC controlled the stimulus presentations and recorded the behavior of the animal and monitored eye position.

3.1.2 Visual stimuli

Random dot patterns (RDPs) of bright dots of the luminance of 55 cd/m^2 were displayed on a dark monitor screen of 0.1 cd/m^2, placed 57 cm away from the animal. The monitor screen was set to a resolution of 33 pixels/^{o} with a refresh rate of 75 Hz. Dots were randomly plotted with a density of 5 dots per degree square within a virtual circle matching the size of the receptive field (RF) of the neuron under study. The speed of all the dots was uniform over the entire RDP and was set to the preferred speed of the neuron. In each trial, dots coherently

moved in one of 12 equally spaced directions. Clockwise direction changes of 25° occurred at random time points between 300 and 4000 ms after the onset of visual motion. 200 ms after each clockwise direction change, a second counterclockwise change returned motion direction to its initial value prior to the change.

3.1.3 Electrophysiological recording

Extracellular single-unit recordings were made from 54 isolated MT cells in two hemispheres of two awake, behaving monkeys seated in a primate chair with the head restrained. The neuronal responses were recorded with tungsten microelectrodes of impedance 0.5–2 Ω, Microprobe and FHC. MT was identified by its anatomical location, a high percentage of direction-selective cells, the eccentricity and the receptive field size of its cells.

3.1.4 Behavioral task

Monkeys were trained to perform a motion direction change detection task. Each trial began with a fixation point displayed on the center of a blank computer screen. After the animal maintained its gaze on the fixation point for 300 ms, a static random dot pattern (RDP) was shown either inside the neuron's receptive field or opposite to the RF, cueing the animal as to the target's location in the upcoming trial. The trial was continued if the monkey touched a lever. 300 ms after the lever was touched, a second similar RDP was displayed at other location and both RDPs began moving in the same direction. At random time points between 300 and 4000 ms after the onset of visual motion the target and distractor directions might undergo transient clockwise changes of +25° for 200 ms. In first distractor change trials, the distractor change occurred at least 600 ms before the target change. The monkey was required to detect the change in the target by releasing the lever in a reaction-time window extending from 250 to 700 ms after the change onset and to ignore distractor changes to get a fluid reward. Trials were aborted without reward if the monkey deviated its gaze outside the fixation window, failed to detect the target change within the

reaction-time window, responded to a distractor change, or release the lever in the absence of stimulus change.

3.1.5 Data analysis

We analyzed the electrophysiological data using custom-written scripts in MATLAB (MathWorks).

Spike density function (SDF): we computed SDF in each trial by convolving the spike train aligned relative to the onset of direction change (or relative to motion onset in the analysis related to the mechanism underlying the overestimated representation of direction change) with a Gaussian kernel of $\sigma = 10, 20, and\ 40\ ms$ at a resolution of 1 ms. The results shown in this report correspond to $\sigma = 20\ ms$, unless otherwise stated.

Neuronal response to a stimulus (trial-averaged response): we averaged the SDFs of a single MT cell in a given attentional condition across multiple presentations of the same visual stimulus (pre-change direction) to estimate the neuronal response to each of 12 stimuli as a function of time.

Time-mean neuronal response: we computed time-mean response by averaging the neuronal response over an analysis time window. In our analysis, we used a pre-change analysis time window from -700 to 0 ms and a post-change window from 100 to 200 ms unless otherwise stated. It has been documented that the transient response induced by change events play a key role in sensation and perception of these rapid events (Britten et al., 1996; Celebrini et al., 1993; Cook & Maunsell, 2002a; Galashan et al., 2013; Ghose & Harrison, 2009; Herrington & Assad, 2009; Macknik & Livingstone, 1998; Mechler et al., 1998; Pack & Born, 2001; Price & Born, 2010; Raiguel et al., 1999b; Smith et al., 2011; Traschütz et al., 2015). We, thereby, considered the post-change analysis time window from 100 to 200 ms following the direction change, similar to Price & Born (Price & Born, 2013), which takes the direction change induced-transient into account. In principle, in agreement with a previous study (Price & Born, 2013), we showed

that any post-change time window, which includes the transient response change yields similar results.

Direction tuning curves: we quantified the direction tuning of MT cells by fitting time-mean neuronal responses to 12 directions with a (symmetric) von Mises function of the form:

$$y(x; a_1, a_2, a_3, a_4) = a_1 + a_2 \exp(a_3 \cos(x - a_4)) \quad \text{(Eq. 1)}$$

or a skewed von Mises function (Swindale, 1998),

$$y(x; a_1, a_2, a_3, a_4, a_5) = a_1 + a_2 \exp\big(a_3 \cos\big((x - a_4) + a_5(cos(x - a_4) - 1)\big)\big) \quad \text{(Eq. 2)}$$

The least squares minimization routine was used to fit the data with the von Mises function.

Population response profile: unattended and attended trial-averaged responses of each neuron to different directions were normalized to the neuron's highest response evoked in either attentional condition. The normalized responses of each neuron were aligned in time to the direction change onset and in direction to the pre-change preferred direction of the neuron. The pre-change preferred direction was the median of preferred directions determined by fitting the responses to different directions with the von Mises function every 10 ms over a time window spanning from -800 ms to the onset of direction change. The normalized, aligned data were averaged across the neurons to construct the population response profile for both unattended (Figure 3a) and attended (Figure 3b) stimuli.

We estimated the location of population peak activity (black solid line in Figure 3) by fitting the population response with the von Mises function every 20 ms.

Population response curves: For each neuron and for each of 12 directions, we computed pre- and post-change response by averaging the neuronal response from -300 to 0 ms and from 100 to 200 ms (relative to the direction change),

respectively. We then determined each of pre- and post-change direction tuning curves by fitting the corresponding neuronal responses to 12 directions with a von Mises function. We averaged pre- and post-change direction tuning curves across neurons after aligning their preferred directions. We used the median of the distribution of tuning shift across cells to locate the peak of population post-change response curve (Figure 8, 9).

Modeling the effects of visual motion adaptation: To model the suppressive effect of adaptation on the pre-change response curve described by a von Mises function located at 25° (Eq. 3) we subtracted a similar profile (Eq. 4) located at the pre-change direction (0°) from the pre-change response curve. We multiplied an inverted von Mises function located at pre-change direction (Eq. 5) by the result of the subtraction of the previous step to model the adaptation effect on the normalization signal. Both von Mises functions used to model the adaptation effects had a bandwidth similar to that of the pre-change response curve. We varied asymptote and amplitude of both von Mises functions to get the best fit to the observed post-change response curve (Eq. 6). We only looked for the parameters resulted in the response curve shift similar to that of the observed post-change curve.

$$y_{unAdapt}(x; a_1, a_2, \omega, a_3) = a_1 + a_2 \exp(\omega \cos(x - a_3)); \quad a_3 = 36\pi/5 \qquad \text{(Eq. 3)}$$

$$y_{supp}(x; b_1, b_2, \omega, b_3) = b_1 + b_2 \exp(\omega \cos(x - b_3)); \quad b_3 = 0 \qquad \text{(Eq. 4)}$$

$$y_{norm}(x; c_1, c_2, \omega, c_3) = c_1 + 2c_2 \cosh(\omega) - c_2 \exp(\omega \cos(x - c_3)); \quad c_3 = 0 \qquad \text{(Eq. 5)}$$

$$y_{post-change\ model}(x; b_1, b_2, c_1, c_2) = y_{norm} \times (y_{unAdapt} - y_{supp}) \qquad \text{(Eq. 6)}$$

3.2 Human psychophysical study

3.2.1 Participants

Twenty-one volunteers, 7 males and 14 females, aged 21-36, with normal or corrected-to-normal vision took part in the experiment. Nineteen were naive to the purpose of the experiments, and all participants signed a written consent

form prior to the experiment. 10 subjects fulfilled the criterion for inclusion in this study (see Procedures).

3.2.2 Apparatus and stimuli

Stimuli were programmed and controlled in an open-source software package MWorks (http://mworks-project.org/) running on a Macintosh computer. They were presented on a monitor screen Samsung (SynsMaster 2233, 1680x1050 pixels) in a dim room. The screen had a refresh rate of 120 Hz, a luminance of 0.1 Cd/m^2, and was subtended 475 mm in width and 295 mm in height resulting in a spatial resolution of 35 pixels/^{o}. The observers viewed the monitor screen binocularly from a distance of 57 cm. A chin and forehead rest was used to reduce their head movements. An eye tracker with a sampling rate of 1000 Hz (EyeLink 1000, SR Research) recorded eye movements in each trial. The subjects used the buttons on a gamepad (Logitech Precision) to initiate each trial and to respond at the end of each trial.

Stimuli were moving random dot patterns. Each RDP consisted of 100 dots (each 0.1^o in diameter), all in white (experiments 1 and 2) or half in white and half in yellow (experiment 3). The white and yellow dots in our experiment had a luminance of 70.2 Cd/m^2 and 58.9 Cd/m^2, respectively. Dots were randomly plotted in a stationary circle of radius 3^o of visual angle and all coherently moved in a specific direction at the speed of 8^o/s.

Mask stimuli were identical, except all dots were always presented in white color, and each dot moved with the speed of 8^o/s in a direction between -45^o and +45^o relative to the post-change motion direction (main experiments) or the motion direction (direction discrimination task). The centers of stimuli were at 5^o eccentricity to the left and right side of the central fixation point. Data were analyzed using custom-written scripts in MATLAB (MathWorks).

3.2.3 Procedures

On each visit, subjects were given both written and verbal information about the tasks. They were also instructed to covertly attend to the right stimulus in all

experiments. Suitability of the subjects for the main experiments and include their data in my analysis was based on their sensitivity in discriminating between upward and downward motion in a direction discrimination experiment: an average discrimination threshold less than 3^o for both rightward and leftward motions. Ten of 21 subjects met the criterion and completed two main tasks. Each subject repeated each experiment 6 times on 3 different days. The order and the type of experiment were randomly chosen each time. The subjects seated in front of the screen and pressed a gamepad button while they maintained eye fixation on a white small square (subtended on each side 0.17^o visual angle) presented in the middle of the screen to begin a trial. If fixation was broken at any time during the trial, the trial was aborted and repeated later.

3.2.4 Experiment 1 (motion direction discrimination task)

Two identical moving RDPs were shown for 200 ms in either visual hemifield at the same eccentricity. The motion direction in each trial was determined using simple 1-up/1-down staircase procedures for rightward and leftward motions. The two coherently moving RDPs were then replaced by the two mask RDPs. 200 ms later, the stimuli disappeared and the subjects were required to press a gamepad button to indicate whether the observed motion direction was upward or downward relative to their reference horizontal lines. Direction discrimination thresholds for each of rightward and leftward motions in each session were estimated by measuring the slope of the psychometric curve fitted with a logistic function of the form:

$$P(x;\alpha,\beta) = \frac{1}{1+\exp\big(-\beta(x-\alpha)\big)}$$

α is the point of subjective equality and $\frac{1}{\beta}$ (slope) is a measure of how accurate a subject is in judging the direction - direction threshold. The average discrimination threshold across sessions was used to determine the discrimination threshold for each subject.

3.2.5 Experiment 2

Two RDPs moving in the same direction were presented in opposite hemifields at equal eccentricity. In each trial, the direction of motion was randomly chosen to be leftward or rightward. A clockwise or counterclockwise change of 22°, 25°, or 27° occurred in the direction of right RDP at a random time between 2000-3200 ms. 200 ms after the change, stimuli were replaced with mask RDPs displayed for 200 ms. Subsequently, the screen went blank and subjects were required to press the buttons of a gamepad to indicate whether the motion direction after the change was upward or downward relative to their reference horizontal line. Post-change motion direction varied from trial to trial according to four simple 1-up/1-down staircase procedures associated with clockwise and counterclockwise direction changes in each of rightward and leftward motions. The post-change motion direction in each staircase began with an angle that was distinctly different from the horizontal line (20°). This angle reduced toward the horizontal line until the reported post-change direction crossed the horizontal line. The procedure was then reversed and increased the angle until the subject's perceived direction of post-change motion did not cross the horizontal line. Each staircase, therefore, yielded the 50% point of subjective equality for the corresponding motion direction and direction change. The error in the perceived direction change for each motion direction was assessed using the average of points of subjective equality measured for clockwise and counterclockwise direction changes in the corresponding direction.

3.2.6 Experiment 3

The design and the time course of this experiment was identical to Experiment 2, except that half of the dots in RDPs were in white, and the other half in yellow and each set of dots moved in one direction offset (22°, 25°, 27°) clockwise from the post-change direction and the other offset counterclockwise by the same absolute angle. When the white dots of the stimulus in right visual hemifield changed direction, the yellow dots simultaneously disappeared. The subject's task was to indicate the post-change direction of white RDP by pressing the gamepad buttons.

4 RESULTS

We investigate the neuronal representation of a change in motion direction in the middle temporal visual area (MT) of the rhesus monkey, demonstrate how spatial attention influences the direction change representation, and examine possible mechanisms underlying the response changes induced by the direction change. We propose a model to explain the response changes following the direction change. We perform a human psychophysical experiment to compare the representation and perception of direction change and to test the predictions of the model. We employ a linking model to account for the perception of direction change based on our neuronal data.

4.1 Representation of direction change in MT and attention influence on it

To study the neuronal representation of a change in the direction of visual motion and the influence of spatial attention on it, we recorded from 52 MT cells in two different hemispheres of two monkeys while they were performing a motion direction change detection task (Figure 1; see Methods). In either spatial attention condition, visual stimulus consisted of visual motion in each of 12 evenly spaced directions shown for 300-4000 ms followed by a clockwise direction change of $+25^{o}$ lasting for 200 ms.

To investigate how the direction change affects neuronal responses, we compared responses of neurons prior to and following the direction change. Figure 2 shows pre- and post-change responses of an example MT cell in both attentional conditions. Figure 2a plots the spike density functions aligned to the

direction change onset (t=0), averaged across trials for two different directions followed by the same direction change. The red curves represent responses when

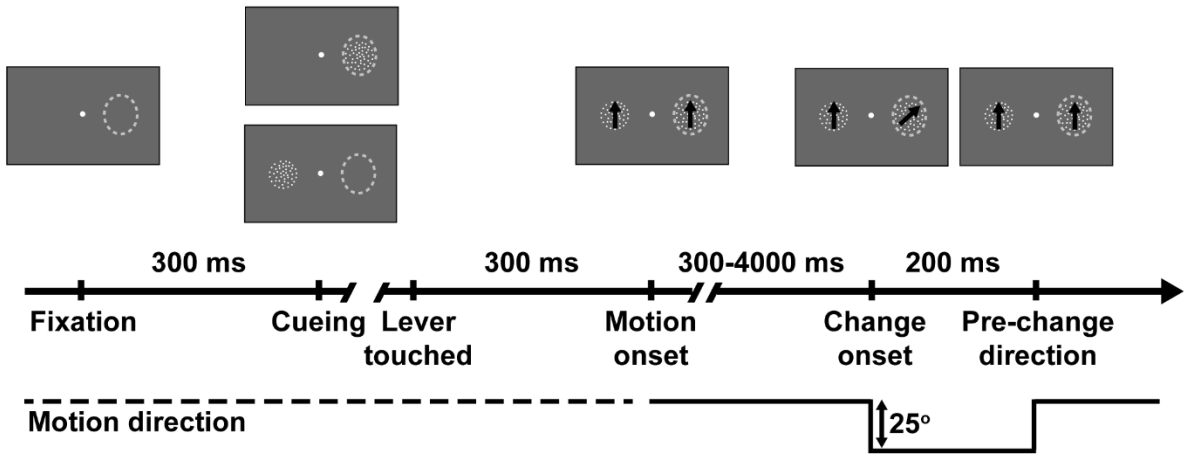

Figure 1 | Paradigm of the motion direction change detection task: a trial began with the appearance of a central fixation point (indicated by a white dot). After the monkey foveated the fixation point, a static random dot pattern was shown either inside the neuron's receptive field (RF) (shown as dashed lines) or opposite to the RF, cueing the animal to the location of the target. The trial was continued if the monkey touched the lever of a primate chair. 300 ms after the lever was touched, another random dot pattern was displayed at other location and both random dot patterns began moving randomly in one of 12 evenly spaced directions. Clockwise direction changes +25° might occur in both target and distractor in a time window from 300 to 4000 ms after the motion onset. The stimulus direction was returned to its pre-change value after 200 ms. The animal was required to detect the change in the target by releasing the lever and to ignore the similar change in the distractor to get a fluid reward. Regarding the type of stimulus inside the RF, each trial belongs to one of two spatial attention conditions: target inside the receptive field (attended) or distractor inside the RF (unattended).

the stimulus inside the receptive field was unattended and blue when it was attended. In line with previous reports, responses to attended stimuli are larger than those to unattended stimuli. The change in motion direction elicited a transient change in the response. To evaluate the effect of direction change on the responses of the neuron, analysis time windows of -700-0 ms (corresponding to pre-change), and 100-200 ms (corresponding to post-change), indicated by the shaded areas in Figure 2a, were used. Although direction change increased responses to one motion direction (top panel) ($p < 0.00004$, two-sided Wilcoxon rank sum test for distributions with equal medians), responses to other direction (bottom panel) were not significantly altered by the direction change ($p > 0.6$, two-sided Wilcoxon rank sum test for distributions with equal medians). The figure also shows that the neuron's response to the same direction is not the same before and following the change (responses in the light shaded area in top panel compared with those in dark shaded area in bottom panel). To examine the effect of unattended and attended direction changes on the responses to different

directions, a comparison was made between pre- and post-change direction tuning curves in both attentional conditions (Figure 2b).

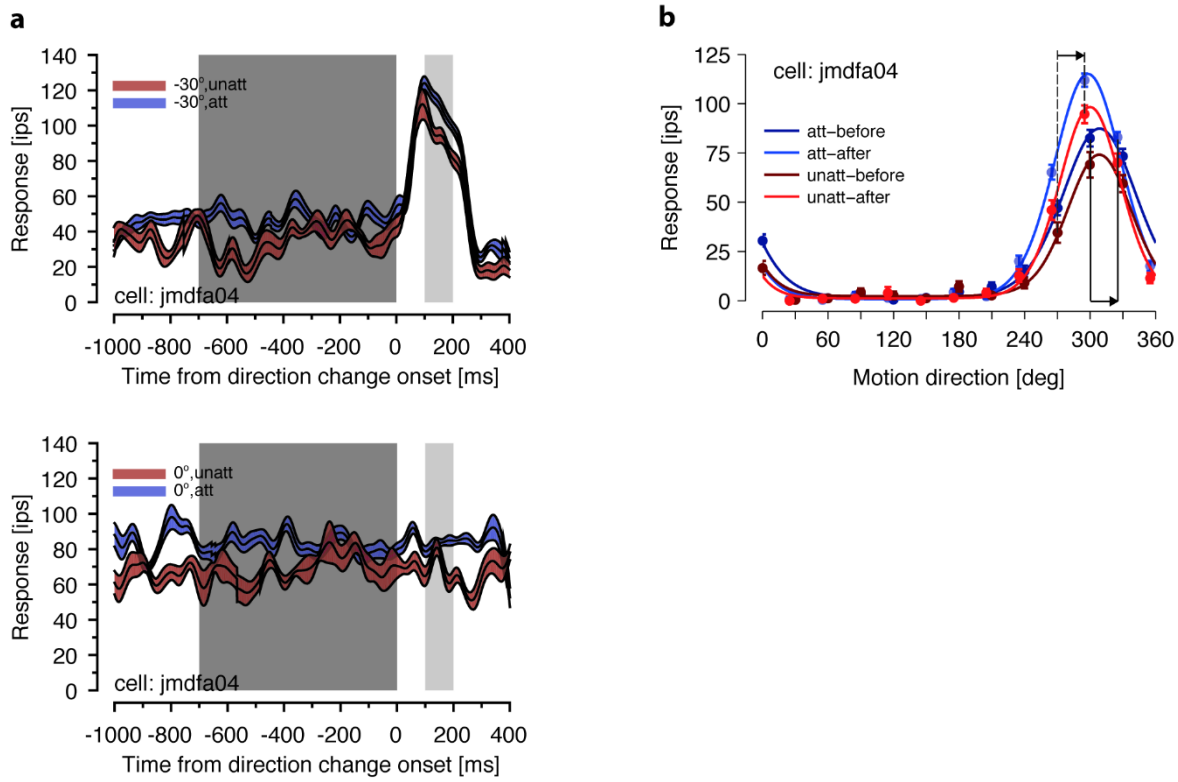

Figure 7 | Influence of unattended and attended direction changes on the responses of an example MT cell: (a) responses of an MT cell to unattended and attended direction changes in the rising flank of tuning (top) and close to the preferred direction (bottom). Dark and light shaded areas show the time windows used to compute the pre- and post-change responses, (b) direction tunings of the same MT cell prior and following the direction change of +25° in both attentional conditions. Two arrows indicate the directions in the flank of tuning (left) and close to the preferred direction (right) we used in Figure 2a. Left and right vertical lines mark pre- and post-change direction of the stimulus, respectively.

Figure 2b depicts time-averaged responses to 12 directions prior to and following the direction change in both attentional conditions. We fitted the von Mises function to the responses to estimate direction-tuning curve in each condition. Vertical dashed and solid lines mark the stimuli used for illustration in the top and bottom panels of Figure 2a, respectively. The dashed lines represent the pre-change direction in the positively sloped flank of direction tuning and the solid lines indicate pre-change direction close to the neuron's preferred direction. The left and right lines in each pair of lines are pre- and post-change motion directions, respectively. Comparison of preferred direction between the pre- and post-change tuning curves in each attention condition showed that the direction change of +25° induced a preferred direction shift of -8° when the stimulus inside the RF was unattended. The shift was increased to -11°

when attention was directed towards the stimulus inside the neuron's receptive field.

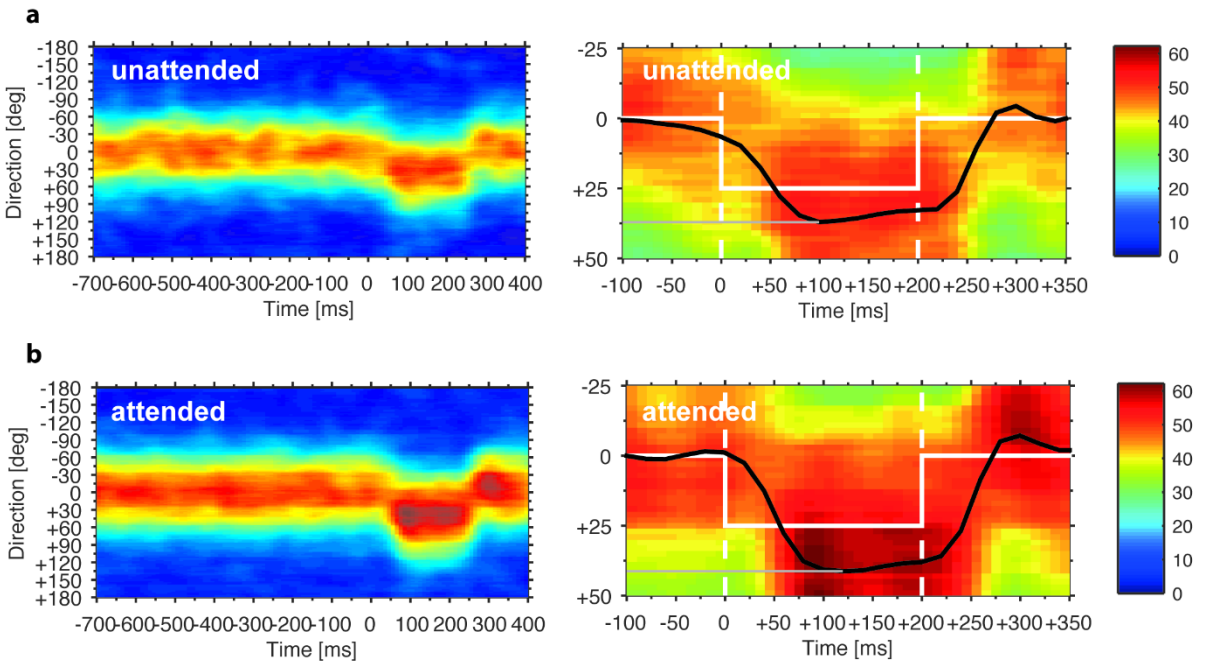

Figure 3 | MT representation of motion and its direction change (n=36) in (a) unattended, (b) attended conditions: response profile of each cell was normalized to its highest response and was aligned to the cell's pre-change preferred direction. The normalized, aligned responses were then averaged across cells. The White solid line indicates the direction of stimulus. The black solid line represents the dynamics of the location of population peak activity. Vertical white dashed lines mark the time points the change in motion direction took place. Right panel plots magnified the response profiles shown in the left panel plots around the direction change event.

We investigated the overall effect of direction change on the MT population response by constructing population response profile as depicted in Figure 3. Responses of each neuron aligned to the pre-change preferred direction were averaged across neurons to construct the population response profile for both unattended (Figure 3a) and attended (Figure 3b) stimuli. X-axis plots time with t=0 corresponding to the direction change onset, the y-axis is the direction, and the population responses are represented with colors as indicated by the color scale in the most right column. As the left panel of the figure indicates, pre- and post-change population responses to attended stimulus are larger than the responses evoked in unattended condition (an average response enhancement about 13% (See Supplementary Information 1)). The figure also shows that the dynamics of moving stimulus are reflected in the population responses. The plots in the middle column of Figure 3 show the same information as the ones in the

left with magnification around the change event. The white solid line represents the direction of the physical stimulus and the black curve is the location of the population peak activity (see Methods). A closer look at the response profile around the direction change event (middle column in Figure 3) reveals that although MT population precisely represented the direction of motion (prior to the direction change), the information of the direction change (following the direction change) was overestimated.

We quantified the effects of unattended and attended direction changes on the population response by determining pre- and post-change population response curves in both attentional conditions (Figure 4e). Population response curves in each attention condition are determined using the average of across-cell population responses over the time period from -700 to 0 ms (pre-change) and +100 ms to +200 ms (post-change). Black and gray solid lines show the motion direction prior to and following the change event, respectively. Dark and light dashed lines represent the peak location of pre- and post-change population response curves. An unattended direction change of 25^{o} induces a repulsive shift of 9^{o} in the peak location of population response curve (location of dashed light red line relative to solid gray). The shift increases to 14^{o} when the stimulus is attended (dashed light blue line relative to solid gray). Changes in other parameters of population response curve induced by unattended and attended direction changes are provided in Supplementary Information 2. Control analysis indicated that these findings do not depend on the selection of pre- and post-change time windows (See Supplementary Information 3).

It is obvious that the effect of a direction change on a given neuron's response depends on its preferred direction. A direction change away from the neuron's preferred direction (or at the preferred direction) should decrease response, while a change towards the preferred direction should cause a response increase. We investigated this by taking a cross-section of the population response profile (Figure 4a-b). Figure 4a-b plots the responses of neurons with 3 different direction preferences of 0^{o}, 25^{o}, and beyond 30° as a function of time. As expected the direction change caused a drop in responses of the neuron preferring

0^o and increased responses for the neuron with the preferred direction of 25°, i.e. when the direction change aligned the stimulus direction to the neuron's preferred direction. Unexpectedly, but in line with the observations from the population plots in Figure 3, the largest response was evoked for neurons where the stimulus change fell short of what would have been needed to overcome the angular distance to the neuron's preferred direction. Dynamics of population activity have characteristics similar to that of a single neuron's responses: (1) a transient response component triggered by the direction change and (2) a difference between pre- and post-change responses to a given direction. Similar to the responses of a single cell (Figure 2a), there is a difference between population responses to the same motion direction prior to and following the direction change. For instance, as illustrated in Figure 4b (attended condition), post-change responses of cells preferring 25^o to the direction of 25^o are different from the pre-change responses of cells preferring 0^o to the stimulus moving in 0^o. Although the abrupt change in motion direction induced a transient change in the neuron's response (Figure 2a), our design was ill-suited to investigate the transient change in the population response beyond 200 ms from direction change onset. This is mainly because: (1) the post-change period in our experiment is relatively short to permit post-change responses to vary with time, (2) the variability between the response latency of different neurons (See Supplementary Information 4) causes the transient change looks stationary in time following the change. We tested whether direction change can induce a transient change in population response if the responses of each individual neuron used to produce the population response profile are aligned to the time of peak response induced by the direction change rather than direction change time (Figure 4c-d). The results show that if the peaks of neuronal responses are aligned (t=0), the population responses following the direction change exhibit a pattern similar to that of a single cell. This implies that a direction change induces a transient change in population response. To investigate how attention affected the response latency to the direction change, we compared the latencies of both attentional conditions. Our analysis showed that the median of response latency to the direction change in both conditions was approximately 80 ms,

which matches well with previously reported neuronal latencies in the area MT. We did not find any significant difference between the latencies of unattended and attended responses to the direction change ($p = 0.3$, paired two-sided Wilcoxon test for distributions with equal medians) (See Figure S2).

We estimated the direction change influence on the direction tuning of individual MT cells in both attentional conditions by examining the histograms of the distribution of change in tuning parameters induced by the direction change. Figure 5a plots the distribution of shift in preferred direction for both unattended and attended stimuli inside the receptive field shown in red and blue. It indicates that the direction change of $+25^{o}$ significantly shifted the preferred direction of MT cells. The median shift when the unattended stimulus was inside the receptive field was -6^{o} ($p = 0.0005$, two-sided Wilcoxon signed rank test for distribution with zero median). The shift became significantly larger for attended stimulus inside the receptive field ($p = 0.001$, paired two-sided Wilcoxon test for distributions with equal medians) with the median of -14^{o} ($p = 0.0000005$, two-sided Wilcoxon test for distribution with zero median). The impact of direction change on the bandwidth, defined as the full width at half height of the tuning, is shown in Figure 5b. Direction change decreased the bandwidth with a post- to the pre-change ratio of 0.93 ($p = 0.00007$, two-sided Wilcoxon signed rank test for distribution with a median equal to 1) when stimulus inside the receptive field was unattended. Although attended direction change made the tuning curves narrower with a post- to pre-change ratio of 0.92 ($p = 0.03$, two-sided Wilcoxon signed rank test for distribution with median equal to 1), the impact of attention on the bandwidth change was not statistically significant ($p = 0.7$, paired two-sided Wilcoxon test for distributions with equal medians).

The amplitude and asymptote of direction tuning indicate the neuronal responses to the preferred and anti-preferred directions, respectively. The distribution of amplitude ratio (Figure 5c) shows a statistically significant increase in amplitude with both unattended and attended direction changes ($p <$

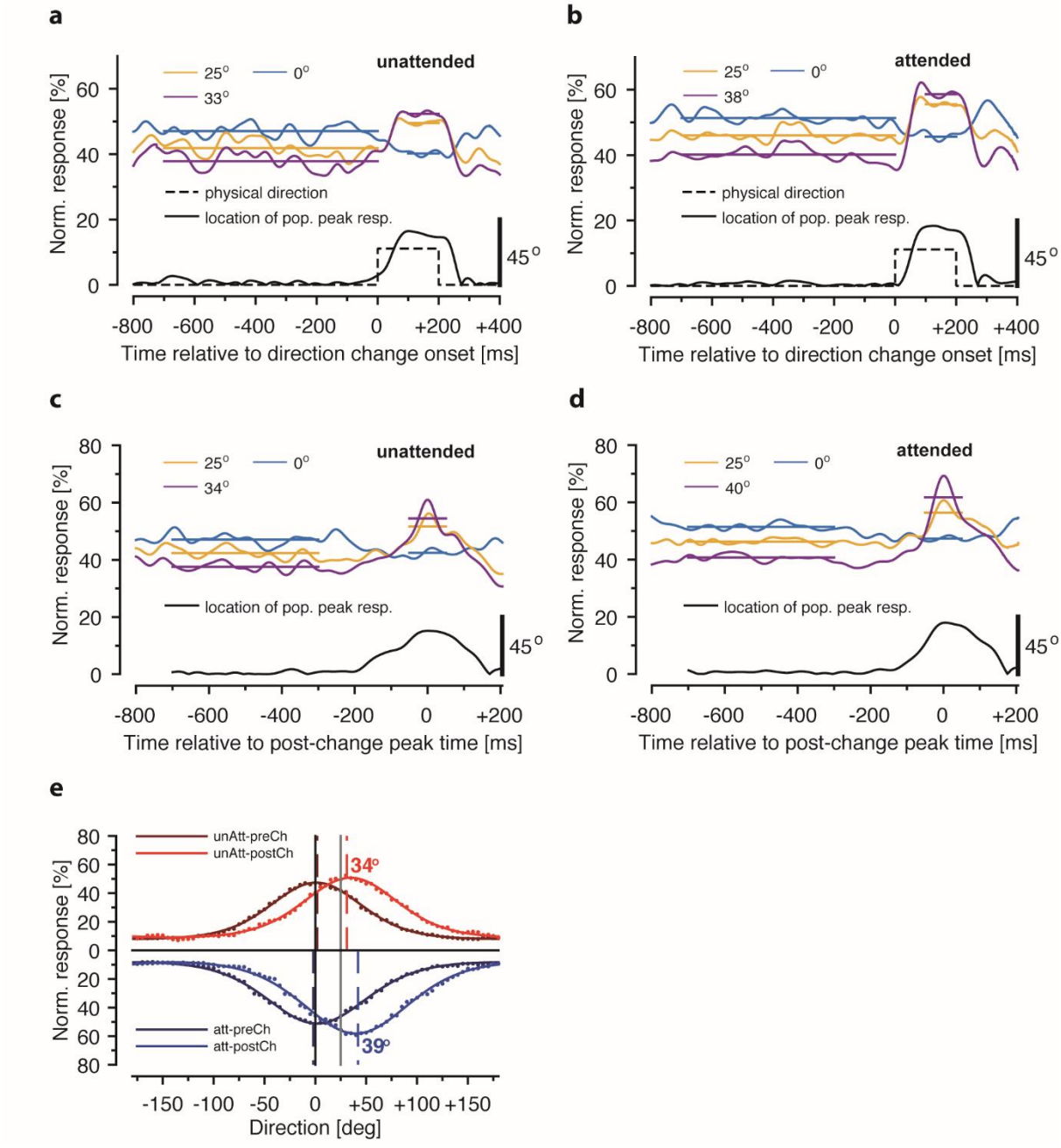

Figure 4 | Population response as a function of time and direction in both attentional conditions: (a-d) population PSTHs: neuronal responses in different directions were aligned to (a, b) onset of direction change, and (c, d) the time of peak response evoked by direction change. PSTHs in different colors represent population responses to different directions, black dashed and solid lines indicate the dynamics of stimulus and the peak location of population response, respectively, (e) population direction tunings: population responses prior (-700-0 ms) and subsequent (100-200 ms) to the direction change of 25°. Black and grey solid lines show the stimulus direction prior and subsequent to the direction change of 25°. The dark and light dashed lines in each attention condition indicate the location of population peak response to motion (pre-change) and direction change (post-change), respectively.

0.0005, two-sided Wilcoxon signed rank test for distribution with a median equal to 1). The median ratio in both attentional conditions was 1.18 (18% increase in the response to preferred directions). Figure 5d shows that the asymptote of direction tuning was significantly enhanced by direction change ($p < 0.05$, two-

sided Wilcoxon signed rank test for distribution with a median equal to 1). The median increase in the response to anti-preferred direction in unattended and attended conditions was 6% and 8%, respectively. We did not find any significant influence of spatial attention on the asymptote change induced by the direction change ($p = 0.4$, paired two-sided Wilcoxon test for distributions with equal medians). We carried out several controls to ensure our results are independent of the standard deviation of the Gaussian kernel used to calculate the spike density function, tuning characteristics of neurons, selection of analysis time windows, and that they are induced by the direction change (See Supplementary Information 5).

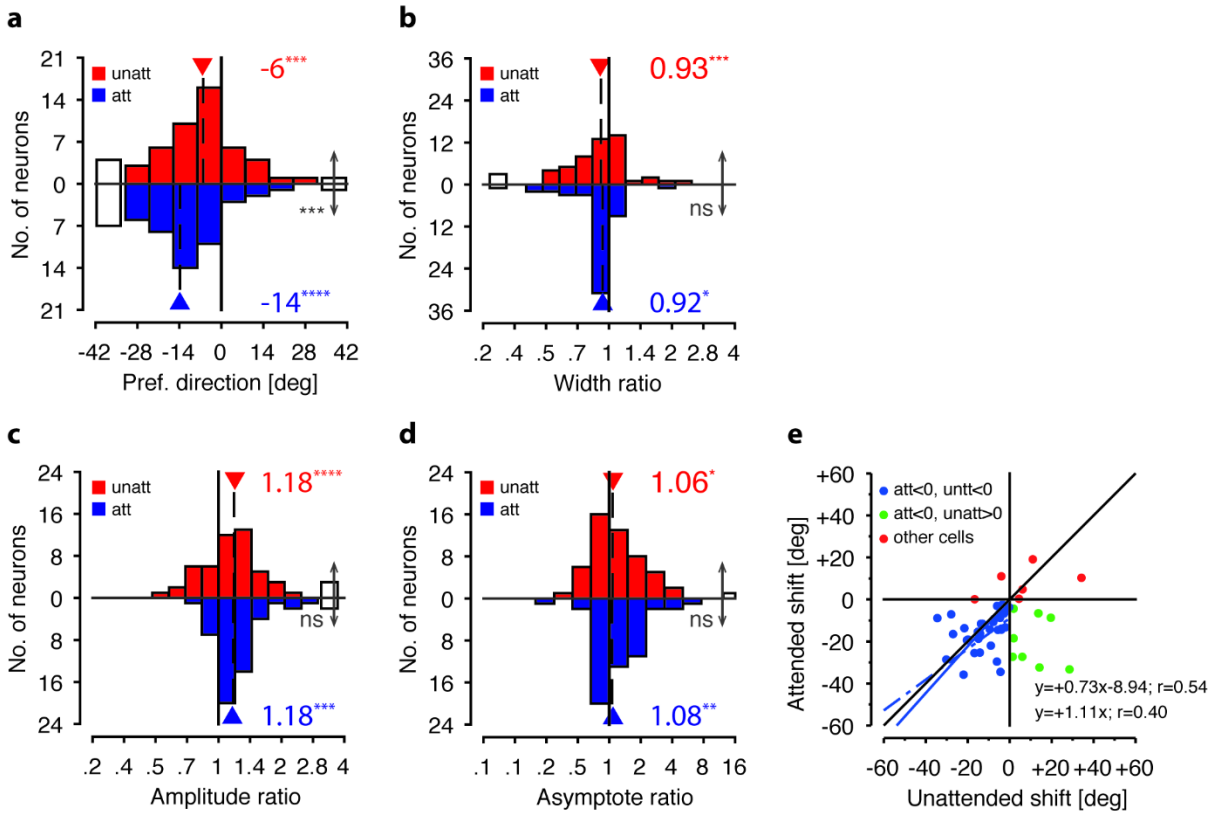

Figure 5 | Direction change influence on the response characteristics of individual MT cells: (a-d) changes of direction tuning parameters caused by unattended (red) and attended (blue) direction changes. Dashed lines and arrowheads indicate the median of change in tuning parameters, which are also shown in the figure, (e) comparison between tuning shifts in unattended and attended conditions across cells (n=52). Most cells had more negative shifts in attended than the unattended condition for a positive direction change (dots below the identity line). Cells were divided into three groups on the basis of the unattended and attended tuning shifts. Almost three-quarters of the cells (indicated by blue circles, n=36) showed negative shifts in both attention conditions. The result of a linear fit to this data (blue lines) shows that the magnitude of tuning shift in attended condition was larger than the unattended condition.

To further examine the shift of direction tuning, we fitted a skewed von Mises function to the tuning curve data. In two separate analyses, we included

tuned-, direction-selective cells from fit to each of symmetric and skewed von Mises functions each time (See Supplementary Information 6). The consistent results indicate that regardless of the symmetry of the function employed to fit the data, post-change direction tuning is shifted from the pre-change tuning and it is larger in attended condition than unattended one. Our analysis, therefore, indicates that although direction change significantly changed different tuning parameters, tuning shift induced by the direction change was the only parameter significantly affected by spatial attention.

To investigate the relationship between tuning shifts in unattended and attended conditions, we compared the tuning shifts in both conditions across the cells (Figure 5e). For most cells, the tuning shift in attended condition is more negative than the unattended condition for the positive direction change (most points below the identity line). For almost three-quarters of the cells that tuning shifts in both unattended and attended conditions were negative (cells in the third quadrant shown as blue points), we performed the simple linear regression analysis with and without an intercept term. Solid and dashed blue lines in the figure represent the results. The Pearson's linear correlation coefficients were 0.54 and 0.40 for these models, respectively. Both regression models, therefore, show a correlation between unattended and attended tuning shifts. The models also predict a more negative shift in attended condition than the unattended condition in the range of observed shifts (for a positive direction change).

4.2 Mechanism underlying the overestimation of direction change

Our results showed that change in motion direction induced a transient change in the neuronal responses. Response change following the direction change resulted in a shift in the direction tuning of MT neurons. The shift was larger in attended condition than the unattended condition. Here we test whether the fatigue-based models of adaptation could explain our observations. To do this, we investigated whether: (1) pre-change spike-rate adaptation correlates with post-change tuning shift, (2) there is any relationship between attentional modulation of pre-change spike-rate adaptation and larger shifts in attended condition, (3)

attentional modulation of pre-change tuning parameters can describe larger tuning shifts in attended condition, (4) the magnitude of tuning shift depends on pre-change motion exposure time (duration scaling).

4.2.1 Correlation between pre-change bandwidth and tuning shift suggests spike-rate adaptation as a cause of tuning shift

It is clear that if pre-change spike-rate adaptation induces the tuning shift, the tuning shift should be correlated with pre-change bandwidth. This means that since cells with narrow tuning curves are less adapted compared with the cells with broad tuning curves, tuning shift of cells with narrow tuning curves should be smaller than that for cells with broad tuning curves. To test this, we examined the relationship between direction tuning parameters before the change and tuning shift induced by the direction change. Figure 6a plots the post-change tuning shift induced by the direction change as a function of pre-change bandwidth in both attentional conditions for all the cells. We used the color-coding introduced in the Figure 5e. To quantify the relationship between tuning shift and pre-change bandwidth we fitted a linear mixed-effects model on the data of the cells that showed negative tuning shifts (for positive direction change) in both attention conditions (blue points). We considered fixed effects for the bandwidth with uncorrelated random effect for the coefficients grouped by the attention condition. Since our analysis indicated that the random-effects term is not statistically significant ($p > 0.1$, t-test), a simple linear regression line ($r = -0.39$, Pearson correlation) describes the relationship between tuning shift and pre-change bandwidth in both attentional conditions (blue solid line in Figure 6a).

Although the intercept term of the regression line was not significantly different from zero ($p = 0.63$, t-statistics for a test that the intercept is zero), the slope showed a significant difference from zero ($p = 0.0006$, t-statistics for a test that the slope is zero). The linear model fit with no significant intercept term suggests that the ratio of the post-change tuning shift to pre-change bandwidth is the same across cells. Our analysis revealed that the width of the pre-change tuning was the only tuning parameter correlated with the tuning shift.

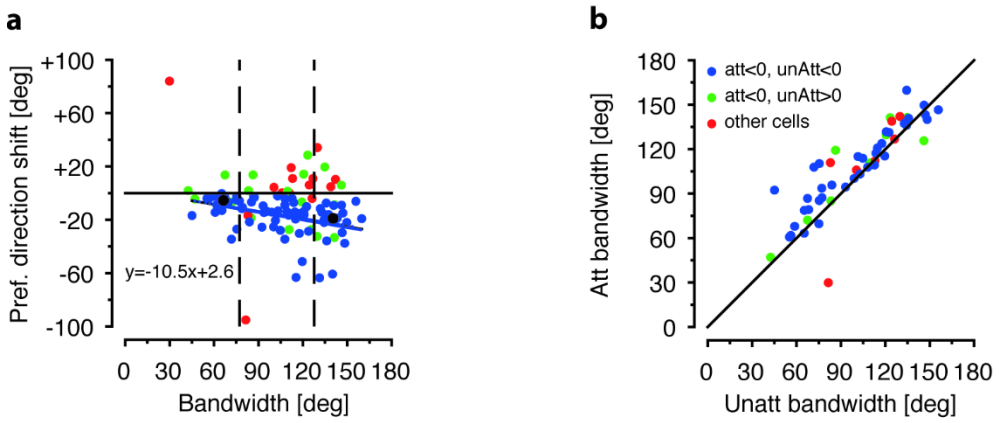

Figure 6 | Correlation between pre-change bandwidth and tuning shift caused by direction change, (a) direction tuning shift as a function of tuning width prior to the direction change. The color code is as same as the Figure 5e. The blue line is the simple linear fit to the data of cells, which showed negative shifts in both attentional conditions (n=36). Black dashed lines show first and third quantiles of bandwidth data. Black circles indicate the average bandwidth and tuning shift of two groups of tuning curves: a group with tuning bandwidths narrower than first quantile and the other group with tunings broader than third quantile, (b) influence of attention on the pre-change tuning bandwidth of the neurons in the direction change detection task (n=52).

We confirmed the relationship between tuning shift induced by the direction change and the pre-change bandwidth by sorting the bandwidth data of the cells that showed negative shifts in both attentional conditions (n=36). The tuning shift was computed for the 25% narrowest and 25% broadest tuning curves. The median bandwidth of the group with 25% narrowest tuning curves was 66^{o} that was significantly less than the median bandwidth of 140^{o} for the group with 25% broadest tuning curves ($p = 0.0000003$, two-sided Wilcoxon rank sum test for distributions with equal medians). Comparison between the medians of tuning shifts in these two groups revealed that the tuning shift for the group with narrow tunings was significantly less than the shift of the group with broad tunings ($p = 0.0005$, two-sided Wilcoxon rank sum test for distributions with equal medians). The group with narrow tuning curves had a median shift of -5^{o}, whereas it was -19^{o} for the group with broad tuning curves. Black filled circles in Figure 6a illustrate the median bandwidth and median tuning shift for each group and the vertical black dashed lines are the first and third quantiles of the bandwidth. We also investigated the difference between the tuning shifts for the groups of tuning curves that had the same median bandwidths ($p > 0.05$, two-sided Wilcoxon rank sum test for distributions with equal medians). We

randomly selected equal numbers of tuning curves for two groups from the data of neurons that showed negative shifts in both attentional conditions. We only considered the two groups with no significant difference between median bandwidths of them and computed the median tuning shifts induced by the direction change for either group. This procedure was repeated for 10,000 times and in about 96% of cases the difference between the tuning shifts did not reach the significance level ($p > 0.05$, two-sided Wilcoxon rank sum test for distributions with equal medians). This indicates that there is no difference between the post-change tuning shifts of the groups with similar pre-change bandwidths.

Our preliminary results suggest that pre-change spike-rate adaptation can account for the tuning shift observed in unattended and attended conditions.

4.2.2 Attentional modulation of pre-change bandwidth cannot explain larger tuning shift in attended condition

We demonstrated that attention increases the shift of tuning curves. We also showed that the tuning shift is correlated with the pre-change bandwidth. Therefore, one may speculate that the increased shift in attended condition might be resulted from broadening the pre-change bandwidth by the attention. In the first attempt to test this idea, we computed attentional modulation of pre-change bandwidth by comparing the pre-change bandwidth of tuning curves in unattended and attended conditions (Figure 6b). We found that attention significantly broadened the pre-change bandwidth of neurons from 104^o to 111^o ($p = 0.00003$, paired two-sided Wilcoxon test for distributions with equal medians). We also determined the attentional modulation of pre-change bandwidth in another dataset including 146 MT cells. The data were collected from the same animals while they were performing a similar task (speed change detection task). The median bandwidth in attended condition was 108^o that showed a statistically significant difference from 104^o observed in unattended condition ($p = 0.000005$, paired two-sided Wilcoxon test for distributions with equal medians) (See Supplementary Information 7). As indicated by blue points in Figure 6b, attention broadened tuning curves of the neurons that showed negative shifts in

both attentional conditions ($p = 0.0001$, paired two-sided Wilcoxon test for distributions with equal medians). The medians of pre-change bandwidth in unattended and attended conditions for these cells were 102^o and 109^o, respectively. Our analysis also showed that attention significantly increased the tuning shift of the cells from -12^o to -14^o ($p = 0.005$, paired two-sided Wilcoxon test for distributions with equal medians). Although we found that attention increased the pre-change bandwidth, we failed to show that the attentional modulation of pre-change bandwidth caused a greater shift of post-change tuning curve (See Supplementary Information 8).

4.2.3 Attentional modulation of parameters of pre-change tuning curve cannot explain larger tuning shift in attended condition

One may suspect that the bigger tuning shift in attended condition could be explained by the difference between tuning parameters prior to the direction change in two attentional conditions. To address this issue, we studied the correlation between attention modulation of different tuning parameters prior to the change, $(X_{att}-X_{unatt})/(X_{att}+X_{unatt})$, and tuning shift change by the attention. Our results (See Supplementary Information 9) show that changes in tuning shift associated by attention do not correlate with modulation of any of pre-change tuning parameters (Pearson's linear correlation coefficient < 0.06) and therefore, larger tuning shift in attended condition cannot be attributed to attentional modulation of different pre-change tuning parameters.

4.2.4 Similarity between pre-change spike-rate adaptation in unattended and attended conditions suggests that larger tuning shift in attended condition is not related to attentional modulation of spike-rate adaptation

To investigate the effect of adaptation on the neuronal responses during the course of exposure to the stimulus prior to the direction change, we compared the parameters of direction tuning between two time windows: a time window from 400 to 700 ms following the motion onset (in the sustained phase of response after motion onset), and a time window lasting 300 ms before the direction change. Figure 7a is the histogram of the distribution of amplitude ratio (before the change to after motion onset) over the course of stimulus exposure prior to

the direction change for both unattended (red) and attended (blue) conditions across all neurons. The median amplitude ratio when the stimulus inside the receptive field was unattended was 0.93 with a significant difference from 1 ($p = 0.0005$, two-sided Wilcoxon signed rank test for distribution with a median equal to 1). In attended condition this ratio changed to 0.94, which was significantly different from 1 ($p = 0.0008$, two-sided Wilcoxon signed rank test for distribution with median equal to 1), but the difference between unattended and attended conditions did not reach significance ($p = 0.8$, paired two-sided Wilcoxon test for distributions with equal medians). The results show that the tuning amplitude in both attentional conditions was the only parameter significantly influenced during exposure to the stimulus before the direction change (changes in other tuning parameters during the course of exposure to the stimulus before the direction change in both attentional conditions are provided in Supplementary Information 10). This implies that although adaptation during the course of stimulus exposure prior to direction change reduces the neuronal responses, there is no statistically significant difference between the adaptation effect in unattended and attended conditions.

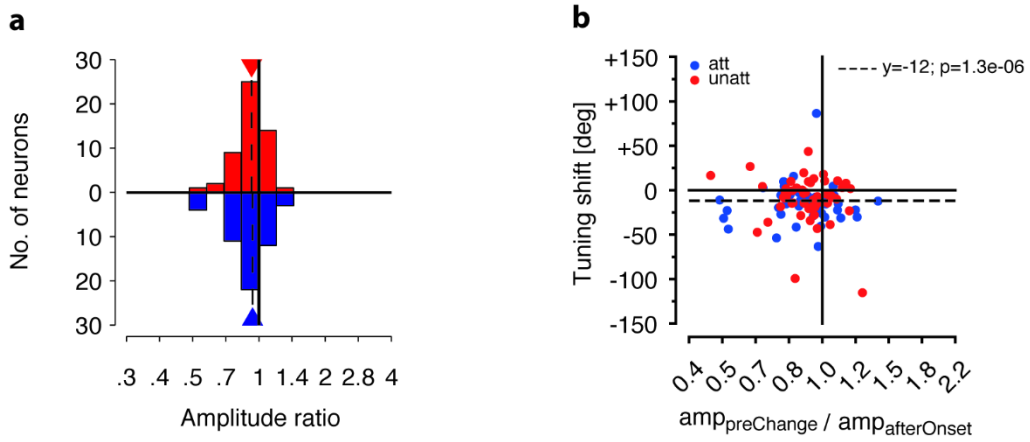

Figure 7 | Spike-rate adaptation over the course of the trial and its relationship with tuning shift in unattended (red) and attended (blue) conditions, (a) influence of pre-change adaptation on the tuning amplitude. Tuning parameters were compared between a time window from 400 to 700 ms following the motion onset (in the sustained phase of response after motion onset) and a time window of 300 ms prior to the direction change. Dashed lines and arrowheads indicate the median of amplitude ratio in each attentional condition, (b) correlation between tuning shift and response change over the course of the trial (n=52).

4.2.5 Pre-change spike-rate adaptation and tuning shift are unrelated

To clarify the role of spike-rate adaptation during the course of trial before direction change, we examined the relationship between the shift of tuning induced by the direction change and the amplitude change during the course of exposure to the stimulus prior to the direction change (Figure 7b). In Figure 7b, red and blue points represent unattended and attended data, respectively and black dashed line is the linear model fit to the data. This line had a statistically significant intercept of -12^{o} ($p = 0.000001$, t statistic for a test that the intercept is zero) with a slope that did not reach significance level ($p = 0.6$, t statistic for a test that the slope is zero). This indicates that independent of response change during the course of stimulus exposure prior to the direction change, the tuning shift caused by the direction change was around -12^{o}.

4.2.6 Tuning shift is unrelated to the stimulus exposure duration prior to the direction change

We performed several analyses to confirm that the stimulus exposure duration prior to the change (300-4000 ms) does not impact the shift of direction tuning subsequent to the change. First, we analyzed the data of the trials that the direction change occurred between 300 and 2700 ms after motion onset. The results indicate that: (1) the magnitude of shift did not change for trials with shorter pre-change exposure duration compared with those having the exposure duration between 300 and 4000 ms, and (2) tuning shift was greater when the stimulus inside the receptive field was attended (See Supplementary Information 11). Second, we divided attended trials into two groups according to the pre-change exposure duration: short trials (early direction change) with exposure duration between 300 and 2700 ms (mean±SD=1870±550 ms), and long trials (late direction change) which change in motion direction happened at least 3100 ms after motion onset (mean±SD=3690±220 ms). Distribution of change in different tuning parameters for both short and long trials (See Supplementary Information 12) revealed that changes of tuning parameters in both groups were in line with the results of our previous analysis (Figure 5a-d, blue histograms). Comparison between changes of tuning parameters induced by the early and late

direction changes, however, did not show any significant difference between them ($p > 0.1$, paired two-sided Wilcoxon test for distributions with equal medians). We, therefore, did not find any relationship between pre-change stimulus exposure duration and tuning shift induced by direction change.

To explore the effects of visual motion adaptation on neural responses, we compared pre- and post-change population response curves (see Methods; Figure 8). As shown in Figure 8a-b, responses following the direction change are enhanced in one flank of the population response curve (right flank), even though in the other flank post-change responses are reduced (left flank). In accordance with this, as we showed earlier that direction change increased both asymptote and amplitude of direction tuning curves (Figure 5c-d). The amplitude of post-change population response curve was also higher than that of pre-change population response curve (Figure 4e). Our finding thus reveals that in contrast to traditional fatigue models of adaptation, neural responses following adaptation are not always reduced.

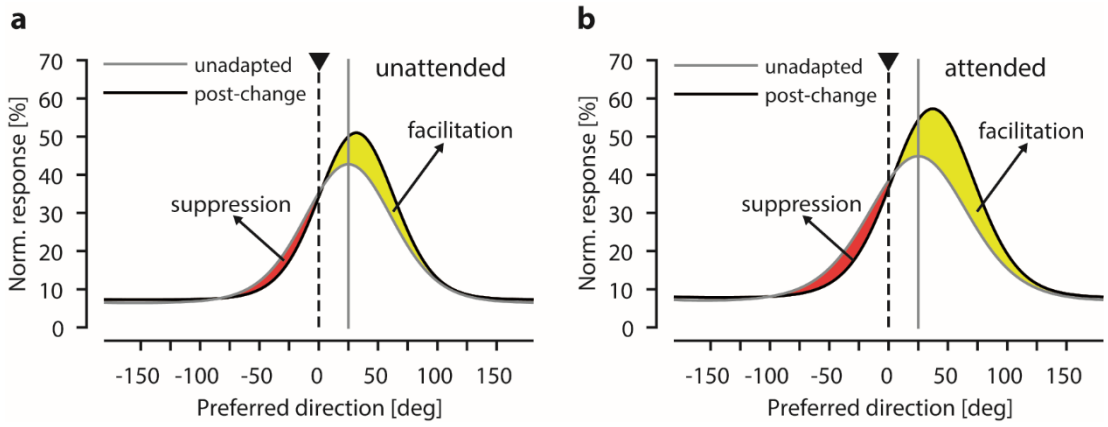

Figure 8 | Population response curves prior to and following the direction change in (a) unattended, (b) attended conditions, For a direction change of +25°, post-change responses (black solid curves) in the positively sloped flank of response curve are suppressed, even though on the other flank responses following the direction change are facilitated. The figure also shows that the effects of adaptation are stimulus-specific, meaning that they are dependent on the pre- and post-change directions. These effects are more pronounced when the stimulus is attended (Fig. 8a compared with 8b). In each attentional condition, we averaged pre- and post-change direction tuning curves across cells after aligning their preferred directions to construct the population response curves prior to and following the direction change (n=52; see Methods).

4.3 Modeling response curves following the direction change

Our results showed that a step change in motion direction shifts the MT response profile and modulates its amplitude. In line with previous reports (Price & Born,

2013; Priebe et al., 2002), we also demonstrated that fatigue hypothesis cannot explain these effects. Here we investigate whether and how a normalization model of adaptation and attention accounts for the effects we observed. This model assumes that visual motion experience not only suppresses the feedforward drive of a neuron (classical receptive field signals) but also weakens the pooled activity of its neighboring neurons (normalization signals) and therefore, facilitates responses of the neuron (S. G. Solomon & Kohn, 2014). We assessed the suppressive effect of adaptation on the response by subtracting the pre-change response profile from a response profile driven by a stimulus *moving* in the post-change direction (Figure 9; see Methods). As we considered a divisive form of tuned normalization (Rust et al., 2006; Simoncelli & Heeger, 1998), the resultant profile was multiplied by an inverted pre-change response profile to model adaptation effect on the normalization signals (Snowden et al., 1991). In each attentional condition, we adjusted the asymptote and amplitude of both suppressive and facilitatory profiles to get the best fit to the observed post-change response curve. We fixed the peak location of the modeled post-change response curve at the location of the peak of the observed post-change population response curve. We found that the model results in an excellent fit to the post-change responses in both attentional conditions. While a large part (77%) of the response profile shift (6.7°) following the direction change in unattended condition is due to the suppression of classical receptive field signals, the adaptation influence on tuned normalization contributed to the remaining shift (23%). Attending to the stimulus modulated both suppressive and facilitatory effects of adaptation by 56% and 180%, respectively. In the attended condition, suppression of classical receptive field signals contributed to 66% of the post-change response curve shift of 12.3°. Strengthened tuned normalization by attention increased its contribution to the post-change response curve shift to 34%. This is consistent with the notion that the strength of tuned normalization covaries with attentional modulation (Ni et al., 2012; Verhoef & Maunsell, 2017).

Modeling, therefore, shows that the tuned normalization model of adaptation which takes into account both the suppressive and facilitatory effects

of visual motion exposure on the neuronal responses successfully captures the post-change responses in both attentional conditions.

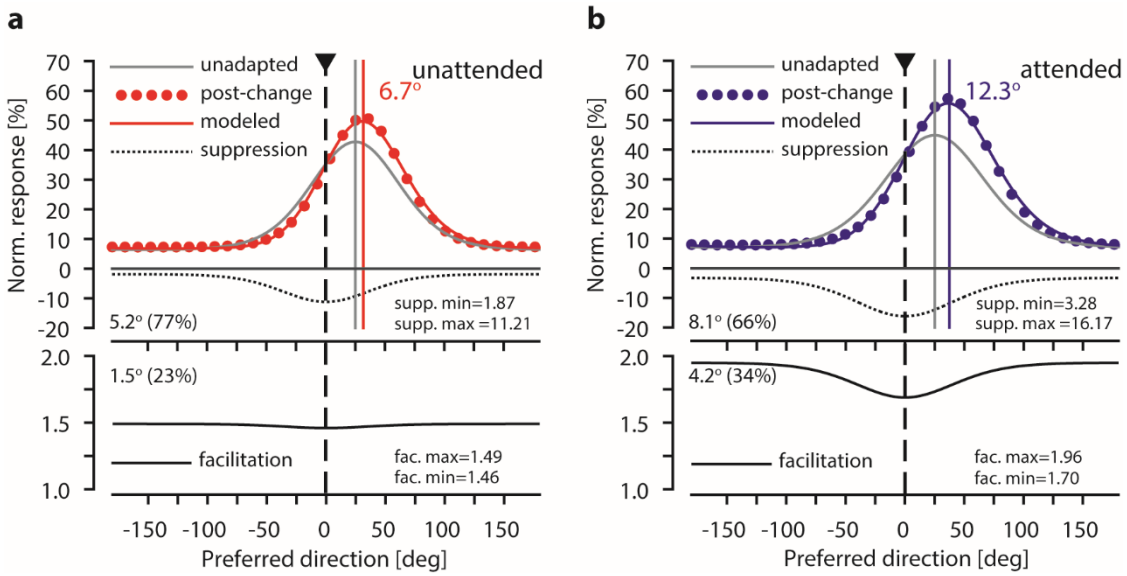

Figure 9 | Modeling of direction change overestimation in (a) unattended, (b) attended condition. Adaptation exerts influences on both feedforward drive of the neurons (suppressive effect of adaptation) and normalization signals (facilitatory effect of adaptation). We modeled the suppressive effect of adaptation by subtracting the pre-change response profile (black dashed curve in the top panel of each figure) from the response curve driven by a stimulus moving in a post-change direction (grey curves). We multiplied the result by an inverted pre-change response profile to take the facilitatory effect of adaptation into account (black solid curve in the bottom panel of each figure). We varied the asymptote and amplitude of both suppressive and facilitatory profiles to get the best fit to the observed post-change response curve (red/blue dotted curves). Peak locations of the modeled post-change response curves (red/blue solid curves) were fixed at the observed post-change peak locations. The x-axis is direction, the y-axis is the normalized response, vertical black dashed lines with downward arrowheads indicate pre-change motion direction, and vertical grey solid lines show post-change direction. Vertical red/blue lines show the peak location of the observed post-change response curve.

4.4 Perception of direction change

Although the findings of the monkey electrophysiology experiment demonstrates that the representation of direction change in area MT of monkey is overestimated, it remains unclear how a change in the direction of a moving stimulus is perceived. To address this issue, we examined the perception of direction change in human subjects using a design, which was similar to the one of monkey electrophysiology experiment (Figure 10a; see Methods). While the subjects gazed at a central fixation point and covertly attended to the right visual hemifield, two random dot patterns moving in the same direction were displayed one in each hemifield. At a random time after motion onset, a direction change occurred in the right stimulus. Figure 10b illustrates four possible conditions of the task: the motion direction could be either leftward or rightward (left column

and right column, respectively). In each case, both clockwise and counterclockwise direction changes occurred with the same probability (first row and second row, respectively). In all cases the post-change motion direction was close to the horizontal. The subject's task was to judge the motion direction following the change relative to the horizontal. This allowed us to estimate the perceived direction change in a counterbalanced design of rightward versus leftward motions and clockwise versus counterclockwise direction changes. For each of rightward and leftward motion directions, the error in the perception of direction change was computed using the point of subjective equality (PSE) measured in the corresponding staircase procedures for clockwise and counterclockwise direction changes (see Methods). Figure 10c summarizes the result of this experiment for 10 subjects (3 males, aged 21-35) and the median effect across all subjects shown in the last bar. We averaged the errors of the perceived direction change in leftward and rightward moving patterns (Supplementary Information 13 provides errors in perceived direction changes computed separately for both leftward and rightward motions). According to the sign convention used in our analysis, positive and negative errors illustrated in the y-axis correspond to overestimation and underestimation of direction change, respectively. The median error in perceived direction change across subjects showed an overestimation of 6^o ($p = 0.004$, two-sided Wilcoxon signed rank test for distribution with zero median). The result of this experiment is in line with the electrophysiological findings and indicates that perceived direction change in human subjects is overestimated.

We demonstrated that both MT representation and perception of direction change are overestimated, but it is not clear whether there is a causal link between these two effects. While MT has been linked causally to motion perception, there are several perceptual motion phenomena, such as reference repulsion, that presumably are higher level and not causal by MT activity. We tested whether repulsion happens even when direction representation in MT is veridical. In order to do this, we designed a second task, which was identical to the first psychophysical experiment in all aspects, except that a perceptually irrelevant random dot pattern was superimposed to each stimulus. The

irrelevant random dot pattern was in yellow color and moved in a direction such that the expected MT overestimation of direction change diminished while the perceptual task remained unchanged (Figure 11a). Each stimulus, therefore, consisted of two sets of dots in white and yellow colors moving in directions

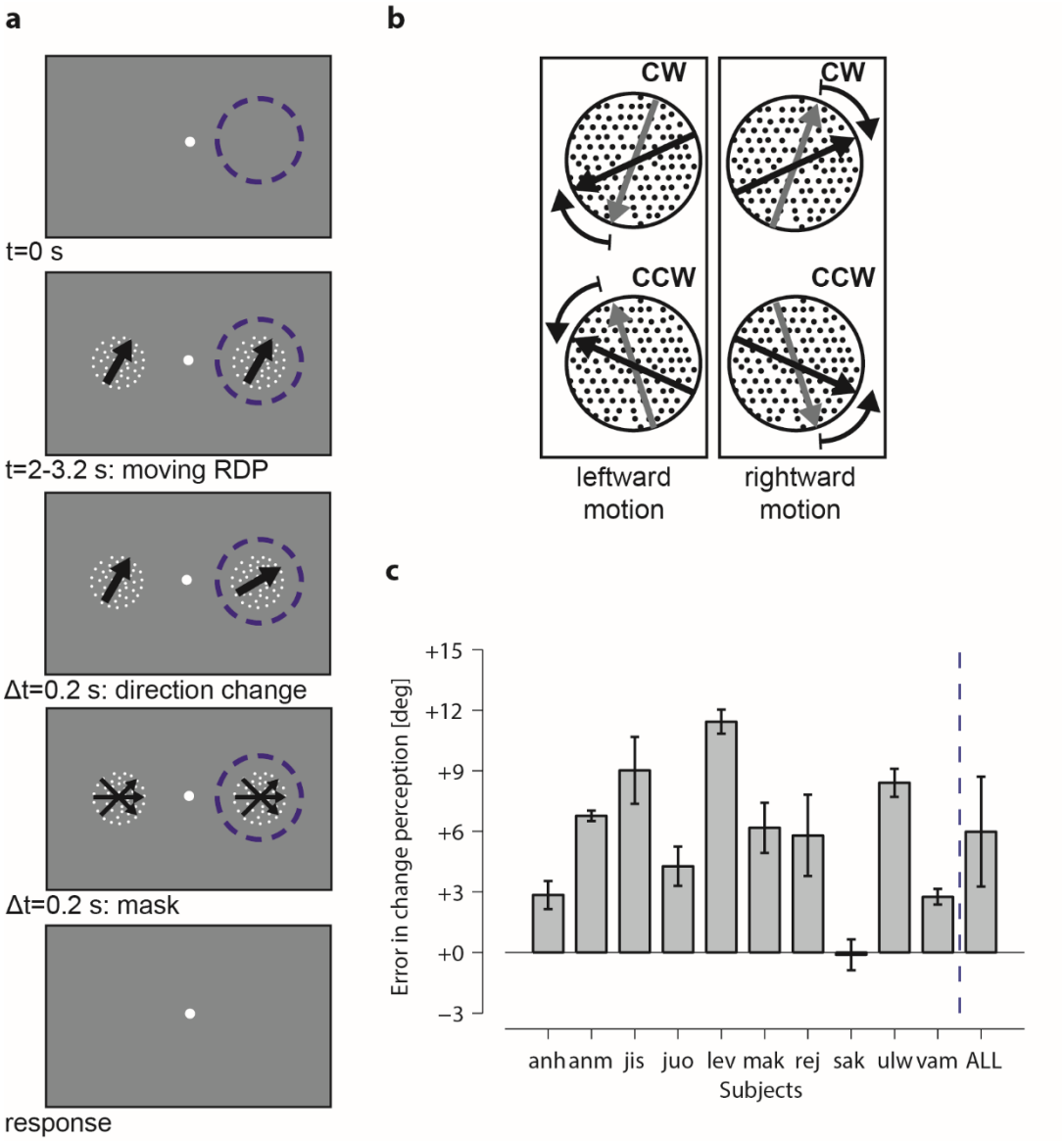

Figure 10 | *Investigation of perceived direction change*, (a) paradigm of human psychophysical experiment: while the subjects maintained fixation on a central small point (white dot) and covertly attended to the stimulus in the right hemifield (dashed circle), they pressed a button of a gamepad to start a trial. Then, two coherent random dot patterns moving in the same direction were simultaneously shown in both visual hemifields. After random time between 2 and 3.2 s a direction change of 25º occurred in the right random dot pattern. 200 ms later, coherent random dot patterns were replaced with two mask random dot patterns, which were displayed for 200 ms. After disappearing the mask stimuli, subjects were required to report the post-change motion direction was upward or downward relative to the horizontal, (b) the stimulus configuration in psychophysical task: in a given trial, random dot patterns could move either leftward (left column) or rightward (right column). For each motion direction, one of two clockwise (CW, first row) and counterclockwise (CCW, second row) could occur. Grey and black arrows indicate pre- and post-change motion directions, respectively. Arc arrows show the direction change, (c) the results of the human psychophysical experiment. Subject names are shown in abscissa (last bar reflects the median effect across all subjects) and ordinate represents the median of error in the perceived direction change. Error bars are the median absolute deviations.

separated by ±25° relative to the post-change direction. The direction change always occurred in the relevant random dot pattern (white dots) of the right stimulus while the irrelevant one (yellow dots) simultaneously disappeared. The subjects were required to report the post-change motion direction of the relevant random dot pattern in the right stimulus relative to the horizontal. Figure 11b, top panel illustrates the physical direction of a stimulus following the change when it is horizontal. Both MT adaptation and higher-level mechanisms may contribute to the overestimation of perceived direction change observed in the first psychophysical experiment (Fig 11b, middle panel). Exposure to two superimposed sets of dots in different colors moving in directions with opposite offsets relative to the post-change direction of stimulus reveals the contributions of adaptation and higher-level mechanisms to the overestimation of post-change

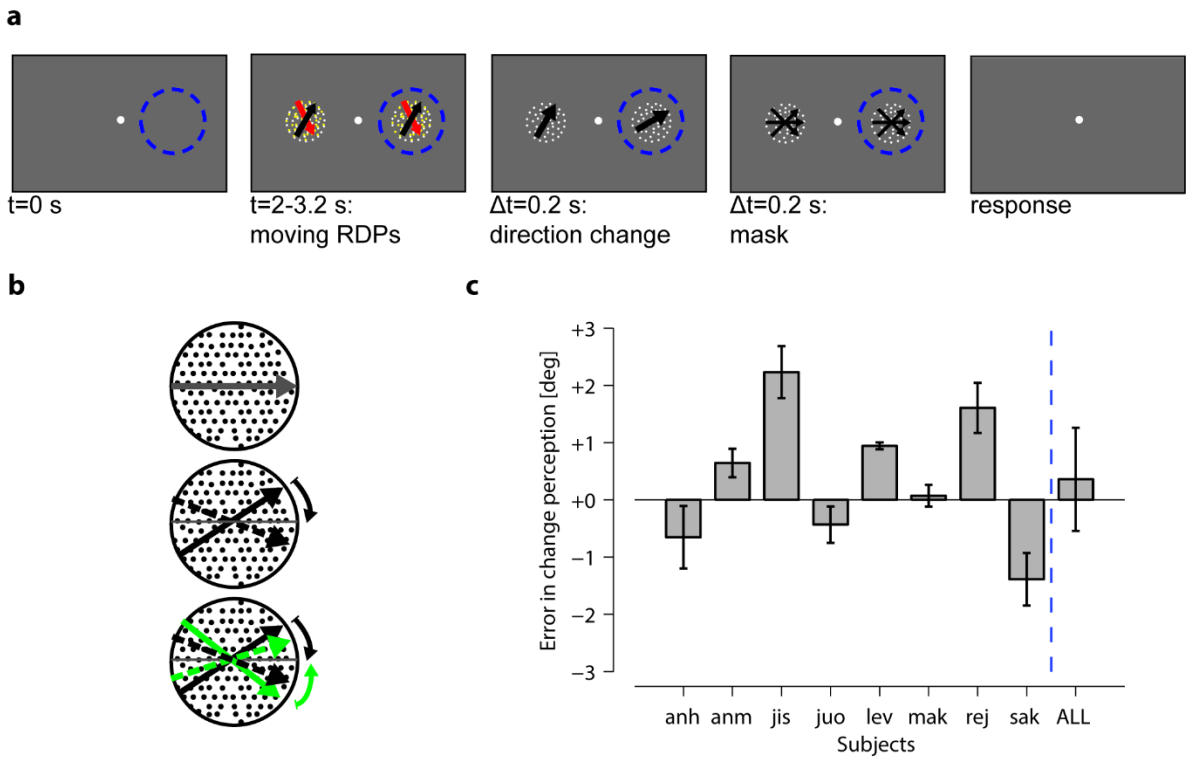

Figure 11 | Causal link between MT representation and perception of direction change, (a) human psychophysical task designed to study the contribution of MT adaptation and higher level effects to the overestimation of perceived direction change. The task was similar to the previous psychophysical task (Figure 10), except that a perceptually irrelevant random dot pattern with a different color (yellow) was superimposed to each of pre-change stimuli. The irrelevant (yellow) and relevant (white) random dot patterns moved with opposite offsets relative to the post-change direction, (b) top: post-change physical direction (horizontal grey arrow), middle: exposure to pre-change direction (solid arrow) causes the post-change horizontal direction (grey line) to appear downward (dashed arrow), bottom: adaptation with random dot patterns with opposite offsets (solid black and solid green arrows) relative to the post-change direction (horizontal grey line) induces errors in the perceived post-change direction (dashed black and dashed green arrows), which cancel out each other's effects, (c) the psychophysical results: subject names are shown in abscissa (the last bar reflects the median effect across all subjects) and ordinate represents the median of error in the perceived direction change. Error bars are the median absolute deviations.

direction. High-level mechanisms suggest a direction change overestimation of the relevant random dot pattern independent of the presence of irrelevant random dot pattern, whereas MT adaptation predicts an accurate perception of post-change direction. This is mainly due to the fact that based on the physiological effect of adaptation in MT, pre-change moving patterns with opposite offsets cancel out each other's influence on the post-change direction and thereby, there will be a diminished or absent overestimation in perceived direction change (Figure 11b, bottom panel). Figure 11c plots the results of this experiment just like Figure 10c (Supplementary Information 14). The median error in the perceived direction change across subjects was $+0.4^{o}$, which was not significantly different from zero ($p > 0.5$, two-sided Wilcoxon signed rank test for distribution with zero median). These results support the hypothesis of a causal link between the MT representation of direction change and perception, however, the results undermine the influence of high-level mechanisms on the misperception of direction change.

4.5 Neural correlate of perceptual direction change overestimation

A linking model can explain how direction tuning shift of MT cells induced by the direction change might underlie the overestimation of perceived direction change.

To explore whether and how a linking model can account for the overestimation of the perceived direction change based on the response characteristics of MT cells, we created MT population response profile by implementation of a labeled-line model and readout the perceived direction from the profile using a winner-take-all approach. In the labeled-line model of direction encoding, there are neurons selective for different directions. For each preferred direction, there is only one representative neuron with the tuning parameters equal to the average of those across all the neurons having the same preferred direction. In this model, the label of each neuron is its pre-change preferred direction and the population response profile is the distribution of responses of the neurons with different labels to the presented stimulus. According to the winner-take-all method, the perceived direction is the label of

neuron responding maximally to the stimulus (peak location of the population response profile). Figure 12 illustrates how shift in the preferred direction of single neurons due to direction change might result in the overestimation of perceived direction change in both unattended (left column) and attended (right column) conditions. Figure 12a plots the tuning curves of four representative neurons shown in different colors prior and subsequent to the direction change of +25° with solid and dashed curves, respectively. The post-change tuning curves are shifted by -7° and -11° following the direction change in unattended and attended stimuli, respectively. Median of the tuning curve parameters prior and subsequent to the direction change were used to construct the pre- and post-change tuning curves of model neurons. The shift was computed as the median

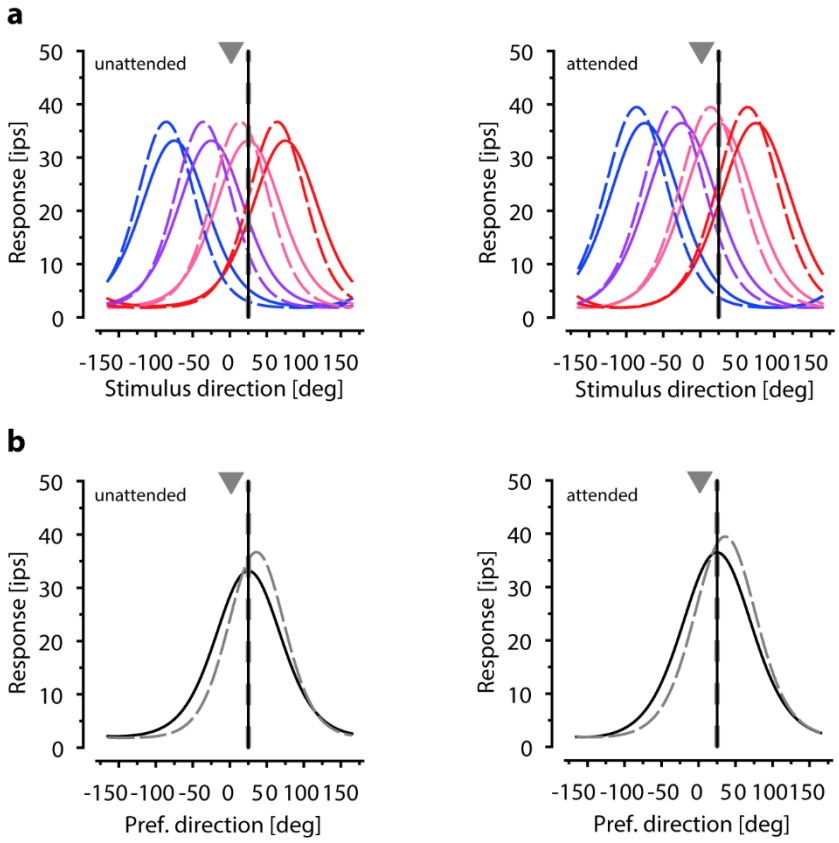

Figure 12 | Link between physiological and perceptual effects of direction change, (a) responses of 4 example neurons (shown in different colors) to a stimulus moving in +25° (solid curves) and a direction change of +25° (dashed curves) in unattended (left panel) and attended (right panel) conditions. Black solid line represents the motion direction, and downward grey arrow and grey dashed line mark the stimulus direction prior to and following the direction change, respectively, (b) population response to the direction (black solid curves) and the direction change (dashed grey curves) of +25° in unattended (left panel) and attended (right panel) conditions. Although population responses to motion direction show a peak for the neurons preferring the same direction in both attention conditions, direction change causes repulsive shifts of the population responses (with the same magnitude as the neuronal tuning shifts, but opposite to it), which is larger in attended condition than unattended condition.

shift of the preferred direction across neurons. Figure 12b demonstrates the population response profiles to a stimulus moving in 25° (solid black curve) and a direction change of 25° (dashed grey curve). Vertical black lines show the motion direction, and the downward grey triangle and the vertical grey dashed line indicate the pre- and post-change motion directions, respectively. Based on the winner-take-all readout of activity, although the perception of motion direction is precise, the shift of population response profile is opposite to the neuronal tuning shift and has the same magnitude. This indicates perceived direction change is exaggerated and spatial attention pronounces the overestimation. This simple model, therefore, can account for the overestimation of perceived direction change and attentional enhancement of overestimation.

5 DISCUSSION

The main goal of this study was to investigate the neuronal representation and perception of unattended and attended change events. Although many studies have investigated the neuronal representation of stimuli with stationary patterns in time, little is known about how changes in these stimuli are encoded in the brain. On the other hand, the influence of attention on the processing of information about stimuli with stationary patterns in time has been well studied, however, to my knowledge, no study has yet demonstrated the attentional influence on the representation of change events. I addressed these questions in the context of MT processing and perception of visual motion with regard to the following considerations: (1) response characteristics of direction-selective cells in MT have been well-documented (Albright et al., 1984; Baker et al., 1981; Felleman & Kaas, 1984; Maunsell & Van Essen, 1983a, 1983b; Van Essen et al., 1981; Zeki, 1974, 1980, 1983), (2) there is a strong evidence indicating the link between the activity of MT neurons and visual motion perception (Britten et al., 1992, 1996; Dodd et al., 2001b; Newsome & Paré, 1988; Newsome et al., 1989; Nichols & Newsome, 2002; Salzman et al., 1990; Zihl et al., 1983), (3) attentional modulation of MT responses have been widely reported (Galashan et al., 2013; Martinez-Trujillo & Treue, 2004; Reynolds & Chelazzi, 2004; Treue, 2001; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996, 1999; Zénon & Krauzlis, 2012), (4) physiological effects of visual motion adaptation in MT have been previously demonstrated (Kar & Krekelberg, 2016; Kohn & Movshon, 2003, 2004; Lisberger & Movshon, 1999; C. A. Patterson, Duijnhouwer, et al., 2014; Petersen et al., 1985; Price & Born, 2013; Priebe & Lisberger, 2002; Priebe et al., 2002; Zavitz et al., 2016), (5) perceptual effects of visual motion adaptation have been

known for many years (Anstis et al., 1998; Clifford, 2002; Glasser et al., 2011; Levinson & Sekuler, 1976; Marshak & Sekuler, 1979; R. Patterson & Becker, 1996; Schrater & Simoncelli, 1998), (6) attention influence on perceptual effects induced by visual motion adaptation has been proved (Alais & Blake, 1999; Berman & Colby, 2002; Blaser & Shepard, 2009; Chaudhuri, 1990; Huk et al., 2001; Lankheet & Verstraten, 1995; Rees et al., 1997; Rezec et al., 2004; Seiffert et al., 2003; Taya et al., 2009). From a different perspective, this study, for the first time, addressed the neuronal substrate of attentional modulation of perceptual effects of adaptation reported in many studies (Alais & Blake, 1999; Berman & Colby, 2002; Blaser & Shepard, 2009; Chaudhuri, 1990; Huk et al., 2001; Lankheet & Verstraten, 1995; Rees et al., 1997; Rezec et al., 2004; Seiffert et al., 2003; Taya et al., 2009).

To accomplish the goal of the study, single-cell recordings were made from the area MT of rhesus monkeys while they performed a motion direction change detection task. The task was designed such that each neuron's responses to unattended and attended stimuli were recorded. In either attentional condition, 12 evenly spaced directions shown for 300-4000 ms preceded a clockwise direction change of $+25^{o}$ for 200 ms.

Most electrophysiological studies documenting the effects of adaptation on the neuronal responses employed a simple adapt-test paradigm (Kar & Krekelberg, 2016; Kohn & Movshon, 2003, 2004; C. A. Patterson et al., 2013; C. A. Patterson, Duijnhouwer, et al., 2014; Petersen et al., 1985; Price & Born, 2013; Priebe & Lisberger, 2002; Priebe et al., 2002). These studies investigated how adaptation to a particular inducing stimulus altered neuronal responses to different test stimuli (adapter: fixed, test: varying) (Kar & Krekelberg, 2016; Kohn & Movshon, 2003, 2004; Price & Born, 2013). On the other hand, some reports indicated how adaptation to different inducing stimuli affected neuronal responses to a particular test stimulus (adapter: varying, test: fixed) (Priebe & Lisberger, 2002). In our paradigm, however, both adapter and test stimuli were varying in a systematic way so that test direction was 25^{o} greater than adapting

direction. This design made it a good candidate for studying the neural representation of direction change events.

The results of our electrophysiological study showed that attention modulated MT responses over the time course of visual stimulation with a median of 13%, which is in the range of attentional signal enhancement previously reported (Seidemann & Newsome, 1999; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996, 1999).

In line with previous studies, I found that direction change induced a transient change in the response (Galashan et al., 2013; Price & Born, 2013; Priebe & Lisberger, 2002; Traschütz et al., 2015). It has been documented that the transient response induced by change events play a key role in sensation and perception of these rapid events (Britten et al., 1996; Celebrini et al., 1993; Cook & Maunsell, 2002b; Galashan et al., 2013; Ghose & Harrison, 2009; Herrington & Assad, 2009; Macknik & Livingstone, 1998; Mechler et al., 1998; Pack & Born, 2001; Price & Born, 2010; Raiguel et al., 1999a; Smith et al., 2011; Traschütz et al., 2015). I, thereby, considered a post-change analysis time window, similar to Price & Born (Price & Born, 2013), from 100 to 200 ms following the direction change, which takes the direction change induced-transient into account. In principle, in agreement with a previous study (Price & Born, 2013), I showed that any post-change time window, which includes the transient response change will yield similar results.

Although MT population response profile (prior to the direction change) showed that the representation of visual motion was precise, comparing the population responses following the direction change and prior to it indicated that a physical direction change of 25^{o} had an unattended MT representation of 34^{o}, an overestimation of 9^{o}. I have demonstrated for the first time that attention modulates the overestimation of direction change represented in MT by about 50%, i.e. an attended overestimation about 39^{o}.

I examined the effects of direction change on the direction tuning of individual MT cells. Consistent with my previous analysis, I found that: (1) a

positive direction change induced a negative shift in the post-change direction tunings, which is similar to the attractive direction tuning shift reported by Kohn & Movshon after prolonged adaptation (40 s, top-up: 5s) to gratings (Kohn & Movshon, 2004), (2) tuning shift was larger in attended than unattended condition, (3) although direction change also affected other direction tuning parameters, our data does not show any significant difference between changes of these parameters in two attentional conditions. These results may provide a detailed picture of speed tuning shifts reported in the study by Price & Born (Price & Born, 2013). Price & Born's study investigated how a speed change affected the speed tuning of MT cells while the duration of exposure to a moving random dot pattern prior to the direction change was very similar to my study (Price & Born, 2013). They reported a statistically significant shift in the speed tuning, which was explained by a lateral shift of preferred speed, vertical gain change, or both since they did not sample data from a full range of speed tuning curve. My results suggest that post-change tuning curves exhibit a lateral shift accompanied by a vertical gain change.

Any sensory experience, adaptation, affects neuronal responses (Glasser et al., 2011; Kar & Krekelberg, 2016; Kohn & Movshon, 2004; C. A. Patterson et al., 2013; Price & Born, 2013; Priebe & Lisberger, 2002; Priebe et al., 2002). My results clearly indicate that neither simple fatigue model nor stimulus-specific fatigue model of adaptation was able to account for the facilitated post-change responses in my study. Consistent with the results of a previous study (Price & Born, 2013): (1) I did not find any link between pre-change tuning parameters and tuning shift, (2) there was no correlation between spike-rate adaptation occurring beyond 300 ms from motion onset and tuning shift.

My electrophysiological results contradict the traditionally held view based on fatigue models of adaptation, which assumes attentional modulation of perceptual effects of adaptation is caused by attentional modulation of pre-change responses (Alais & Blake, 1999; Berman & Colby, 2002; Chaudhuri, 1990; Lankheet & Verstraten, 1995). I showed that there is no relationship between

attentional modulation of pre-change responses and larger tuning shifts observed in attended condition compared with the unattended condition.

My results also did not show any dependency on the visual motion exposure time between 300 and 4000 ms, which is remarkably in accordance with previously published results (C. A. Patterson et al., 2013; C. A. Patterson, Duijnhouwer, et al., 2014; Price & Born, 2013). The study by Patterson and colleagues demonstrated that adaptation effects in early response epoch are independent of adaptation duration between 400 ms and 40 s (C. A. Patterson et al., 2013; C. A. Patterson, Duijnhouwer, et al., 2014). Price & Born also did not observe any evidence that exposure duration of 500-5000 ms influences the tuning shift (Price & Born, 2013).

In contrast to fatigue models, we quantitatively showed that a tuned normalization model of adaptation and attention (Rust et al., 2006; S. G. Solomon & Kohn, 2014) can account for the effects induced by unattended and attended direction changes. In this model, adaptation reduces feedforward drive of the neurons and has a suppressive effect on the neural responses, whereas adaptation decreases normalization signals (disinhibition) and ultimately facilitates neural responses. Transient change (increase or decrease) in the response following the direction changes reflects the interaction between these suppressive and facilitatory effects. Post-change responses greater than expected from unadapted response curve indicate stronger disinhibition and reduced post-change responses relative to the responses predicted by unadapted response curve might imply stronger suppression. The results of the model suggest that direction change overestimation in MT results from both suppression of feedforward drive of the neurons and weakened tuned normalization following the visual motion exposure. Attention increases the overestimation by modulating both components. Strengthened tuned normalization when the stimulus is attended increases its contribution to the direction change overestimation (Figure 9). This might go in line with attention studies attributing attention effects to the changed tuned normalization (Ni et al., 2012; Verhoef & Maunsell, 2017).

Because of the restrictions imposed by our physiological experiment, I was unable to test the spatial specificity of adaptation effects or existence of similar adaptation-induced effects in V1. My study, therefore, could not ascertain whether the effects of adaptation in my study were inherited from V1 or they were locally produced in MT. However, I speculate that the effects induced by adaptation (post-change transient response change, which is the basis for the direction change overestimation) in our experiment most likely stemmed from MT intrinsic circuitry. This claim is based primarily on the difference between the source of adaptation to gratings and random dot patterns. Adaptation studies (mostly with prolonged adaptation duration) using gratings as adapter have shown that the effects of adaptation are inherited from V1 (Glasser et al., 2011; Kohn, 2007; Kohn & Movshon, 2003, 2004), whereas other studies in which random dot pattern is used as the adapter have proposed that adaption effects are generated locally in MT (Kohn, 2007; Price & Born, 2013; Priebe et al., 2002; Traschütz et al., 2015; Zavitz et al., 2016). It has been shown that random dot pattern does not produce strong adaptation in V1 (Glasser et al., 2011; Kohn, 2007; Kohn & Movshon, 2004; Price & Born, 2013; Priebe et al., 2002; Snowden et al., 1992; Traschütz et al., 2015; Zavitz et al., 2016).

To examine how a change in the direction of visual motion is perceived I conducted a human psychophysical experiment, which was similar to the monkey task in many aspects, e.g. the timescale of pre-change visual motion (~ 2 s), the magnitude of direction change (~ 25^{o}), and no prolonged adaptation over trials as the motion direction in each trial was randomly chosen. Since designing an experiment, which allows measuring the percept in a spatially unattended location is not straightforward, my paradigm only yielded the perception of attended direction change. The results showed that the perception of attended direction change of 25^{o} in human subjects is overestimated by about 7^{o}. Further psychophysical experiments demonstrated that the overestimated representation and perception of direction change were causally linked.

Using a linking model, similar to the one employed by Kohn & Movshon (Kohn & Movshon, 2004) and Jin et al (Jin et al., 2005), showed that neuronal

overestimation of direction change in MT might underlie the perceived direction change overestimation. This simple model suggested an overestimation of perceived direction change as large as the tuning shift observed at the neuronal level. Although the results of my human psychophysical experiment showed an overestimation (~7°) smaller than the one predicted by the model (~14°), which might be explained by differences across species and experimental paradigms used in electrophysiological and psychophysical studies and the simplicity of the model, the shift of direction tuning of MT cells might account for the overestimation of the perceived direction change.

In summary, we find that the neuronal representation and perception of a sudden stimulus change are overestimated. We show that, in a change detection task, attending to the stimulus makes the overestimation of the neuronal representation even more pronounced. One might speculate that attention, to improve the behavioral performance, enhances the change overestimation in a change detection task, whereas it reduces (corrects) the overestimation when it is detrimental to performance, e.g. in a discrimination task. Our results also indicate that fatigue-based adaptation models cannot explain effects induced by direction changes and attention. The effect of direction change on the neuronal responses and its attentional modulation are well described within the framework of a tuned normalization model.

6 SUPPLEMENTARY INFORMATION

My thesis dissertation includes this part as I followed the format of many international journals that offer the possibility to provide extensive background information that is not critical for the publication as Supplementary Information.

6.1 Supplementary Information 1

Attentional modulation of MT responses prior and following the direction change:

The effect of attention on the neuronal responses was investigated by computing the attention index ($\frac{Res_{att}-Res_{unatt}}{Res_{att}+Res_{unatt}}$) of the neurons for both pre- and post-change intervals. The analysis showed that directing attention into the receptive field of neurons significantly enhanced the pre- and post-change neuronal responses by 13 and 14%, respectively ($p < 0.001$, two-sided Wilcoxon signed rank test for distribution with median equal to 1.)

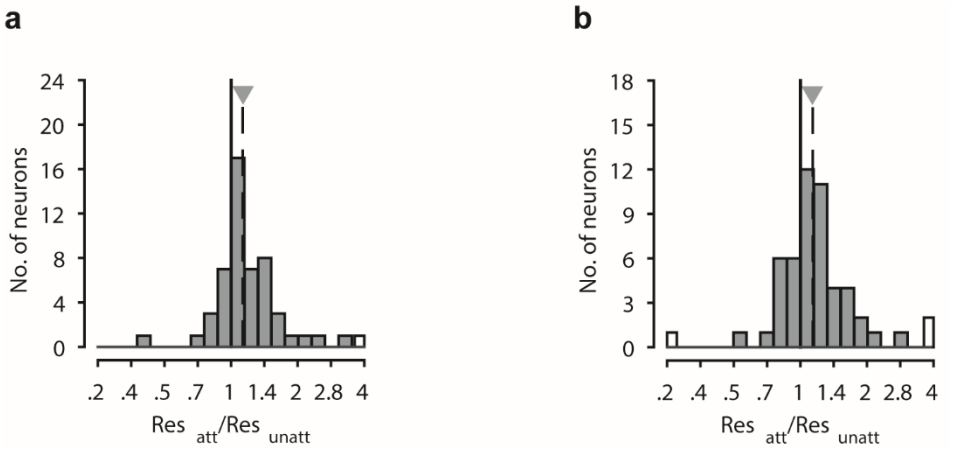

Figure SI 1 | Attentional modulation of neuronal responses: (a) prior, and (b) following the direction change. Dashed lines and arrowheads indicate the median attentional modulation.

6.2 Supplementary Information 2

Direction change effect on the parameters of population response curve (Fig. 4e):

An unattended direction change of 25^{o} induced a repulsive shift of 9^{o} in the peak location of population response curve. The shift increased to 14^{o} when the stimulus was attended. Bandwidth ratio (ratio of post- to pre-change bandwidths) of 1.03 in unattended condition was increased to 1.05 when the stimulus was attended. Change in the amplitude (ratio of post- to pre-change amplitudes) of unattended population response was 1.07 that increased to 1.14 by the attention. Attention also reduced the change in the asymptote (ratio of post- to pre-asymptotes) of the population response curve from 1.13 to 0.99.

6.3 Supplementary Information 3

Changes of population response curve induced by direction change are independent of the selection of pre- and post-change time windows:

- A control analysis employed different population response curves. Pre- and post-change population response curves were determined by using the across-cell population responses at a random time prior to the change and at the time point following the change when the location of population peak activity had the greatest deviation from the pre-change motion direction. The results of this analysis were consistent with the previous analysis (Figure 4e) and are summarized in the Table SI 1.

Parameter	Unattended	Attended
Peak location (post-pre)	11°	15°
Bandwidth (post/pre)	1.09	1.08
Amplitude (post/pre)	1.10	1.12
Asymptote (post/pre)	1.00	1.07

Table SI 1 | Change in the parameters of population response curve caused by unattended and attended direction changes. Pre- and post-change response curves were estimated at a random time point before the direction change and at the time of response peak following the direction change, respectively.

- We carried out another control analysis to ensure our findings based on the population response curves do not depend on the selection of pre- and post-change time points. We computed the average of peak locations of population response every one millisecond for pre- (-700-0 ms) and post-change (50-150 ms) time intervals. The results summarized in Table SI 2 show that the change of 25° in the direction of motion induced an average repulsive shift of 10° in the population response curve away from the direction of pre-change stimulus when it was not attended and attention increased the shift by 4°.

Parameter	Unattended	Attended
Peak location (post-pre)	10°	14°
Bandwidth (post/pre)	1.05	1.06
Amplitude (post/pre)	1.08	1.13
Asymptote (post/pre)	1.11	1.05

Table SI 2 | Median of the changes in the population response curve parameters induced by the direction change of 25° in both spatial attention conditions. We computed population response curves every millisecond for pre- and post-change time intervals of -700-0 ms and 50-150 ms, respectively. We averaged different parameters of population response curves over pre- and post-change time intervals.

6.4 Supplementary Information 4

The latency of MT responses to unattended and attended direction changes:

We determined the response latency of neurons to direction change (time point at which 75% of peak response - relative to the pre-change response - is exceeded) in both attentional conditions (Figure SI 2). The scatter plot shows the latency in attended condition against the latency in unattended condition across MT cells. Red and blue histograms are the distributions of latencies in unattended and attended conditions, respectively. The arrowheads point to the medians of the distributions. The results showed that the response latency to the direction change in unattended and attended conditions were 80±22 and 81±29 ms (median±SD), respectively. We did not find any significant difference between the latencies of unattended and attended responses to the direction change ($p = 0.3$, paired two-sided Wilcoxon test for distributions with equal medians).

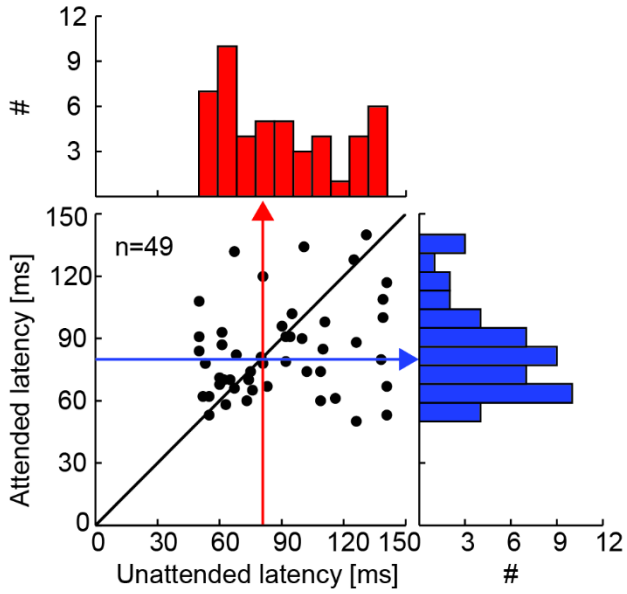

Figure SI 2 | Comparison of response latencies in unattended and attended conditions across MT cells (n=49). Red and blue arrows point to the median of latency in unattended and attended conditions, respectively.

6.5 Supplementary Information 5

Change of tuning curves are induced by direction change and are independent of the standard deviation of Gaussian kernel used to smooth the spike trains, inclusion criteria for MT cells, and post-change analysis time window:

- We convolved the spike trains with a Gaussian kernel to compute the spike density functions. As the results summarized in the Table SI 3-5 indicate changes in the parameters of direction tuning are, to a large extent, independent of the standard deviation used to smooth the spike trains.

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (post-pre)	-7° p'=0.0005	-14° p'=0.0000005	0.004
Bandwidth (post/pre)	0.94 p"=0.0001	0.90 p"=0.03	0.8
Amplitude (post/pre)	1.18 p"=0.00000005	1.19 p"=0.0002	0.4
Asymptote (post/pre)	1.06 p"=0.05	1.05 p"=0.02	0.5

Table SI 3 | Median of changes in the parameters of direction tuning curves caused by unattended and attended direction changes. A Gaussian with a standard deviation of 10 ms was used to compute the spike density functions.

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (post-pre)	-6° p'=0.0005	-14° p'=0.0000005	0.001
Bandwidth (post/pre)	0.93 p"=0.00007	0.92 p"=0.02	0.8
Amplitude (post/pre)	1.18 p"=0.00000004	1.19 p"=0.0004	0.4
Asymptote (post/pre)	1.06 p"=0.05	1.08 p"=0.01	0.4

Table SI 4 | Median of changes in the parameters of direction tuning curves caused by unattended and attended direction changes. A Gaussian with a standard deviation of 20 ms was used to compute the spike density functions.

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (post-pre)	-6° p'=0.0003	-12° p'=0.0000006	0.01
Bandwidth (post/pre)	0.95 p"=0.0002	0.93 p"=0.04	0.6
Amplitude (post/pre)	1.17 p"=0.00000008	1.14 p"=0.0003	0.1
Asymptote (post/pre)	1.07 p"=0.06	1.10 p"=0.006	0.3

Table SI 5 | Median of changes in the parameters of direction tuning curves caused by unattended and attended direction changes. A Gaussian with a standard deviation of 40 ms was used to compute the spike density functions.

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p": two-sided Wilcoxon signed rank test for distribution with a median equal to 1

- To make sure that the results do not depend on the tuning characteristics of MT cells, we repeated the analysis by applying the following inclusion criteria: (1) neurons were highly direction selective (response to the preferred direction was at least 5 times greater the response to the anti-preferred direction), (2) the neurons were well tuned (goodness of fit greater than 0.7). The results of this analysis were consistent with those presented before (See Table SI 6).

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (post-pre)	-5° p'=0.002	-13° p'=0.0005	0.02
Bandwidth (post/pre)	0.93 p"=0.001	0.93 p"=0.1	0.3
Amplitude (post/pre)	1.19 p"=0.0001	1.19 p"=0.01	0.06
Asymptote (post/pre)	0.98 p"=0.4	1.00 p"=0.2	0.5

Table SI 6 | Median of changes in the parameters of direction tuning curves caused by unattended and attended direction changes. We selected the MT cells that met the following criteria: (1) response to the preferred direction was at least 5 times greater the response to the anti-preferred direction; (2) goodness of fit greater than 0.7. These cells comprised half of the population of MT cells (25 out of 50).

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p": two-sided Wilcoxon signed rank test for distribution with a median equal to 1

- We performed a control analysis to show that the results are not affected by the selection of post-change time window. This analysis used the time-averaged responses in a post-change time window between +150 and +250 ms to assess the

tuning curve parameters following the change. The results confirmed the previous findings shown in Figure 5 (See Table SI 7).

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (post-pre)	-7° p'=0.0001	-10° p'=0.0000006	0.02
Bandwidth (post/pre)	0.95 p"=0.00005	0.92 p"=0.004	0.7
Amplitude (post/pre)	1.15 p"=0.00000002	1.10 p"=0.0001	0.1
Asymptote (post/pre)	1.00 p"=0.3	1.06 p"=0.007	0.4

Table SI 7 | Median of changes in the parameters of direction tuning curves caused by unattended and attended direction changes (n=52). We used a time window from 150 to 250 ms following the direction change to analyze the post-change data.

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p": two-sided Wilcoxon signed rank test for distribution with a median equal to 1

- We demonstrated that the observed changes in the tuning parameters were induced by the direction change and are not analysis artifacts or caused by different sizes of pre- and post-change time windows. To do this, we repeated the analysis and determined the tuning curves of cells in two time windows with sizes identical to those used before, but both windows were chosen to be prior to the change: from -700 ms to -100 ms and from -100 ms to 0 ms. The analysis showed that the change of none of tuning parameters between these time windows reached statistical significance ($p >> 0.05$, two-sided Wilcoxon signed rank test. See Table SI 8). This indicates that the changes in tuning parameters caused by direction change were neither analysis artifacts and nor caused by different sizes of pre- and post-change analysis windows.

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (win2-win1)	0° p'=0.9	0° p'=0.8	0.6
Bandwidth (win2/win1)	0.99 p"=0.2	0.98 p"=0.2	0.9
Amplitude (win2/win1)	1.00 p"=1.0	1.01 p"=0.2	0.5
Asymptote (win2/win1)	1.06 p"=0.02	0.95 p"=1.0	0.3

Table SI 8 | Median of changes in the parameters of direction tuning curves caused by unattended and attended direction changes (n=52). We used two time windows from -700 to -100 ms (win1) and from -100 to 0 ms (win2) prior to the direction change to analyze the data.

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p": two-sided Wilcoxon signed rank test for distribution with a median equal to 1

6.6 Supplementary Information 6

Investigation of tuning shift induced by direction change in different attentional conditions using skewed von Mises function:

Direction tuning shifts were computed after we fitted the pre- and post-change data separately with skewed von Mises function. Direction-selective (response to the preferred direction at least 5-fold larger than the response to anti-preferred direction), tuned (goodness of fit greater than 0.7) cells were included in our analysis.

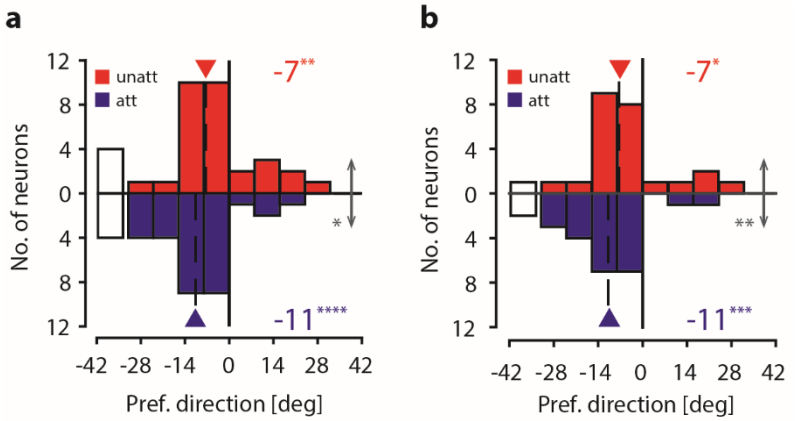

Figure SI 3 | shift of direction tunings in unattended (red) and attended (blue) conditions, (a) direction-selective, tuned cells were selected based on the result of fitting the data with skewed von Mises function (n=34), (b) direction-selective, tuned cells were selected based on the result of fitting the data with symmetric von Mises function (n=25; See Table SI 6). Dashed lines and arrowheads indicate the median shifts, which are also shown in the figure.

6.7 Supplementary Information 7

Influence of attention on the bandwidth of direction tuning of MT cells:

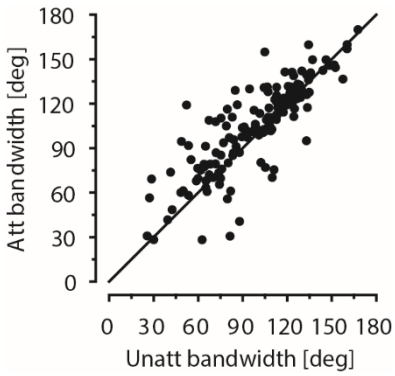

Figure SI 4 | Attentional effect on the pre-change bandwidth: attention significantly (p = 0.000005, paired two-sided Wilcoxon test for distributions with equal medians) broadened the pre-change bandwidth of direction tuning of MT cells (104º) in speed-change detection task to 108º (n=146).

6.8 Supplementary Information 8

Correlation between changes in pre-change bandwidth and direction change induced-tuning shift associated with attention:

If the increase of pre-change bandwidth in attended condition results in larger tuning shifts, there should be a negative correlation between the pre-change bandwidth change by attention and the change in tuning shift by attention (expected from Figure 6a). For the cells which showed negative shifts in both attentional conditions, the correlation between tuning shift change by attention and the change of pre-change bandwidth by attention is positive ($r = +0.42$, Pearson correlation) and has a slope that is significantly different from zero ($p = 0.01$, t-test). This indicates that broadening the pre-change tuning curves by attention cannot account for the greater negative shifts in attended condition.

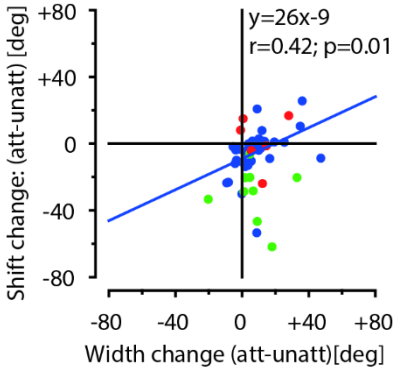

Figure SI 5 | Correlation between the attentional effect on pre-change bandwidth and tuning shift. Circles with different colors correspond to different groups of cells introduced in Figure 5e. The solid line is the result of simple linear regression fit to the data.

6.9 Supplementary Information 9

Correlation between attentional modulation of different parameters of pre-change direction tuning and change of tuning shift associated with attention:

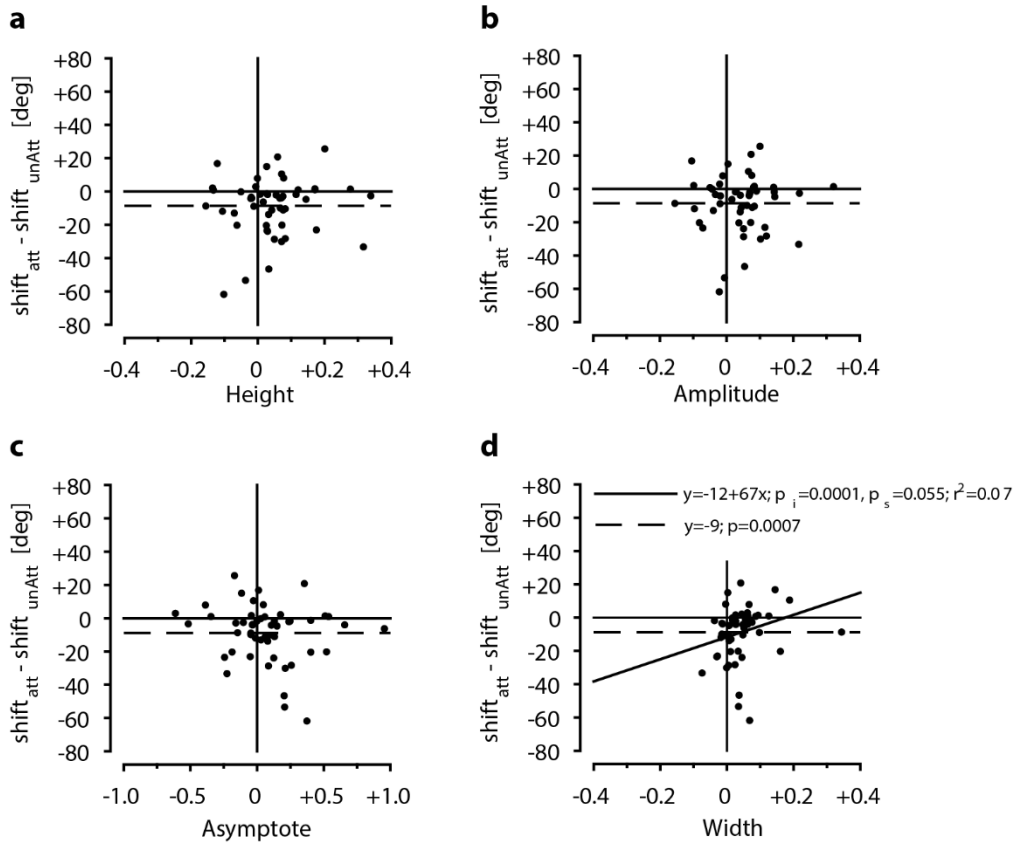

Figure SI 6 | Correlation between attention modulation of pre-change tuning parameters and shift change by attention (n=51), (a) height, (b) amplitude, (c) asymptote, and (d) bandwidth. The differences of slopes of linear fits to the data were not statistically significant from zero ($p_s >> 0.05$, t-test; except for bandwidth). The dashed lines show the average (mean) of attentional effect on tuning shift. For bandwidth, similar to Supplementary Information 8, there is a positive correlation between attentional modulation of width and shift change by attention (solid line).

6.10 Supplementary Information 10

Influence of adaptation to unattended and attended visual motion prior to the direction change on the parameters of direction tunings:

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (preDC-postOnset)	-0.2° p'=0.8	+0.1° p'=0.5	0.9
Bandwidth (preDC/postOnset)	0.99 p''=0.99	1.03 p''=0.005	0.1
Amplitude (preDC/postOnset)	0.93 p''=0.0005	0.94 p''=0.0008	0.8
Asymptote (preDC/postOnset)	1.14 p''=0.04	1.08 p''=0.04	0.8
Height (preDC/postOnset)	0.90 p''=0.002	0.91 p''=0.0002	0.6

Table SI 9| Median of changes in the parameters of direction tuning curves caused by unattended and attended motion adaptation prior to the direction change (n=52). We compared the tuning parameters in the time window lasting 300 ms prior to the direction change (preDC) with the ones in the sustained period after motion onset (400-700 ms after motion onset, postOnset).

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p'': two-sided Wilcoxon signed rank test for distribution with a median equal to 1

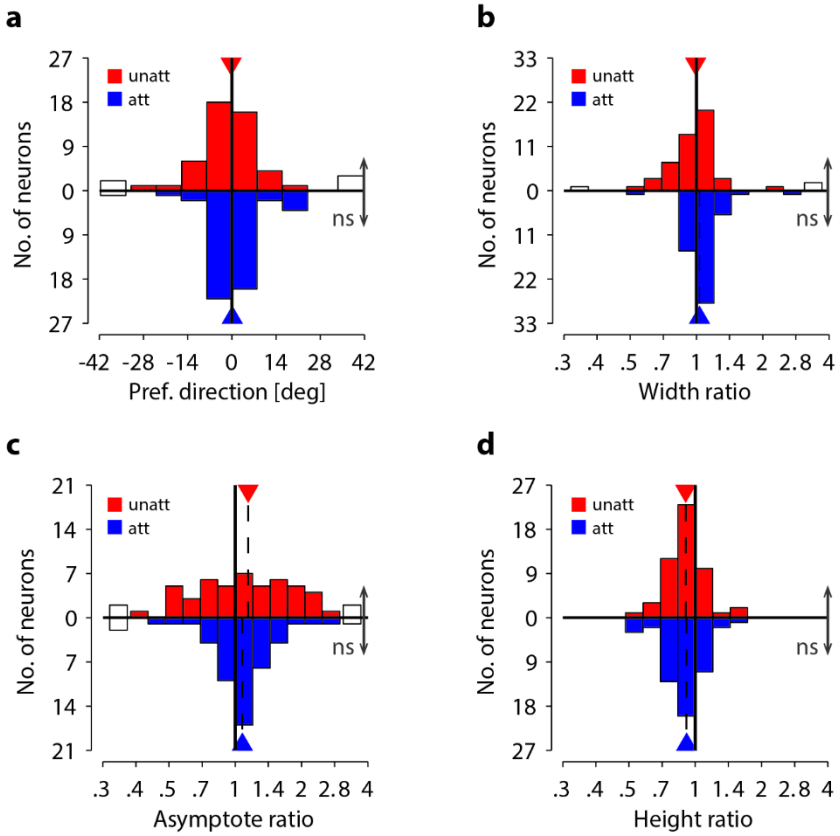

Figure SI 7 | Influence of pre-change adaptation on the direction tuning parameters in unattended (red) and attended (blue) conditions, (a) preferred direction, (b) width, (c) asymptote, (d) height. Statistics are given in Table SI 9. Dashed lines and arrowheads indicate the median of change in tuning parameters.

6.11 Supplementary Information 11

Changes in the direction tuning parameters following the unattended and attended direction changes are independent of (pre-change) motion adaptation duration:

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (post-pre)	-6° p'=0.0004	-13° p'=0.000002	0.0009
Bandwidth (post/pre)	0.92 p"=0.001	0.92 p"=0.05	0.2
Amplitude (post/pre)	1.22 p"=0.0000002	1.18 p"=0.0002	0.3
Asymptote (post/pre)	1.08 p"=0.01	1.03 p"=0.04	0.9

Table SI 10 | Median of changes in the parameters of direction tuning curves caused by unattended and attended direction changes (n=50). We selected trials that the direction change occurred between 300 and 2700 ms after the visual motion onset.

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p": two-sided Wilcoxon signed rank test for distribution with a median equal to 1

6.12 Supplementary Information 12

Changes in the parameters of direction tuning induced by direction change are independent of (pre-change) motion adaptation duration in attended condition:

Parameter	Short trials	Long trials	Exposure time impact (p)
Preferred direction (post-pre)	-13° p'=0.0003	-15° p'=0.00008	0.1
Bandwidth (post/pre)	0.90 p"=0.004	0.92 p"=0.009	0.7
Amplitude (post/pre)	1.22 p"=0.000003	1.21 p"=0.00003	0.9
Asymptote (post/pre)	1.17 p"=0.008	1.03 p"=0.05	0.1

Table SI 11 | Median of changes in the parameters of direction tuning curves caused by early and late direction changes in attended trials (n=32). Direction change time varies from 300 to 2700 ms ($mean \pm SD = 1870 \pm 550\ ms$) in short trials, and from 3100 to 4000 ms ($mean \pm SD = 3690 \pm 220\ ms$) in long trials.

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p": two-sided Wilcoxon signed rank test for distribution with a median equal to 1

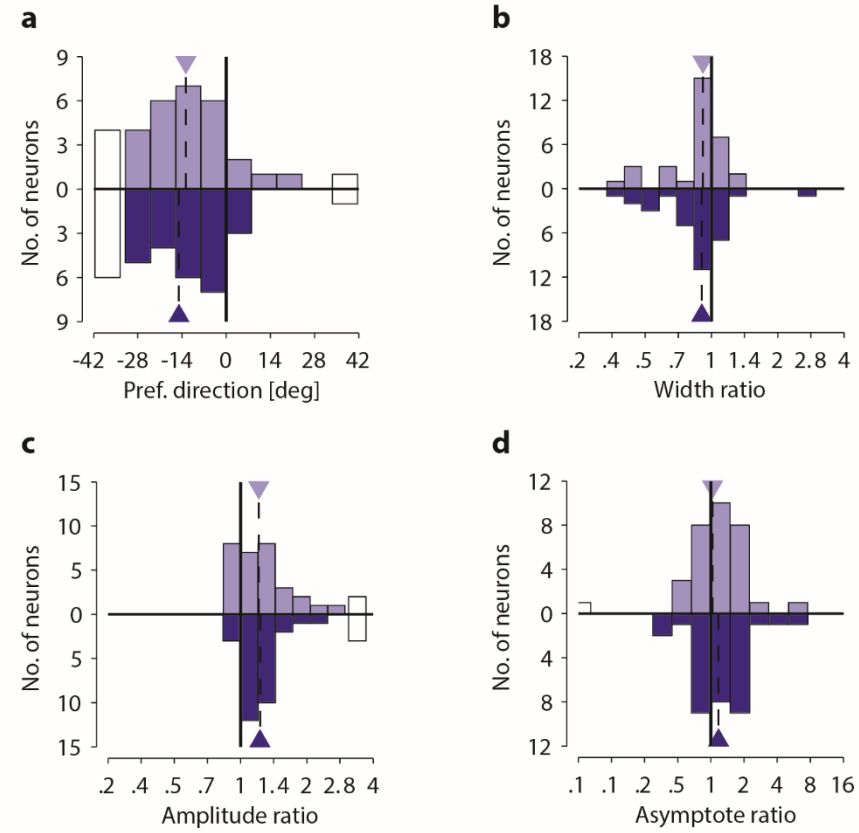

Figure SI 8 | Change of tuning parameters in short (light blue) and long (dark blue) attended trials (n=32), (a) preferred direction, (b) width, (c) amplitude, (d) asymptote. Statistics are given in Table SI 11. Dashed lines and arrowheads indicate the median of change in tuning parameters.

6.13 Supplementary Information 13

Errors in the perceived direction change computed separately for both rightward and leftward motions (first human psychophysical experiment, Figure 10a):

Subject	median leftward	MAD leftward	median rightward	MAD rightward	median average both	MAD average both
anh	+3.9	+1.4	+2.7	+0.5	+2.8	+0.7
anm	+8.3	+0.7	+6.8	+0.5	+6.8	+0.3
jis	+11.3	+2.2	+6.4	+0.9	+9.0	+1.7
juo	+2.6	+1.7	+4.3	+0.8	+4.3	+1.0
lev	+9.9	+0.4	+13.3	+0.5	+11.4	+0.6
mak	+8.6	+1.9	+5.3	+1.6	+6.2	+1.2
rej	+12.5	+2.4	-0.4	+2.3	+5.8	+2.0
sak	-0.2	+0.9	-0.8	+0.3	-0.1	+0.8
ulw	+10.1	+0.1	+6.7	+1.3	+8.4	+0.7
vam	+3.7	+0.3	+1.7	+0.1	+2.8	+0.4

Table SI 12 | Error in the perception of direction change. The first column is name of participants in the experiment; second and fourth columns indicate the median error of perceived direction change for each subject averaged across sessions when RDPs moved leftward and rightward, respectively; third and fifth columns show the median of absolute deviation of the error values for each subject for the corresponding motion direction; the sixth column is the median of the average (mean) error across leftward and rightward motions; the last column indicates the median of absolute deviation of the averaged errors.

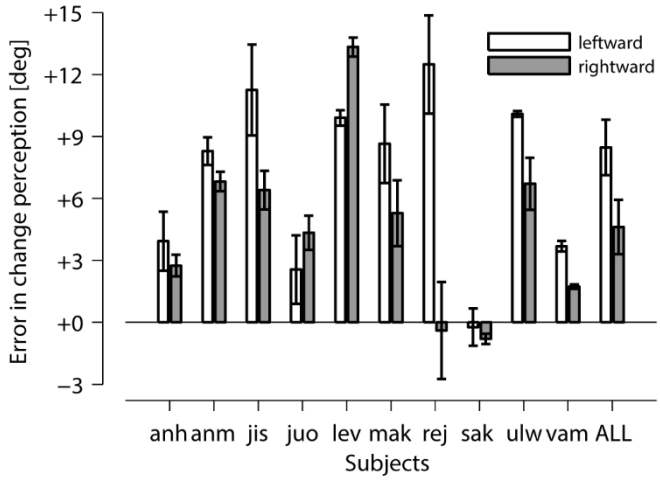

Figure SI 9 | Perception of direction change: errors in perceived direction change are computed separately for leftward and rightward motions. Subject names are shown in abscissa (last bars denoted by 'ALL' reflect the median effect across all subjects) and ordinate represents the median of error in the perceived direction change. Error bars are the median absolute deviations.

6.14 Supplementary Information 14

Errors in the perceived direction change computed separately for both rightward and leftward motions (second human psychophysical experiment, Figure 11a):

Subject	median leftward	MAD leftward	median rightward	MAD rightward	median average both	MAD average both
anh	-0.9	+0.8	-0.5	+0.3	-0.7	+0.5
anm	+0.6	+0.3	+0.7	+0.6	+0.6	+0.2
jis	+2.4	+0.5	+2.1	+0.5	+2.2	+0.5
juo	-0.9	+0.3	-0.0	+0.1	-0.4	+0.3
lev	+0.9	+0.2	+0.9	+0.2	+0.9	+0.1
mak	-0.1	+0.2	+0.3	+0.4	+0.1	+0.2
rej	+1.3	+0.5	+2.0	+0.2	+1.6	+0.4
sak	-1.5	+0.6	-1.2	+0.3	-1.4	+0.5

Table SI 13 | Error in the perception of direction change. The first column is name of participants in the experiment; second and fourth columns indicate the median error of perceived direction change for each subject averaged across sessions when RDPs moved leftward and rightward, respectively; third and fifth columns show the median of absolute deviation of the error values for each subject for the corresponding motion direction; the sixth column is the median of the average (mean) error across leftward and rightward motions; the last column indicates the median of absolute deviation of the averaged errors.

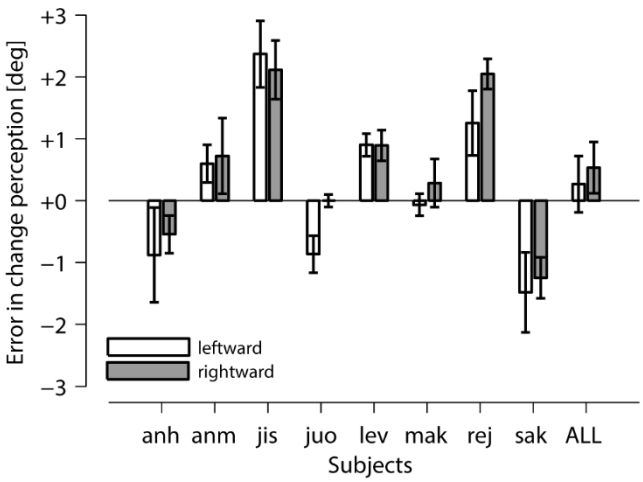

Figure SI 10 | Perception of direction change following exposure to two superimposed random dot patterns: errors in perceived direction change are computed separately for leftward and rightward motions. Subject names are shown in abscissa (last bars denoted by 'ALL' reflect the median effect across all subjects) and ordinate represents the median of error in the perceived direction change. Error bars are the median absolute deviations.

6.15 Supplementary Information 15

Direction change influence on the parameters of direction tuning in each of two monkeys ('f' and 'm') performing motion direction change detection task:

Monkey 'f':

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (post-pre)	-4° p'=0.2	-16° p'=0.0005	0.01
Bandwidth (post/pre)	0.91 p"=0.05	0.80 p"=0.03	0.9
Amplitude (post/pre)	1.25 p"=0.007	1.32 p"=0.02	0.9
Asymptote (post/pre)	1.34 p"=0.04	1.21 p"=0.2	0.9

Table SI 14 | Median of changes in the parameters of direction tuning caused by unattended and attended direction changes for monkey 'f' (n=12). A Gaussian kernel with a standard deviation of 20 ms was used to compute the spike density functions.

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p": two-sided Wilcoxon signed rank test for distribution with median equal to 1

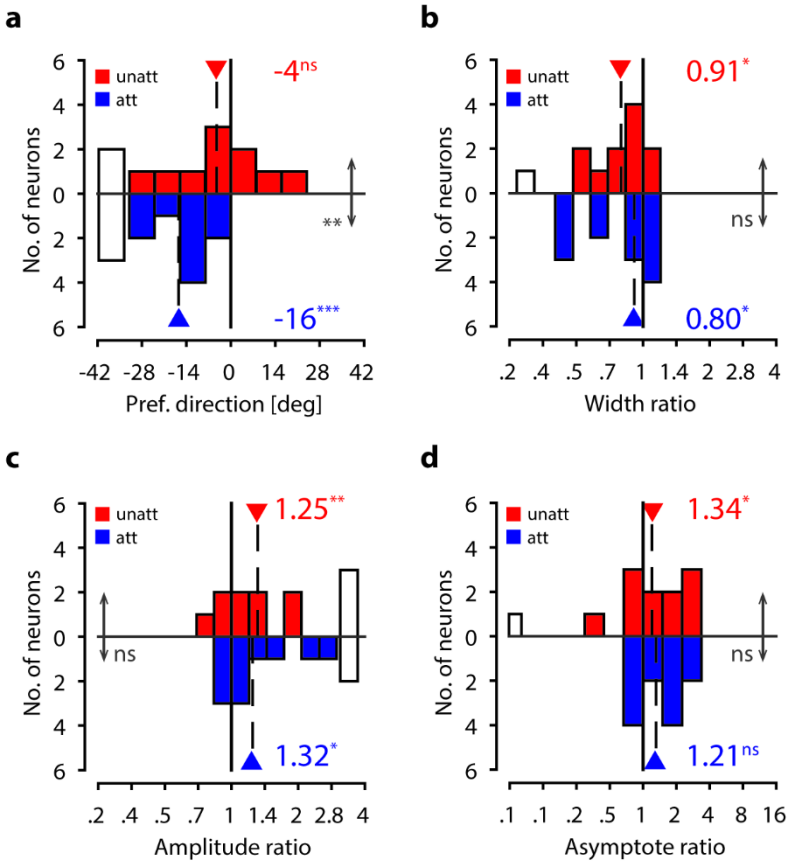

Figure SI 11 | Change of tuning parameters following the unattended and attended direction changes for monkey 'f' (n=12), (a) preferred direction, (b) width, (c) amplitude, (d) asymptote. Statistics are given in Table SI 14. Dashed lines and arrowheads indicate the median of change in tuning parameters.

Monkey 'm':

Parameter	Unattended	Attended	Attention impact (p)
Preferred direction (post-pre)	-8° p'=0.002	-14° p'=0.0001	0.04
Bandwidth (post/pre)	0.94 p"=0.002	0.95 p"=0. 3	0.8
Amplitude (post/pre)	1.15 p"=0.000002	1.21 p"=0.004	0.7
Asymptote (post/pre)	1.07 p"=0.2	1.10 p"=0.02	0.3

Table SI 15 | Median of changes in the parameters of direction tuning caused by unattended and attended direction changes for monkey 'm' (n=38). A Gaussian kernel with a standard deviation of 20 ms was used to compute the spike density functions.

p: p-value of the paired two-sided Wilcoxon test for distributions with equal medians
p': p-value of the two-sided Wilcoxon signed rank test for distribution with 0 median
p": two-sided Wilcoxon signed rank test for distribution with a median equal to 1

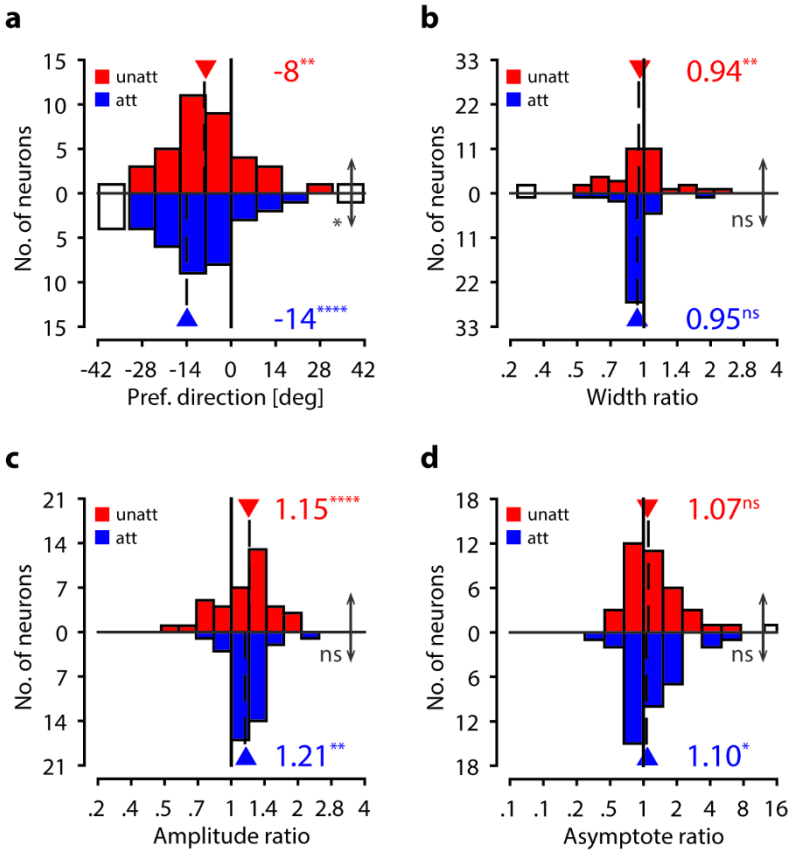

Figure SI 12 | Change of tuning parameters following the unattended and attended direction changes for monkey 'm' (n=38), (a) preferred direction, (b) width, (c) amplitude, (d) asymptote. Statistics are given in Table SI 15. Dashed lines and arrowheads indicate the median of change in tuning parameters.

6.16 Supplementary Information 16

List of MT cells used in the electrophysiological study:

No.	Cell ID	Animal ID	Note†
1	jffna01	f	-
2	jffoa50	f	jffoa01, jffoa02
3	jffob50	f	jffob01, jffob02
4	jfftb50	f	jfftb02, jfftb03, jfftb04
5	jffza04	f	-
6	jfgaa01	f	-
7	jfgab00	f	-
8	jfgcb01	f	-
9	jfgfa01	f	-
10	jfgha50	f	jfgha04, jfgha05, jfgha06
11	jfgka50	f	jfgka05, jfgka06
12	jfgwa02	f	-
13	jmbvb50	m	jmbvb01, jmbvb02
14	jmbvd50	m	jmbvd01, jmbvd02, jmbvd03, jmbvd04, jmbvd05, jmbvd06
15	jmbwa01	m	-
16	jmbya50	m	jmbya02, jmbya03, jmbya04, jmbya05, jmbya06
17	jmbyb50	m	jmbyb01, jmbyb02, jmbyb03, jmbyb04
18	jmbza01	m	-
19	jmcaa01	m	-
20	jmcab50	m	jmcab01, jmcab02, jmcab03, jmcab04
21	jmcda01	m	-
22	jmcdb50	m	jmcdb01, jmcdb02
23	jmcea50	m	jmcea01, jmcea02, jmcea03
24	jmcha01	m	-
25	jmchb01	m	-
26	jmclc01	m	-
27	jmcma50	m	jmcma02, jmcma03
28	jmcna50	m	jmcna01, jmcna02, jmcna03, jmcna04

29	jmcoa50	m	jmcoa01, jmcoa02
30	jmcpa04	m	-
31	jmcqa50	m	jmcqa01, jmcqa02
32	jmcsa50	m	jmcsa01, jmcsa02
33	jmcta01	m	-
34	jmcua01	m	-
35	jmcwa02	m	-
36	jmcxa50	m	jmcxa01, jmcxa02
37	jmcxc00	m	-
38	jmdaa50	m	jmdaa01, jmdaa02, jmdaa03, jmdaa04
39	jmdda01	m	-
40	jmdfa04	m	-
41	jmdga01	m	-
42	jmdgb01	m	-
43	jmdgc01	m	-
44	jmdia50	m	jmdia01, jmdia02, jmdia03
45	jmdib50	m	jmdib01, jmdib02, jmdib03, jmdib04, jmdib05, jmdib06
46	jmdla50	m	jmdla01, jmdla02
47	jmdna50	m	jmdna04, jmdna05
48	jmdqb50	m	jmdqb01, jmdqb02
49	jmdua01	m	-
50	jmdva50	m	jmdva05, jmdva06, jmdva07, jmdva08
51	jmdwa04	m	-
52	jmdyb50	m	jmdyb03, jmdyb04

† 'Note' column lists the cell IDs merged to generate the files ending in 50.

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Number of trials for different motion directions for each MT cell:

(A) Unattended condition:

No.	Cell ID	# trials  0°	# trials  30°	# trials  60°	# trials  90°	# trials  120°	# trials  150°
1	jffna01	4	5	4	5	5	5
2	jffoa50	7	6	6	6	6	6
3	jffob50	3	3	4	4	4	3
4	jfftb50	4	3	4	4	4	4
5	jffza04	4	4	3	4	4	4
6	jfgaa01	2	2	1	2	2	2
7	jfgab00	4	4	4	5	4	5
8	jfgcb01	7	8	8	7	11	7
9	jfgfa01	4	3	4	4	4	3
10	jfgha50	3	4	4	4	4	5
11	jfgka50	5	4	5	4	5	4
12	jfgwa02	5	5	5	5	5	5
13	jmbvb50	4	3	4	5	4	4
14	jmbvd50	3	3	3	3	5	3
15	jmbwa01	4	5	4	4	4	4
16	jmbya50	2	2	1	2	3	2
17	jmbyb50	5	5	4	4	5	6
18	jmbza01	5	5	6	5	5	5
19	jmcaa01	6	6	6	5	5	6
20	jmcab50	4	5	6	6	5	5
21	jmcda01	5	5	5	5	5	5
22	jmcdb50	4	4	4	3	4	4
23	jmcea50	4	6	4	6	4	4

24	jmcha01	6	6	6	6	6	6
25	jmchb01	4	5	4	4	4	4
26	jmclc01	3	3	3	3	3	3
27	jmcma50	3	4	4	3	3	3
28	jmcna50	6	5	6	6	6	5
29	jmcoa50	3	3	3	3	3	3
30	jmcpa04	3	3	3	3	3	3
31	jmcqa50	7	7	6	7	7	7
32	jmcsa50	4	4	4	4	4	4
33	jmcta01	4	3	3	3	3	4
34	jmcua01	5	5	4	5	4	5
35	jmcwa02	5	5	5	5	5	5
36	jmcxa50	1	1	1	2	1	1
37	jmcxc00	4	4	4	4	4	4
38	jmdaa50	2	3	2	3	3	3
39	jmdda01	4	4	4	4	5	4
40	jmdfa04	8	9	8	8	8	9
41	jmdga01	5	6	5	5	5	6
42	jmdgb01	4	4	4	4	4	4
43	jmdgc01	7	5	5	4	4	4
44	jmdia50	5	5	6	3	5	5
45	jmdib50	7	6	8	5	6	4
46	jmdla50	6	6	6	6	6	6
47	jmdna50	7	7	7	7	8	7
48	jmdqb50	5	5	4	6	5	6
49	jmdua01	6	6	6	6	6	6
50	jmdva50	7	8	6	6	5	6
51	jmdwa04	6	5	5	6	6	5
52	jmdyb50	4	4	4	3	4	4

No.	Cell ID	# trials  180°	# trials  210°	# trials  240°	# trials  270°	# trials  300°	# trials  330°
1	jffna01	4	5	4	5	5	4
2	jffoa50	5	7	6	6	5	7
3	jffob50	3	4	4	4	4	4
4	jfftb50	3	3	3	3	3	2
5	jffza04	4	4	4	4	4	3
6	jfgaa01	2	1	2	2	2	1
7	jfgab00	4	4	4	4	4	5
8	jfgcb01	5	7	5	5	5	6
9	jfgfa01	2	3	3	4	4	4
10	jfgha50	4	4	4	4	5	4
11	jfgka50	4	5	5	5	5	5
12	jfgwa02	5	5	5	5	5	5
13	jmbvb50	4	4	4	4	4	3
14	jmbvd50	3	3	6	5	4	4
15	jmbwa01	5	5	5	4	4	4
16	jmbya50	1	2	2	3	2	2
17	jmbyb50	5	5	4	6	4	4
18	jmbza01	5	5	6	5	5	5
19	jmcaa01	5	5	5	5	5	6
20	jmcab50	6	6	5	5	5	4
21	jmcda01	5	5	5	5	5	5
22	jmcdb50	3	4	4	4	3	4
23	jmcea50	4	4	5	4	4	4
24	jmcha01	6	6	6	6	6	6
25	jmchb01	4	4	4	4	4	4
26	jmclc01	3	3	3	3	3	3
27	jmcma50	3	4	3	3	3	4

28	jmcna50	7	6	6	7	5	6
29	jmcoa50	2	3	3	3	3	3
30	jmcpa04	3	3	3	3	3	3
31	jmcqa50	7	6	7	7	7	7
32	jmcsa50	4	4	4	4	5	4
33	jmcta01	3	3	4	3	3	3
34	jmcua01	5	5	4	5	4	4
35	jmcwa02	5	5	5	5	5	5
36	jmcxa50	1	2	2	1	1	1
37	jmcxc00	4	4	4	4	4	4
38	jmdaa50	3	3	2	3	2	3
39	jmdda01	4	4	4	4	4	5
40	jmdfa04	9	9	8	9	9	9
41	jmdga01	6	6	5	6	6	6
42	jmdgb01	4	4	4	4	4	4
43	jmdgc01	4	4	4	4	5	4
44	jmdia50	3	6	3	6	5	3
45	jmdib50	5	6	8	7	5	6
46	jmdla50	5	6	6	6	6	6
47	jmdna50	8	8	8	8	7	7
48	jmdqb50	5	5	4	5	6	6
49	jmdua01	6	6	6	6	6	6
50	jmdva50	6	6	5	6	7	6
51	jmdwa04	5	6	5	5	5	6
52	jmdyb50	5	4	4	4	4	3

(B) Attended condition:

No.	Cell ID	# trials  0°	# trials  30°	# trials  60°	# trials  90°	# trials  120°	# trials  150°
1	jffna01	10	10	10	10	10	9
2	jffoa50	11	12	14	13	13	12
3	jffob50	6	6	8	8	7	8
4	jfftb50	7	5	7	8	6	7
5	jffza04	8	7	7	8	8	8
6	jfgaa01	4	3	4	3	4	4
7	jfgab00	8	10	8	9	8	10
8	jfgcb01	14	14	14	14	15	14
9	jfgfa01	8	7	8	7	6	7
10	jfgha50	10	9	9	8	9	9
11	jfgka50	9	9	10	9	9	9
12	jfgwa02	10	10	11	11	10	10
13	jmbvb50	7	8	7	9	7	7
14	jmbvd50	8	6	8	6	5	7
15	jmbwa01	10	9	6	9	10	9
16	jmbya50	6	5	4	4	5	5
17	jmbyb50	10	11	10	11	8	8
18	jmbza01	10	10	10	11	10	10
19	jmcaa01	12	12	12	10	10	10
20	jmcab50	9	9	11	11	10	11
21	jmcda01	10	10	10	10	10	10
22	jmcdb50	7	9	8	8	7	8
23	jmcea50	9	9	8	9	8	8
24	jmcha01	12	12	12	12	12	13
25	jmchb01	8	8	8	8	8	8
26	jmclc01	6	6	6	6	6	6

27	jmcma50	7	7	6	8	7	6
28	jmcna50	13	11	11	13	12	12
29	jmcoa50	6	6	6	5	5	5
30	jmcpa04	6	7	6	7	6	7
31	jmcqa50	14	14	13	14	14	14
32	jmcsa50	8	8	8	8	8	8
33	jmcta01	7	7	8	7	7	6
34	jmcua01	10	10	10	9	9	10
35	jmcwa02	10	10	10	10	10	10
36	jmcxa50	3	4	2	4	2	2
37	jmcxc00	8	8	8	8	8	8
38	jmdaa50	4	5	4	4	6	5
39	jmdda01	8	8	8	8	8	8
40	jmdfa04	18	17	18	17	17	17
41	jmdga01	10	11	11	11	10	10
42	jmdgb01	8	8	8	8	8	5
43	jmdgc01	8	8	8	9	8	8
44	jmdia50	9	10	9	10	9	8
45	jmdib50	12	10	12	11	13	11
46	jmdla50	12	12	10	11	12	12
47	jmdna50	14	14	15	14	14	16
48	jmdqb50	10	10	10	10	11	10
49	jmdua01	12	12	12	12	12	11
50	jmdva50	11	12	12	13	14	11
51	jmdwa04	10	10	10	12	10	11
52	jmdyb50	9	8	8	8	8	9

No.	Cell ID	# trials  180°	# trials  210°	# trials  240°	# trials  270°	# trials  300°	# trials  330°
1	jffna01	10	10	10	10	8	9
2	jffoa50	13	13	13	12	12	11
3	jffob50	7	8	8	7	7	8
4	jfftb50	7	7	8	7	6	6
5	jffza04	8	8	8	8	8	8
6	jfgaa01	4	4	2	3	4	4
7	jfgab00	9	9	9	8	9	8
8	jfgcb01	14	14	11	10	11	10
9	jfgfa01	7	7	8	8	9	8
10	jfgha50	10	8	8	9	8	8
11	jfgka50	10	9	8	10	8	10
12	jfgwa02	10	10	11	10	11	11
13	jmbvb50	8	6	6	8	8	9
14	jmbvd50	7	6	7	6	9	8
15	jmbwa01	9	8	10	9	8	9
16	jmbya50	3	4	4	5	4	4
17	jmbyb50	11	9	8	10	10	8
18	jmbza01	10	10	10	11	10	11
19	jmcaa01	10	10	10	10	11	12
20	jmcab50	11	12	9	9	10	10
21	jmcda01	10	11	10	10	10	10
22	jmcdb50	8	7	7	8	8	8
23	jmcea50	9	8	9	8	9	9
24	jmcha01	13	12	12	12	12	12
25	jmchb01	8	8	8	8	8	8
26	jmclc01	6	6	6	6	7	6
27	jmcma50	6	7	6	6	6	6

28	jmcna50	10	12	11	12	13	12
29	jmcoa50	6	6	6	5	5	5
30	jmcpa04	6	6	6	6	6	6
31	jmcqa50	13	14	13	14	14	13
32	jmcsa50	8	8	8	8	8	8
33	jmcta01	8	8	8	7	8	7
34	jmcua01	8	9	13	13	12	8
35	jmcwa02	10	10	10	10	10	10
36	jmcxa50	2	2	1	2	3	1
37	jmcxc00	8	8	8	8	8	8
38	jmdaa50	4	7	6	7	6	7
39	jmdda01	8	8	8	9	8	8
40	jmdfa04	17	17	17	18	17	17
41	jmdga01	11	11	10	10	11	11
42	jmdgb01	8	8	8	8	8	8
43	jmdgc01	8	8	8	8	8	8
44	jmdia50	10	10	10	10	11	8
45	jmdib50	12	11	11	13	11	11
46	jmdla50	12	11	12	12	12	12
47	jmdna50	14	15	14	15	16	15
48	jmdqb50	10	9	9	10	10	11
49	jmdua01	12	11	12	12	12	11
50	jmdva50	12	13	15	11	16	13
51	jmdwa04	12	10	12	11	10	10
52	jmdyb50	10	7	9	9	8	7

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List of subjects participated in the psychophysical experiments:

No.	Subject ID	Age	Gender	Naive	Handedness†	Exp. 2	Exp. 3
1	anh	28	f	yes	right	✓	✓
2	anm	27	f	yes	-	✓	✓
3	jis	22	f	yes	right	✓	✓
4	juo	36	m	yes	right	✓	✓
5	lev	23	f	no	right	✓	✓
6	mak	22	f	yes	right	✓	✓
7	rej	31	f	yes	left	✓	✓
8	sak	35	m	yes	-	✓	✓
9	ulw	27	f	yes	right	✓	X
10	vam	31	m	no	right	✓	X

† Here, the handedness is defined based on the hand used to write.

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Consent form for the psychophysical experiment:

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Information for subjects participating in psychophysical tests in the Cognitive Neuroscience Laboratory, German Primate Center (DPZ)

Name of subject: _____

Project leader: _____
Cognitive Neuroscience Laboratory, DPZ

I. Subject requirements

Participation in the tests requires normal or corrected-to-normal vision, and unrestricted arm- and hand-mobility.

II. Aim of the study and benefit for the subject

You participate voluntarily in this study. The purpose of the study is an improved knowledge of human perception and behavior. With your participation you contribute to our understanding of brain functions, especially of perception, the planning of movement, and the role of selective attention. We investigate how the efficiency of the sensorimotor system is influenced by prior knowledge and by the exact sensory circumstances of a particular experimental situation. For example, your performance will be compared between tasks, which differ only in the focus of your visual attention. Differences in performance between these task conditions allow conclusions about the influence of selective attention to the processing of sensory information.

A detailed understanding of the function of the healthy organism and brain is an important prerequisite for helping patients suffering from specific visual or motor deficits. The participation in the tests per se does not yield any direct health benefit.

III. Design of the study

You will participate in measurements, in which we will test your sensory or sensorimotor performance. For this, a number of different stimuli will be presented in random order on a computer screen or with a tactile stimulator. You will sit on a chair in front of these devices, sometimes with your chin on a chin rest in order to guarantee a defined distance to the monitor. You will respond by pressing a button on a computer keyboard, by touching a touch-screen, by making an eye movement or by pressing a foot-switch (for simplicity we only speak of 'keystroke' in the following). A test consists of several trials. In each trial one or more visual stimuli will be presented. At the end of each trial you will respond with a keystroke. For example, the stimulus could consist of a moving pattern and you will have to decide if it is moving to the left or to the right. For some tests, it is important, that you change your direction of gaze as little as possible. For those tests, you will have to maintain your gaze on a small stimulus on the screen during the trials.

IV. Procedure

A single test normally consists of 50 to 200 trials of a few seconds duration each. A test will be finished after 5 to 20 minutes. During one session several tests and different tasks will be conducted. Before each new task you will have opportunity to practice. A session typically takes one hour, including breaks between the tests. You will set the pace as in most measurements you start every trial yourself and because you can take breaks whenever you choose. There are also breaks between the tests and the task of the next test will be explained. Typically, a study consists of several sessions and the first sessions are used for training. It is very important for us, that you finish a study completely. But

09_02 Probandenaufklaerung-EN.pdf

you are free to abort the measurements at any time.

V. Side effects

These tests are absolutely non-invasive experiments. There are no adverse effects. The computers and screens in use are standard equipment as used in offices and for computer games.

VI. Voluntariness of participation

The participation in the study is absolutely voluntary. You are entitled to quit the study at any time and without giving reasons.

VII. Payment

For the participation in the measurements you receive a payment. In some of our studies we investigate the influence of such payments on the performance of the subjects. In these sessions a basic payment is combined with an amount that depends on the psychophysical performance or is chosen at random.

VIII. Passing on of the data

The data collected in these studies will only be used or passed on anonymously.

Consent form:
I read and understood this information carefully. The experimenter answered all my questions. By signing this form I agree to

a) participate in the study and
b) to the publication of the collected data in an anonymous form.

I received a copy of this information sheet.

_____ _____

Place and date Subject's signature

Cognitive Neuroscience Laboratory
German Primate Center – Leibniz Institute for Primate Research
Prof. Dr. Stefan Treue
Kellnerweg 4, 37077 Goettingen
Tel: 0551-3851-118

September 2012

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Written information for doing the psychophysical experiment:

INSTRUCTIONS

1. Before you start with the experiment, make sure that you are sitting comfortably in the chair and that your head lies comfortably in the chin rest.
2. Kindly turn off your mobile phone or any other distracting devices.
3. The experiment consists of 2 blocks; each one lasting approx. 25 minutes.
4. The first session is a training to make you feel comfortable with the experimental task. Additional blocks will be presented during this session, lasting 10 – 15 minutes each. Please make sure that you fully understand the instructions and the task during the training phase and feel free to ask questions.

Experiment 1

1. Every block will start with brief session of eye-calibration followed by the experiment. In this phase you will have to keep your gaze on a small spot as it moves around the screen.
2. The main experimental task is depicted in the Fig 1. In each trial: (a) you will see a central fixation point. You have to look at this point and when you are ready, (b) press the right button on a gamepad. (c) You will see two stimuli in both visual fields; each containing dots moving linearly in a circular region. Please remember, that you need to look at the central fixation point throughout whole experiment. (d) The linear motion is followed by a short masking stimulus. Your task will be to judge whether the direction of motion was directing **up or down.** Make this judgment as accurately as possible and indicate your answer (e) pressing up or down buttons on the right side of the gamepad. If you cannot decide, please make your best guess.

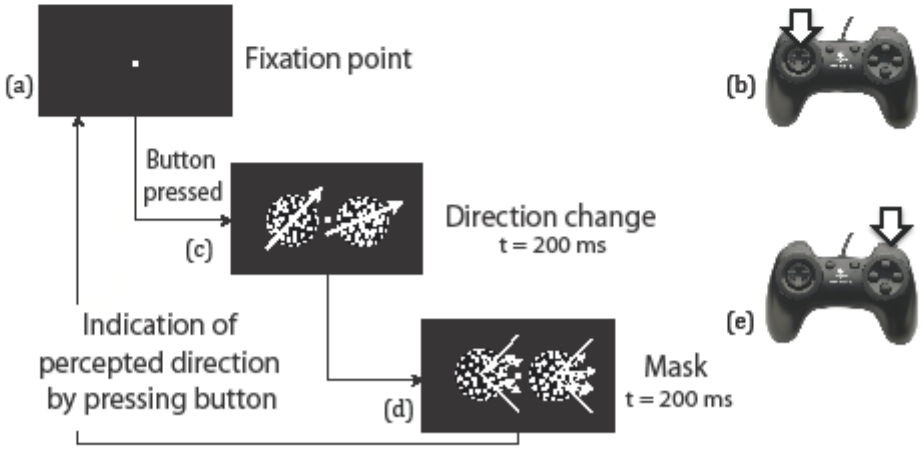

Fig.1

3. After making your choice, you can start next trial when you are ready, by pressing (b) the right button on the gamepad.

Experiment 2:

1. Every block will start with brief session of eye-calibration followed by the actual experiment. In this phase you will have to keep your gaze on a small spot as it moves around the screen.
2. The main experimental task is depicted in the Fig 2. In each trial: (a) you will see a central fixation point. You have to look at this point and when you are ready, (b) press the right button on a gamepad. (c) You will see two stimuli in both visual fields; each containing dots moving linearly in a circular region. Please remember, that you need to look at the central fixation point throughout whole experiment. (d) After 2-3 seconds, you will observe a change in the motion direction of dots **in the right visual field.** (e) The direction change is followed by a short masking stimulus. (f) Your task will be to judge whether the final direction of motion (after the change occurred) was directing **up or down.** Make this judgment as accurately as possible and indicate your answer pressing up or down buttons on the right side of the gamepad. If you cannot decide, please make your best guess.
3. After making your choice, you can start next trial when you are ready, by pressing (b) the right button on the gamepad.

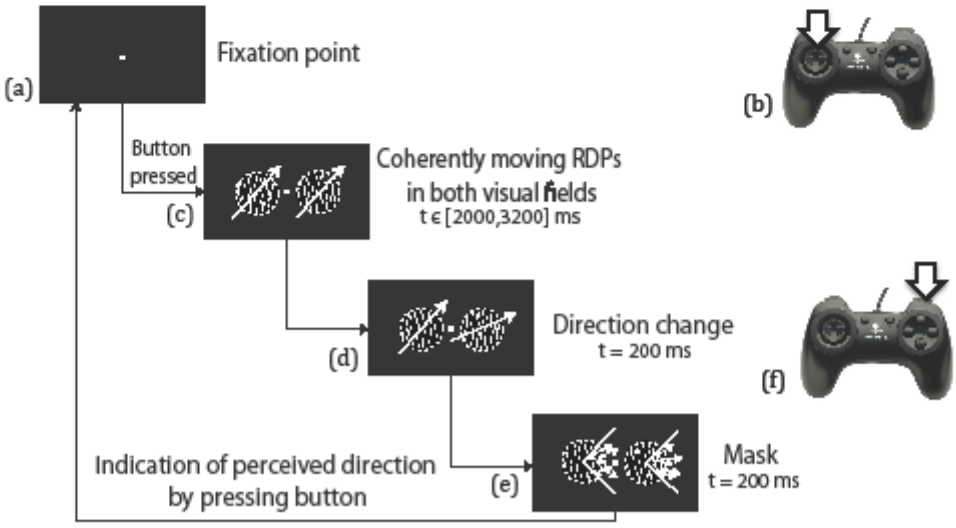

Fig.2

Thank you for your participation.

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VAHID MEHRPOUR, MSc in Physics

Cognitive Neuroscience Laboratory (CNL)
German Primate Center (DPZ)
Kellnerweg 4
37077 Göttingen, Germany
+49 551 3851-301, vmehrpour@dpz.eu

EDUCATION

2013 – 2017 **Doctoral Student**, Neuroscience, German Primate Center (DPZ), Göttingen, Germany

Thesis: "The role of attention and adaptation in shaping cortical representations and the perception of abrupt changes in the visual environment"
Supervisor: Prof. Dr. Stefan Treue

2010 – 2013 **Researcher Assistant**, German Primate Center (DPZ), Göttingen, Germany

Supervisor: Prof. Dr. Stefan Treue

TECHNINCAL SKILLS

- **Operating Systems:** Mac OS, Windows, Linux
- **Data Analysis & Modeling Tools**: MATLAB [extensive], Maple [extensive], C++ [intermediate]
- **Project Management**: Merlin Project, Microsoft Project
- **Other**: Microsoft Office applications, Adobe Illustrator, Adobe Photoshop, Adobe InDesign, Origin

TEACHING EXPERIENCE

- **Teaching Assistant**, *Mathematics for physics students II*, B.Sc., University of Göttingen, Germany (2015)
- **Teaching Assistant**, *Introduction to MATLAB in systems neuroscience*, GGNB doctoral course, University of Göttingen, Germany (2015)
- **Project supervisor**, *Effects of spatial attention on direction change perception in human subjects*, lab rotation project, German Primate Center, Göttingen, Germany (2015)
- **Teaching Assistant**, *Introduction to MATLAB in systems neuroscience*, GGNB doctoral course, University of Göttingen, Germany (2014)
- **Project supervisor**, *Psychophysical investigation of the perception of complex visual motion patterns*, lab rotation project, German Primate Center, Göttingen, Germany (2012)

ABSTRACTS & CONFERENCE PRESENTATIONS

- ***Poster* at the Bernstein Conference 2017 - Göttingen, Germany**, *Environmental change events: neural encoding, attentional modulation, and perceptual correlates*, V. Mehrpour, J. C. Martinez-Trujillo, S. Treue
- ***Poster* at the Primate Neurobiology Meeting 2016 - Tübingen, Germany**, *A unified approach of animal care journaling*, M. Niessing, V. Mehrpour, A. Gail, S. Treue
- ***Poster* at the Society for Neuroscience's Annual Meeting 2014 - Washington, D.C., US**, *Attention sharpens the tuning curves of MT neurons during the on-response to moving stimuli*, V. Mehrpour, J. C. Martinez-Trujillo, S. Treue
- ***Poster* at the Bernstein Conference 2014 - Göttingen, Germany**, *Attentional influence on neuronal responses in primate visual cortex to the onset of visual motion*, V. Mehrpour, J. C. Martinez-Trujillo, S. Treue
- ***Poster* at the Society for Neuroscience's Annual Meeting 2013 - San Diego, California, US**, *Spatial attention enhances the saliency of changes in motion direction at the expense of an accurate representation in area MT*, V. Mehrpour, J. C. Martinez-Trujillo, S. Treue
- ***Poster* at the 11th Göttingen Meeting of the German Neuroscience Society 2013 - Göttingen, Germany,** *Spatial attention suppresses MT responses to motion onset in macaque monkeys*, V. Mehrpour, J. C. Martinez-Trujillo, S. Treue
- ***Talk & Poster* at the Bernstein Conference 2013 - Tübingen, Germany**, *Saliency enhancement by attention in area MT of the visual cortex of rhesus monkeys*, V. Mehrpour, J. C. Martinez-Trujillo, S. Treue
- ***Poster* at the 10th Göttingen Meeting of the German Neuroscience Society 2013 - Göttingen, Germany**, *Stimulus salience enhancement at the expense of accurate representation: MT responses to transient direction changes and their attentional enhancement*, V. Mehrpour, J. C. Martinez-Trujillo, S. Treue

ATTENDED COURSES

- *Theoretical and computational neuroscience: collective dynamics biological neural networks*, GGNB, Göttingen, October 2015-February 2015
- *Analysis and models in neurophysiology*, BCCN, Freiburg, Germany, October 6-11, 2013
- *Scientific integrity & the responsible conduct of research*, DPZ, Göttingen, March 2nd, 2012
- *Introductory course in laboratory animals: handling, techniques and theory*, MPI, Göttingen, February 20-24, 2012
- *From vision to action*, DPZ, Göttingen, October 2010-February 2011

REFEREES

- **Prof. Dr. Stefan Treue**, Professor for Cognitive Neurosciences at the University of Göttingen, Director of the German Primate Center, Head of the Cognitive Neuroscience Laboratory at the DPZ, treue@gwdg.de
- **Prof. Dr. Alexander Gail**, Professor for Sensorimotor Neuroscience and Neuroprosthetics at the University of Göttingen, Head of the Sensorimotor Group at the DPZ, agail@gwdg.de