Feature-based attention in primate visual cortex

Mechanisms and limitations of color- and motion-selection as assessed by neurophysiology, psychophysics and computational modeling

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“[…] an understanding of consciousness must rest on an appreciation of the brain networks that subserve attention, in much the same way as a scientific analysis of life without consideration of the structure of DNA would seem vacuous.” (Posner, 1994)

Contents

Chapter 1 - Introduction

1.1 General introduction and motivation

A long time has passed since it was proposed that attention is the control of a central swinging latch in a Y-shaped tube maze in which balls represent information traveling downwards through either of the branches of the Y (Broadbent, 1957). If this simplistic model of information processing in humans is confronted with more input (balls) than it can process, jamming occurs and information is ultimately dropped. Given input from multiple channels (i.e. branches of the Y), the swinging latch controls which one of the branches currently feeds information to the next processing stage, thereby blocking all other streams of information.

As primitive as this model might appear in the scope of today's research on attention and our current knowledge of the brain, it already incorporates many of the central ideas about cortical processing and attentional selection of information that we still consider valid. First of all, it is generally accepted that the processing capacity of the brain is limited (Broadbent, 1958; but see Krauzlis et al., 2014; Schneider and Shiffrin, 1977; Tsotsos, 2011). It is therefore necessary that some (potentially relevant) information is actively propagated to be processed, while other (potentially irrelevant) information is dropped.

Secondly, attention is hypothesized to be a mechanism that acts at the core of this selection process, by controlling which of the arriving information is to be forwarded to a central processing stage. This process is called gating and its perceptual effects become evident when human subjects have to selectively attend to stimuli that are presented in rapid serial visual presentation (Potter and Levy, 1969; Raymond et al., 1992). Those experiments require subjects to report the presence of specific stimuli (e.g. the letter A and/or the number 1) among numerous distractor stimuli. While attention facilitates detection of the searched-for stimuli in these tasks, the temporal order in which stimuli were presented is rarely perceived by the subjects (Reeves and Sperling, 1986). This is consistent with the idea that attention selectively gates relevant information to a central processing stage, thereby perturbing the temporal order of events. This idea is summarized in the (generalized) attentional gating model (Reeves and Sperling, 1986).

To date, many models of attentional modulation have been proposed. A short review article summarizing the core ideas of top-down attentional modulation is part of this work (Schwedhelm and Treue, 2015 chapter 2.1).

The scope of this thesis, however, is not primarily a description of the perceptual effects of attention, but rather incorporates two empirical studies that aim at shedding some light on the cortical control circuit underlying the deployment of feature-based attention. The first study (Chapter 2.2) attempts to deduce from human psychophysical performance how an attentional signal acts on a local sensory population of motion-selective neurons. In a theoretical framework of cortical normalization I describe a stimulus-independent influence of attention on neuronal responses. This provides a testable prediction of a local and feature-specific top-down modulation in the case of feature-based attention.

The second empirical study (Chapter 2.3) attempts to identify and characterize resource limitations for the deployment of feature-based attention in macaque monkeys. In particular, the aim of the study was to compare neuronal modulations of motion-selective neurons in three cases: First when attention was directed to the encoded feature (attention to motion), second when the attended feature did not match the encoded feature (attention to color), and third when two features were attended simultaneously (attention to a conjunction of motion and color). Neuronal modulations recorded in macaque motion-selective area MT (see Chapter 1.2.1) indicated that feature-based attention enhances neuronal responses when the attended feature matches the neuronal preferences, but also when attention is directed to color. In the latter case, however, modulation onset was delayed, supporting a theory of sequential activation of cortical modules leading up to the enhancement of all features of a stimulus, rather than only one. Further, a possible resource limitation of attention was identified when multiple features were to be attended simultaneously. In those cases we found motion-selective area MT to respond significantly more strongly to stimuli containing at least one of the attended features, without further enhancement for stimuli matching both attended features. This indicates that feature-based attention directed to motion and color cannot be deployed independently and that it might be of limited use when subjects need to employ complex task rules to guide behavioral responses.

This first chapter will give a broad overview of the relevant structures of the visual system subserving motion and color processing and perception. I will then summarize the current state of knowledge of the attentional system, describing different forms of attention and their effects on neuronal responses and visual perception. Finally, I will describe prominent theories of the attention control circuit, leading up to the most debated topics related to the attentional system.

1.2 Motion processing in visual cortex

In mammals, visual information travels from the retina through the optic nerve, traverses the subcortical lateral geniculate nucleus (LGN) and arrives in the occipital cortex. While some image features, like contrast boundaries, are decoded from the retinal image as early as in the retina, motion information needs to be inferred from the visual input by taking into account the temporal sequence of stimulation (Frechette et al., 2005; Wandell, 1995). This type of decoding first takes place in the primary visual cortex (but see Barlow et al., 1964; V1; Hubel and Wiesel, 1968). V1 makes up most of the volume of the occipital cortex and is organized in a retinotopic fashion (Hubel and Wiesel, 1965; 1968; but see Przybyszewski et al., 2014). Being a central structure in primates, V1 is hypothesized to be equivalent in humans, non-human primates and other higher mammals (e.g. Blakemore and Campbell, 1969).

Directionally selective neurons in monkey V1 are mostly constrained to layers 4a, 4b, 4α and layer 6 (Hawken et al., 1988). They make up for roughly 25% of the neurons in V1 (Hubel and Wiesel, 1968). However, directional selectivity in V1 is highly constrained by the aperture problem (e.g. Pack and Born, 2001), which constitutes that the motion direction of a local contour (like a straight contrast boundary) can only be decoded as orthogonal (i.e. with the smallest velocity) to the contour, if the terminals of the contour are occluded by an aperture. Such a scenario exists when viewing the local boundary through an aperture, like the very small receptive field (RF[i]) of a V1 neuron.

The aperture problem can be solved when information from many neurons is pooled together, and thus the edges of the contour are detected. Also, by combination of many neurons sampling the same moving object, a solution to the aperture problem is the calculation of the intersection of (individual) constraints (Adelson and Movshon, 1982; Rust et al., 2006; Simoncelli and Heeger, 1998). It was hypothesized that this process begins when motion information is forwarded to the second visual cortex (V2), where receptive fields are larger and neurons are

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[i] A (classical) receptive field (RF) is the region of visual space a neuron responds to. In human early visual cortex, RFs represent stimuli in a retinotopic reference frame, as shown by fMRI measurements (but see d'Avossa et al., 2007; Gardner et al., 2008).

progressively more sensitive to motion (Hubel and Wiesel, 1965). In parallel, V1 also feeds to the middle temporal area (MT or V5), which is a densely myelinated area with strong reciprocal connectivity to V1 and V2 (Gattass et al., 2005; Van Essen et al., 1981). MT was first classified as a direction-selective area by Dubner and Zeki (1971; Zeki, 1974) and it can be localized in the human by positron emission tomography and functional magnetic resonance imaging (O'Craven et al., 1997; Saproo and Serences, 2014; Tootell et al., 1995; Zeki, 1991).

1.2.1 Area MT

Movshon et al. (Adelson and Movshon, 1982; 1985) used plaid stimuli to test the directionality of MT neurons. Plaid stimuli are a combination of two drifting, sinusoidal gratings, usually with the same spatial frequency and speed, but different motion vectors. Plaids are perceived by humans as moving in the pattern direction (Adelson and Movshon, 1982), which can be computed by the intersection of constraints. In V1, motion-selective neurons respond to the two single pattern directions, but in area MT about ~25% of the neurons are pattern-selective (but see Guo et al., 2004; and Kumano and Uka, 2013 for a different estimate; Movshon et al., 1985; Tinsley et al., 2003). This led to the hypothesis that MT computes the motion of whole objects, or patterns, by pooling and recombination of the motion information it inherits from V1, thereby (at least partly) solving the aperture problem (Born and Bradley, 2005; Movshon et al., 1985; Simoncelli and Heeger, 1998). Majaj et al. (2007) tested this pooling hypothesis by recording from MT pattern-selective cells, but found that placing the two gratings side-by-side in the RF largely abolished pattern selectivity. This suggests that MT does not simply pool directional inputs from V1 but instead performs input recombination on a smaller spatial scale than that of their RFs (Rust et al., 2006), possibly by pooling over a small population of differentially tuned neurons from V1 (Perrone, 2004; Perrone and Krauzlis, 2008).

Area MT is organized in a columnar fashion, with neurons across cortical layers exhibiting similar motion tuning preferences (Albright, 1984; Dubner and Zeki, 1971; Geesaman et al., 1997). Neighboring columns have similar spatial preferences, such that the fovea is represented laterally, the periphery medially, the upper visual field anterior and the lower visual field posterior (Gattass and Gross, 1981; Gattass et al., 2005). The majority of neurons found in area MT are motion-selective, typically with a (circular) Gaussian tuning of 40-60 degrees width (Albright, 1984; Britten and Newsome, 1998; Snowden et al., 1992) and receptive field sizes of 4 degrees diameter at the fovea (Felleman and Kaas, 1984) and increasingly bigger RFs in the peripheral visual field (Born and Bradley, 2005; Desimone and Ungerleider, 1986; Raiguel et al., 1995; Richert et al., 2013). Many neurons in MT are also tuned to binocular disparity and integrate this stimulus feature with motion (see also Krug and Parker, 2011; Rokers et al., 2009). In fact, recent recordings from anaesthetized macaques show that the majority of MT cells integrate planar motion with binocular disparity to form a tuning to 3D motion (Czuba et al., 2014). The selectivity for binocular disparity is also organized in a columnar fashion (DeAngelis and Newsome, 1999), suggesting that single columns in MT encode similar 3D motion trajectories. Speed and velocity preferences, however, are not organized in a columnar fashion (Liu and Newsome, 2003), and typical peak sensitivities for the speed of motion lie within the range of 5-30 degrees/s (Albright, 1984; Britten, 2004). This is largely compatible with the finding that MT detects motion in depth mostly based on interocular velocity differences, rather than by integrating the change in disparity over time (Rokers et al., 2009; Sanada and DeAngelis, 2014). Tuning for motion in 3D makes area MT an important processing stage for the decoding of self-motion from optic flow (Britten, 2008), or for computing object motion beyond the retinotopic reference frame (Fajen and Matthis, 2013; Warren and Rushton, 2009).

1.2.2 Perception of motion

That area MT contains neurons decoding the perceived motion of plaid stimuli (Adelson and Movshon, 1982; Movshon et al., 1985) led to the hypothesis that MT is a key player not only in motion decoding but also in motion perception (Born and Bradley, 2005; but see Tailby et al., 2010). Experimental support for this hypothesis comes from lesion studies. Lesions of area MT were found to elevate psychophysical thresholds in motion detection and discrimination tasks (Lauwers et al., 2000; Newsome and Pare, 1988; Pasternak and Merigan, 1994) although threshold recovery could take place within a few weeks and contrast thresholds were unaffected (Newsome and Pare, 1988). This indicates that rudimentary motion perception may take place even with a (partly) lesioned area MT. Lesions of MT further did not affect detection thresholds for color and texture differences, indicating the specific role of MT in motion processing and perception (Schiller, 2009).

Recording the activity of single cells in area MT while monkeys performed a direction discrimination experiment showed that the sensitivity of individual neurons in area MT is comparable to the sensitivity of the animal (Newsome et al., 1989), as indicated by signal detection theory (Tanner and Swets, 1954). Similar results were obtained for coarse depth-discrimination (Uka and DeAngelis, 2003). Britten et al. (1996) showed that when monkeys chose between one of two motion directions based on a stimulus of uncorrelated noise, the activity of the neurons encoding that stimulus predicted the choice of the animal. Furthermore, in a similar experiment, the choice of monkeys could be biased by microstimulating a direction sensitive column, especially when the sensory evidence was sparse (Salzman et al., 1990; 1992). Microstimulation of MT was further shown to have an effect on speed perception (Liu and Newsome, 2005) and stereoscopic depth perception (DeAngelis et al., 1998), as well as on the perception of structure from motion (Krug et al., 2013). These experiments may be discussed critically due to advantageously long analysis periods compared to the reaction time of the animal (Cook and Maunsell, 2002), or the potentially biased estimation of choices from trial-to-trial fluctuations in neuronal firing (Kang and Maunsell, 2012). Further, it was found that area MT can be less sensitive than the animal in tasks requiring fine direction discrimination (Liu and

Newsome, 2005; Purushothaman and Bradley, 2005). Still, area MT remains a key player in visual motion detection and perception. Neurophysiological studies involving MT as a key area in the motion processing pathway of the brain are of particular importance in order to understand higher-order brain functions like attention (see Chapter 1.4). This is particularly meaningful due to the homologous nature of motion processing streams in macaque and human (Curran and Lynn, 2009; Lynn and Curran, 2010).

1.3 Color Processing in the primate brain

As opposed to visual motion, color is an image feature that can be decoded directly from the retinal image. For this purpose, evolution has provided humans and old world monkeys (e.g. macaques) with three cone receptor types, each with a different chromatic sensitivity profile. They are commonly referred to as L-, M- and S-cones, with respective peak sensitivities of ~560nm, ~530nm and ~450nm (Stockman and Sharpe, 2000; Stockman et al., 1999). Because of the principle of univariance (Rushton, 1972) one photoreceptor cannot distinguish changes in wavelength from changes in intensity, such that in order to sense the chromatic properties of a stimulation, information from different types of cones has to be combined.

Hering (1920) argued that this would best be done by contrasting information in a color opponent manner, such that the weights between the activation of different receptors can be calculated. It was proposed that this happens predominantly on red-green and blue-yellow color-opponent axes. Wiesel and Hubel (1966) then reported the existence of two chromatic opponent cell types in the macaque LGN: Type 1 had an On/Off-center-surround receptive field with predominantly red-green color opponency. Type 2, which did not have a center-surround receptive field, showed color-opponent responses predominantly between blue and yellow spots of light. Both cell types were not sensitive to white-light contrast boundaries, making them the hypothetical building blocks for color processing in cortex.

In striate cortex, color-selective cells are clustered in cytochrome oxidase-rich blobs (Livingstone and Hubel, 1982; 1984; Ts'o and Gilbert, 1988), where information from color opponent cells converges. Here, more complex spatially and chromatically opponent cell types are found, including double opponent cells with opposite chromatic tuning (and different spatial selectivity) for the receptive field center and surround (Conway, 2001; Michael, 1978). Such cells detect chromatic properties of a stimulus in relation to surrounding colors and thus detect local color contrasts irrespective of illumination condition. Local color contrasts can be used to achieve color constancy (Gegenfurtner, 1999; Kraft and Brainard, 1999; Land and McCann, 1971). This brings color coding in V1 closer to color perception as the perception of a color is heavily dependent on the light reflected from surrounding objects (Land and McCann, 1971).

However, the cortical mechanisms underlying color processing are still heavily debated. In particular, it is not very well understood how S-cone information is integrated with L- and M-cone information (Johnson et al., 2004) and which parts of the circuit are crucial for color vision (Schiller et al., 1990). As this thesis focuses primarily on motion processing and perception the reader is advised to refer to Gegenfurtner (2003), Conway (2009), Solomon and Lennie (2007) and Shapley and Hawken (2011) for reviews on the topic.

1.3.1 Area V4

V4 is a midlevel area in the visual processing hierarchy, commonly referred to as the first area of the ventral stream. It was first classified as a color-selective area (Zeki, 1983b; 1983a; 1973), but later was found to be strongly selective for the orientation of stimuli (Mountcastle et al., 1987; Schein et al., 1982; van Essen and Zeki, 1978). The resulting controversy is likely attributable to the patchy organization of V4, with clusters of cells preferring specific colors, orientations or object shapes, as revealed by optical imaging studies (Ghose and Ts'o, 1997; Tanigawa et al., 2010). In fact, attempts to map out a general pattern of intra-areal organization (like DeAngelis and Newsome, 1999 did for area MT) have so far not been conclusive (Youakim et al., 2001).

V4 thus combines information inherited from upstream V1, in which image features like stimulus color and orientation, are encoded by mostly separate populations of neurons. Both V1 and V2 (which receives input predominantly from V1) directly project to V4 (Nakamura et al., 1993; Yukie and Iwai, 1985). In V4 different subclasses of neurons were found: color-selective and color-constant cells, orientation-selective cells, complex shape-selective cells, motion-selective cells and cells that signal relative disparities for stimuli. In summary, V4 detects and segregates objects by using color, motion, disparity and luminance cues (Bushnell et al., 2011a; 2011b; Desimone and Schein, 1987; Hegdé and Van Essen, 2005b; 2005a; Hinkle and Connor, 2001; 2002; 2005; Kobatake and Tanaka, 1994; Kusunoki et al., 2006; Schein and Desimone, 1990; Umeda et al., 2007; Zeki, 1983b), for review see (Roe et al., 2012).

Lesions of macaque V4 illustrate the functional importance of this area. After lesions, monkeys show impairments in color vision and in a range of complex tasks involving object recognition (Heywood and Cowey, 1987; Walsh et al., 1992a; 1992b; 1993). A specific loss of color-constant perception after lesion shows that V4 color cells must play an important role in color perception, but less so in color processing.

Overall, it seems difficult to assign a clear functional label to V4. Undoubtedly however, it is an important visual area, central to a brain network subserving color and object perception (Roe et al., 2012). Further, like motion-selective area MT, V4 is not exclusively modulated by bottom-up sensory input but seems to receive strong top-down modulatory input. In fact, V4 has been intensely studied regarding its attentional modulation (see next section), which makes it an interesting area for the study of higher cognitive functions.

1.4 Attention

The brain is not a feed-forward image processor. McManus et al. (2011) showed that units in area V1 dynamically respond to stimuli given specific stimulus expectation. This demonstrates, as one example of many, that already early on in the visual processing stream, neurons change their responses to sensory input based on prior knowledge, or assumptions, of the visual environment. The connectivity profile of visual areas supports this notion: for almost all of the feed-forward connections from lower to higher visual areas, there exist feedback, or top-down projections (e.g. Felleman and Van Essen, 1991). In fact, even the subcortical lateral geniculate nucleus, which is commonly referred to as visual relay between the retina and primary visual cortex, receives strong descending input from V1 (and also weakly from MT; for review see Kaas and Huerta, 1988). Those top-down projections (originating in layer 6 of V1) might subserve shaping of receptive fields, define the tuning profiles of individual cells, or could be involved in even more complex tasks like the modulation of neuronal responses based on the current behavioral need of the organism. In fact, some modulations of responses observed in the LGN closely resemble cortical modulations observed in the context of visual attention (McAlonan et al., 2006; 2008; O'Connor et al., 2002), although it should be noted here that there exist evidence for a clear separability of the coding of contrast and attention in primary visual cortex (Pooresmaeili et al., 2010), which could be an alternative explanation of the observed modulations in all but one report (McAlonan et al., 2008).

Selective visual attention (Desimone and Duncan, 1995; Kastner and Ungerleider, 2000; Treue, 2001) can be defined as a dynamic adaptation of the visual system to current behavioral needs. Either attention is deployed automatically (bottom-up), like the sudden focusing of resources on novel or unexpected stimuli, or it is deployed voluntarily (top-down) including a slight latency compared to bottom-up selection (but also see Awh et al., 2012; for review see Theeuwes, 2010). Bottom-up deployment, since it is involuntary, might be a result of the complex network structure of the visual system and possibly involves subcortical areas like the superior colliculus, pretectum or the reticular nucleus of the thalamus (Kaas and

Huerta, 1988; McAlonan et al., 2000; 2006). Top-down attention, on the other hand, is flexible in its deployment and its specificity: Spatial attention is directed to specific parts of the visual field and is commonly compared to a 'spotlight' (Brefczynski and DeYoe, 1999; Crick, 1984; Eriksen and Eriksen, 1974; Posner et al., 1980; Treisman and Gelade, 1980) enhancing all stimuli whose spatial positions coincide with the location of attention. Feature-based attention acts on all spatial positions, but enhances stimuli with a specific image feature (e.g. a specific color or motion direction), and object-based attention promotes processing of the representation of a specific object (including all its features, but bound by the object rather than globally).

1.4.1 Spatial attention

On a neuronal level, spatial attention was found to increase the firing rate of single units when the receptive fields of those units code for attended spatial locations (Brefczynski and DeYoe, 1999; Luck et al., 1997b; Sundberg et al., 2012; Treue and Maunsell, 1996). Neurons in both V4 (McAdams and Maunsell, 1999b) and area MT (Treue and Martinez-Trujillo, 1999; Treue and Maunsell, 1999) were found to be enhanced by spatial attention, without changing their tuning functions (but see David et al., 2008; Ling et al., 2009). This led to the conclusion that attention multiplicatively scales responses on the single neuron level. Such a scaling affects responses most strongly when the activity of a neuron is already high, and less so when either the stimulus is not preferred by the neuron or is of low contrast. Thus, when plotting responses to stimuli of varying contrast, attention would scale up the resulting contrast response function (CRF). An alternative to this response gain modulation, which was found for single neurons in area MT (Lee and Maunsell, 2010b), would be to not scale, but shift the CRF such that stimuli with intermediate contrasts are modulated most strongly and already highly salient stimuli (Treue, 2003) at high contrasts are not modulated further. Indeed, such a contrast gain effect was found in V4 (Reynolds et al., 2000) and also in area MT (Martinez-Trujillo and Treue, 2002). Williford and Maunsell (2006) set out to test whether spatial attention in V4 modulated responses by contrast or response gain, but found intermediate effects with good explanatory power of an activity gain model. Here, attention additively scales responses by a fixed factor, independent of stimulus contrast or neuronal preference, which was also found to be the case for single neurons in V1 (Thiele et al., 2009), or in the BOLD signal recorded from human V1 (Buracas and Boynton, 2007). Those seemingly conflicting findings were later unified by the Normalization Model of Attention (NMoA; Reynolds and Heeger, 2009), which postulates a relationship between the different sizes of the stimuli used in the above mentioned experiments relative to the assumed spatial spread of attention. In the NMoA, the ratio between stimulus size and attentional spread determines whether attention has a contrast or response gain effect on the CRF. This prediction was later supported for the case of spatial attention by an fMRI study in humans (Herrmann et al., 2010).

Spatial attention was also found to cause small shifts in the location of V4 RFs of neurons close to, but not at the attended location (Connor et al., 1997). Receptive fields of MT single units also shifted towards the attended locations and were mildly reduced in size when attention was directed inside (Womelsdorf et al., 2006) and increased in size when attention was directed outside the receptive field (Anton-Erxleben et al., 2009; Niebergall et al., 2011a). This effect of shifting RFs can be accounted for by assuming selective multiplicative scaling of neurons in upstream visual areas contributing to the pool of information summed by the downstream RF (Compte and Wang, 2006). Input from a lower visual area biased in this way would create the observed differences in higher visual areas like V4 and MT (Maunsell and McAdams, 2001; McAdams and Maunsell, 1999a).

Finally, spatial attention can be divided into several spotlights and filter out interspersed stimuli. Niebergall et al. (2011b) recorded from single units in area MT while monkeys were required to attend to two RDPs traversing the screen, but not entering the RF of the recorded units. They found that while monkeys showed clear behavioral effects of attention, a stimulus directly in between two attended stimuli was not enhanced by attention. Similar results confirming the ability to split spatial attention were obtained using fMRI or EEG in humans (Drew et al., 2009; McMains and Somers, 2004; Morawetz et al., 2007; Müller et al., 2003; but see Scalf and Beck, 2010).

Among the various types of attentional deployment, visual spatial attention is likely the best understood. In fact, the effects of spatial attention extend far beyond what can be covered in this format. Since this thesis focuses primarily (but not exclusively) on the effects of feature-based attention, the reader is referred to the excellent review of Anton-Erxleben & Carrasco (2013).

1.4.2 Feature-based attention

Attention was found to selectively bias single neurons in area V4 to process one of two stimuli falling in their receptive fields (Moran and Desimone, 1985). The hypothesized mechanism behind this stimulus selection inside a neuron's RF is an attentional enhancement of one of the inputs from lower sensory areas converging in a higher processing stage, effectively giving one input an advantage in the competition for processing resources in the higher area (Desimone, 1998). This idea of a 'biased competition' (Desimone, 1996; Desimone and Duncan, 1995; Duncan et al., 1997) has received support from a number of empirical studies (for review see Beck and Kastner, 2009; Chelazzi et al., 1998; 2001; but see Lee and Maunsell, 2009; 2010a for an alternative account of those findings; Luck et al., 1997a; Reddy et al., 2009; Reynolds et al., 1999).

However, the larger body of studies investigating the effects of feature-based attention on neuronal responses (e.g. Maunsell and Treue, 2006; McAdams and Maunsell, 2000) observed scaling of neuronal firing rates that could not readily be explained by a competition between the inputs to a visual area. To account for this pattern of results, a 'feature similarity gain model' was proposed (Treue and Martinez-Trujillo, 1999). In this model, the amount of feature-based modulation acting on a given neuron is dependent on the similarity between its preferred feature and the attended feature, regardless of the location of spatial attention and the actual sensory input to the cell. This model, although conceptually different, makes similar predictions to the biased competition model (for review see Boynton, 2009). If the underlying gain function becomes smaller than 1 for unattended features, it also predicts suppression of unattended features, as measured in macaque MT neurons (Khayat et al., 2010; Martinez-Trujillo and Treue, 2004), or in the modulations of human visual cortex when subjects attend to colors (Störmer and Alvarez, 2014), spatial frequency and orientation of gratings (Flevaris and Murray, 2015) or motion (Stoppel et al., 2011).

Typical reports of feature-based attention in visual cortex measure the responses of neurons or populations of neurons when they encode stimuli that are not currently relevant for the task, but share the attended feature of the relevant stimulus. Given that in those cases, neuronal responses are enhanced by feature-based attention, but not spatial attention (Lu and Itti, 2005; Martinez-Trujillo and Treue, 2004; Melcher et al., 2005; Motter, 1994; Saenz et al., 2002; 2003; Treue and Martinez-Trujillo, 1999), it has been hypothesized that feature-based attention enhances responses globally throughout the visual field. Further evidence for this 'globalness' of feature-based attention comes from a number of fMRI and EEG experiments, or psychophysical studies in humans (Boynton et al., 2006; Melcher et al., 2005; Saenz et al., 2002; 2003; but see Stoppel et al., 2007). A global enhancement of specific visual features is particularly useful in tasks requiring subjects to find a stimulus with a unique feature or feature conjunction at an unknown location (Andersen et al., 2008; Buracas and Albright, 2009; Kristjánsson and Sigurdardottir, 2008; visual search; Maljkovic and Nakayama, 1994; Wolfe, 1994b; Zhou and Desimone, 2011). Painter et al. (2014) recently confirmed this beneficial global enhancement by feature-based attention in visual search, using steady-state visual evoked potentials (SSVEP) tagged by unique frequencies and measured using EEG in humans.

However, the 'globalness' of feature-based attention can also be detrimental to task performance when a feature has to be attended at a specific spatial location, but ignored in another (Andersen et al., 2013). Since even in those situations, feature enhancement was not constrained to the location of the stimuli, it was suggested that visual feature-based attention is obligatory global and cannot be constrained to spatial locations. Consequently, it was found that if spatial attention and feature-based attention are deployed simultaneously, both enhancements interact only mildly (Andersen et al., 2011; Hayden and Gallant, 2005; 2009; Patzwahl and Treue, 2009; but see Serences and Boynton, 2007). On a neuronal level, feature-based modulation seems to be coordinated across the two hemispheres of the brain, as opposed to spatial attention (Cohen and Maunsell, 2010; 2011), further strengthening the theory that features are enhanced throughout the whole visual field, even at locations where this enhancement has no behavioral benefit (White and Carrasco, 2011).

When human subjects are required to divide feature-based attention to multiple features (e.g. multiple directions of motion), a capacity limit of attentional deployment becomes evident (Ernst et al., 2012; Liu et al., 2013). Despite this finding, it is possible to attend to two feature dimensions (e.g. color and orientation) without the involvement of a central bottleneck, providing a ‘double dose’ of facilitation to stimuli matching both attended features (Andersen et al., 2015).

1.4.3 Object-based attention

It has been found that when monkeys are cued to attend to a specific feature, responses of neurons encoding features different from the attended feature, but originating from the same stimulus were also enhanced. Katzner et al. (2009) showed that neurons in area MT increase their firing rates in a similar way whether monkeys attended to the motion or the color of a moving random dot pattern (see also Chen et al., 2012). A possible explanation for this finding is the deployment of object-based attention (Blaser et al., 2000; Duncan, 1984; Duncan and Nimmo-Smith, 1996; Treisman and Kanwisher, 1998). In this selection mechanism, attention is directed not to a single feature, but instead to all features constituting an object[ii]. The existence of an object-specific enhancement is a well-known phenomenon intensely studied using human psychophysics (for review see Chen, 2012), but conclusive neurophysiological evidence is surprisingly scarce. Roelfsema et al. (1998) showed that neurons in V1 responded more strongly when they encoded parts of a currently relevant object (a curve that monkeys had to mentally trace to find a saccade target). Wannig et al. (2011) showed, also for V1, that recorded neuronal populations were enhanced by the presence of a saccade target in their RFs, and also when they encoded a stimulus that was not the target, but grouped to the target by Gestalt

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[ii] Unfortunately, *object* does not have an unambiguous definition in the scope of visual neuroscience. For the purpose of this work it shall be defined as any visual stimulus or grouping of visual stimuli organized by at least one Gestalt grouping principle[iii].

principles[iii]. Interestingly, stimuli identical to the target stimulus, but presented as separate objects were not enhanced, indicating that this type of attention does not simply deploy feature-based selection to all features grouped by an object (but see Boehler et al., 2011; Lustig and Beck, 2012).

Area MT was also shown to be enhanced by attention when monkeys attended to one surface of a rotating transparent motion display. Here, neither spatial nor feature-based attention could have been the reason for an enhancement in MT, so it was hypothesized that the selection of the surface caused an object-based enhancement (Wannig et al., 2007).

Similar experiments using superimposed objects with different feature-properties were also done in humans, and the modulation of feature-selective brain areas recorded by means of fMRI or MEG. Typically the transparent stimulus consisted of a house and a face and subjects attended to either of the two, resulting in attention-related activity differences in house- and face-coding regions, respectively (Al-Aidroos et al., 2012; Baldauf and Desimone, 2014; Cohen and Tong, 2015; Serences et al., 2004; Yantis and Serences, 2003). Interestingly, the onset of object-based modulation was found to be delayed by ~100ms compared to the onset of feature-based modulation (Schoenfeld et al., 2014). This demonstrates an important constraint of object-based selection mechanisms: the attended object has to be identified for attention to selectively enhance it. In fact, brain areas encoding higher-order objects like houses and faces were found to selectively synchronize with early feature-selective brain areas (e.g. MT and/or V4; Al-Aidroos et al., 2012), likely providing important top-down input for the guidance of object-based selection, at least when directed to complex objects. Simpler objects, like surfaces of colored, moving dots bound by color, speed or motion direction (Schoenfeld et al., 2011; Wegener et al., 2014) might be selected faster. However, these results indicate that object-based attention is a selection mechanism highly related to feature-based attention, which was hypothesized to be necessary for object perception (Stojanoski

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[iii] Gestalt grouping principles first introduced by Wertheimer (1923) are a set of rules for the composition of stimuli to be perceived as one stimulus object. Commonly, they are summarized in six categories for stimulus grouping: proximity, similarity, closure (completeness), good continuation, common fate, and good form.

and Niemeier, 2007) and therewith necessary for the top-down deployment of object-based attention.

1.4.4 The premotor theory of attention

Probably the most influential theory of the control circuit subservient of the deployment of visual attention is the premotor theory of attention (Rizzolatti et al., 1987). In short, a motor plan (especially a saccade plan) is hypothesized to be both necessary and sufficient for the deployment of visual attention. This follows a stringent logic considering that the primary purpose of attention is to focus processing capacities - and therewith the orienting of sensory organs - onto the potentially relevant stimulus. It is therefore a parsimonious explanation that the same neuronal populations that are used to reorient sensory organs - in the case of visual attention, the eyes - are also used to reorient attention.

A line of fMRI experiments shows that exactly this is the case when human subjects attend to spatial locations with or without executing a saccade to the same location (Astafiev et al., 2003; Corbetta and Shulman, 2002; Corbetta et al., 1998; Shulman et al., 2010). Specifically, the reciprocal network between the frontal eye fields (FEF) and the intraparietal sulcus is known to be involved in planning and executing saccades and is also activated when subjects covertly attend to spatial locations (for review see Noudoost et al., 2010). As this network is thought to be homologous in the monkey (Mantini et al., 2013), those findings can be contrasted with electrophysiological recordings and electrical stimulation of the relevant areas in the macaque. Electrical stimulation of sites in FEF usually results in the execution of saccades, however when currents are used that do not elicit saccades but nonetheless excite the reciprocal network, neuronal activity in sensory area V4 is altered in a way closely resembling the effect of deployed spatial visual attention (Armstrong and Moore, 2007; Armstrong et al., 2006; Moore and Armstrong, 2003; Moore and Fallah, 2001). This effect is absent without concurrent visual stimulation of the sensory area (Ekstrom et al., 2008), providing evidence for the modulatory nature of this top-down input from FEF to sensory cortex.

Most interestingly, modulating the activity in FEF can also modulate the effects of deployed feature-based attention. Zhou and Desimone (2011) showed that during visual search, feature-based attention could be measured both in monkey V4 and FEF and that the modulation in FEF preceded the modulation in V4. Heinen et al. (2014) showed with fMRI in humans, that when activity in FEF is disrupted by means of transcranial magnetic stimulation, the activity of motion-selective human MT+ is affected when subjects attend to the motion of transparent motion-face stimuli, but not when attending to faces or passively viewing the stimuli (see also Liu et al., 2011). This is surprising since global feature-based attention is unlikely to be preceded by saccade planning – the core assumption of the premotor theory of attention. It is, however, known that FEF can selectively highlight task relevant features (Schall and Hanes, 1993), synchronize selectively to currently relevant feature-processing populations (Fries, 2009; Gregoriou et al., 2009; Womelsdorf et al., 2007), to which it has direct projections (Ninomiya et al., 2012), and thus contains populations of neurons not primarily engaged in saccade motor preparations. In fact, since the location of the FEF is often determined functionally rather than anatomically and borders to neighboring areas are not very well confined in prefrontal cortex, the above mentioned results can be explained by the inclusion of feature-selective populations from adjacent areas 8A (Zaksas and Pasternak, 2006) or the posterior part of dorsolateral prefrontal cortex (Lennert and Martinez-Trujillo, 2011), both of which were indicated to be involved in the deployment of feature-based attention.

In summary, what started with the idea that a motor plan is sufficient for the deployment of attention might in the scope of recent research become a unified theory of visual attention. However, especially in the scope of feature-based and object-based attention (Pooresmaeili et al., 2014) a motor plan is neither sufficient nor necessary for attentional deployment. Yet, the FEF and surrounding feature-responsive areas seem to be key players in the cortical network guiding top-down attention.

Chapter 2 - Original Manuscripts

This chapter consists of 3 original manuscripts:

- Schwedhelm, P and Treue, S (2014)

  Attentional Top-Down Modulation, Models of
  Encyclopedia of Computational Neuroscience
  (New York, NY: Springer New York), 1–5.
  doi:10.1007/978-1-4614-7320-6_566-1.

- Schwedhelm, P, Krishna, BS and Treue, S

  An extended Normalization Model of Attention accounts for feature-based attentional enhancement of both response and coherence gain
  The Journal of Neuroscience
  In Revision

- Schwedhelm, P and Treue, S

  Attention to features modulates MT units in a delayed match-to-sample task: feature-based enhancement precedes object-based attention
  prepared for submission

2.1 Models of Attentional Top-Down Modulation

This manuscript constitutes an entry in the *Encyclopedia of Computational Neuroscience* (2015), and aims to give a broad overview of current models of top-down selection mainly in the scope of visual search tasks. Search tasks require subjects to find a particular target stimulus among various distractors as fast and accurately as possible. Interestingly, it was shown that when the searched-for stimuli have unique visual features among distractors, those targets are found very fast as they tend to 'pop-out' for selection. Conversely, when target stimuli are defined by a unique conjunction of features, selection takes up more time, and is dependent on the number of distractors.

Top-down visual attention is generally thought to play an important role in the selection of target stimuli (see also Chapter 2.3). The following article will give an overview of the general ideas linking attentional selection to the selection of behaviorally relevant targets. Moving on from the general gating hypothesis (introduced in Chapter 1.1), it provides a more detailed description of current theories of the attentional system, with a strong emphasis on portraying possible theoretical frameworks in which attention guides selection, rather than focusing on the actual implementation of an attentional control circuit in the brain.

Author contributions:
PS and ST wrote the paper.

Attentional Top-Down Modulation, Models of

Encyclopedia of Computational Neuroscience
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Definition

Attention – the ability of a sensory system to facilitate the processing of specific information at the expense of disregarding the remainder.

Bottom-up processes – information processing in the nervous system that operates in a feedforward way, advancing from sensory organs or areas at a low level of the cortical processing hierarchy.

Top-down influence – modulatory signals in the nervous system that originate from areas at a high level of the cortical processing hierarchy, influencing information processing in lower areas.

Saliency – a measure of the magnitude of the difference of a stimulus from its neighbors in space and time.

Detailed Description

The Case for Attention

Evolution has provided humans and other highly evolved species with powerful sensory systems. While our cortical processing capacity has also evolved and grown impressively, the torrent of information provided by our sensors far outstrips our ability to process it all. In addition, most of the sensory information picked up at any moment has little importance for our survival. Complex nervous systems faced with this challenge have developed sophisticated selection mechanism to identify the most relevant incoming information and to focus processing resources (and ultimately perception) onto this small fraction. This process is called attention and for the purpose of this entry can be defined as the selective modulation of sensory information based on its assumed behavioral relevance.

Bottom-Up Versus Top-Down

The selection processes underlying attention need to fulfill two requirements: on the one hand their ubiquitous (central and incessant) role in the continuous stream of perceptual decisions requires that they operate efficiently and as fast as possible. At the same time, the selection processes' purpose of dynamically identifying the most relevant components of the sensory input demands harnessing as much of the cognitive power of the species' central nervous system as possible.

These seemingly incompatible demands, efficient and fast vs. computationally demanding and thus slow, have created two flavors of selection:

1. A bottom-up (automatic, exogenous) attentional selection that exploits the realization that the most informative aspects of our sensory environments are those where one stimulus differs from their neighbors in space and time. This local saliency can be identified and enhanced by simple feedforward filter mechanisms embedded throughout the processing of sensory signals in the nervous system.
2. A top-down (voluntary, endogenous) attentional selection that integrates any information available to the organism about the current situation to make the most informed decision about which sensory input component represents the most relevant information in the given situation.

In the visual domain, this distinction is well illustrated with visual search tasks: If we are confronted with a fairly homogenous visual scene, any outlier will be identified, enhanced, and selected by the continuous parallel computation of local saliency, creating the perceptual "pop-out" characteristic of simple search tasks where the features of the target stimulus differ substantially from the distribution of features of the distractors. Conversely, a target stimulus, which is less distinct, either because it is defined as a conjunction of more than one feature or because it does not differ substantially from the distribution of distractor features, does not pop out, but rather requires a more demanding and correspondingly slower selection process.

Taking a Computational Approach to Attention

Here we illustrate how the attentional modulation of sensory information processing is implemented in computational models. Due to the brevity of the entry, we focus on a few examples of models of top-down attentional modulation in the visual system of man and other primates.

One of the most influential computational models of visual attention is the **feature integration theory** (FIT; Treisman and Gelade, 1980). In the FIT, information about different features of stimulus, such as its shape, color, orientation, and movement, is extracted in parallel, automatically and effortlessly through a system of feature maps, which topographically represent the spatial distribution of specific features in the visual scene. This process detects and locates a target stimulus defined by a single unique feature value (such as the color red) because it is represented by a unique hotspot in a single feature map (with each distractor represented by a hotspot in its corresponding feature map, such as the one for the color blue). This target detection is very quick and is unaffected by the numerosity of distractor stimuli, matching the experimental observation that human reaction times in such simple search tasks are independent of the number of distractor items. If the target stimulus is not defined by a single feature alone, but by a conjunction of multiple features, information from different feature maps needs to be integrated to detect and localize a target. This requires a serial process that actively integrates information from different maps to detect the target's unique feature conjunction at one topographical location, matching the linear increase in reaction time observed with an increase in the number of distracters in a conjunctive search task. The FIT proposes that this serial integration process is accomplished by means of a top-down, spatial "spotlight" of attention.

An alternative account for the pattern of reaction times in search experiments is offered by the **guided search theory** (GST; Wolfe, 1994a), which does not assume an attentional spotlight. Instead, the top-down attentional signal changes the weight of activation maps before they are combined to create a ranking of all present stimuli based on their likelihood to represent a target. The selection of stimuli is then again performed serially, from high to low probability, until the target stimulus is detected.

While the FIT and the GST emphasize the role of feature maps in attentional selection, the theory of visual attention (TVA; Bundesen, 1990) takes a different approach. Here the selection of stimuli is dependent on their processing speed. Before a stimulus can be encoded in visual short-term memory and thus enter awareness, it needs to compete in a computational race with other stimuli. In the TVA top-down attention speeds up the processing of certain items, making them likely to win the race.

While the FIT, GST, and TVA have been developed to account for the perceptual data available at the time, more recent models of attention have been developed to capture data from single-cell recordings from monkey visual cortex. Two early conceptual models attempted to account for the enhanced neuronal response to attended stimuli and the reduced response to unattended stimuli. The biased competition model of attention (Desimone and Duncan, 1995) envisages a competition between the stimulus representation of attended and unattended stimuli that can be biased by a top-down attentional signal in favor of the attended stimulus' representation. The feature similarity gain model of attention (Treue and Martinez-Trujillo, 1999) alternatively proposes that the enhancement of neural responses by attention reflects a process where top-down attentional signals enhance the gain of those neurons whose preferred features match the current attentional state of the organism, independent of the stimulus that currently activates a neuron.

These two conceptual models have inspired a large number of computational models. The most prominent of those are models that emphasize an interaction of top-down attention with the normalization process that creates the sigmoidal contrast response functions typical for neurons throughout sensory cortex. Multiple varieties of such normalization models of attention have been proposed (Boynton, 2009; Ghose, 2009; Ghose and Maunsell, 2008; Lee and Maunsell, 2009; 2010a; Reynolds and Heeger, 2009). They all emphasize the similarity, in perception, as well as in the neural encoding and also in the central role of the response normalization process between two influences on the strength a neural stimulus representation. One is the physical (bottom-up) strength of the stimulus (most directly represented by its contrast) and the other is the attentional weight (implemented as a kind of sensory prior) assigned to them through a top-down attentional signal.

Beyond models that emphasize response normalization, there have been numerous other approaches to model the attentional modulation of sensory information processing. They include the selective tuning model (Tsotsos et al., 2005) that proposes a layered network architecture (representing the hierarchy of cortical areas) to implement a spatial "spotlight of attention" that endows certain regions of the visual scene with enhanced processing. The spiking network model (Deco and Rolls, 2005; Deco and Thiele, 2011) places much more emphasis than any of the models discussed above on building its approach on biological components, such as spiking neurons and specific neurotransmitters.

The Integrated Saliency Map

It should be noted that almost all models of attention incorporate the concept of an integrated saliency map (Treue, 2003), that is, a topographic representation of the stimuli in the current visual scene that combines their relative physical strength and their assumed behavioral relevance. This combination implements a weighing of bottom-up and top-down aspects of a stimulus, providing processing resources to strong unattended stimuli as well as to weak attended ones. While such an integrated saliency map is consistent with a number of perceptual phenomena and is ideally suited to guide eye movements across a visual scene, it is a matter of some debate which of the many topographically organized areas in the visual cortex represents this map or whether multiple such maps exist.

Similarly, while functional imaging and single-cell recording studies have implicated a network of frontoparietal areas in the guidance process that is necessary to appropriately allocate processing resources (Corbetta and Shulman, 2002; Kastner and Ungerleider, 2001), such anatomic specificity is rarely included in current computational models of attention.

Conclusion

In conclusion, in the last decade, a large number of computational models of top-down attention have been developed that can account for a large variety of perceptual and physiological aspects of the attentional modulation of sensory information processing. These models emphasize several core issues, such as the response normalization in cortical networks, the multistage nature of cortical information processing, and the concept of an integrated saliency map. Despite this progress much more work is needed to achieve a complete computational description of top-down attentional modulation.

2.2 An extended Normalization Model of Attention accounts for feature-based attentional enhancement of both response and coherence gain

On a neuronal level, feature-based attention modulates single neurons in visual cortex according to the potential behavioral significance their encoded information currently has for the organism. This modulation leads to response differences (e.g. reflected in an increased firing rate) for attended stimuli relative to physically identical unattended stimuli. While this effect of attention has been repeatedly demonstrated, in particular for macaque visual areas MT and V4 (Chapter 1.4), it is a matter of speculation where the attentional signal originates and how exactly it influences local neuronal populations. In particular, it is still unclear which types of neurons in a given cortical area are modulated by attention (i.e. whether specific cortical layers receive the attentional signal) and how this input is then translated into a change in activity. The biased competition model of attention (Desimone and Duncan, 1995) proposes that attention modulates neuronal activity by a change in the sensory input strength of attended features, thereby increasing the probability of attended stimuli to be encoded by a given neuronal population. The feature similarity gain model of attention (Treue and Martinez-Trujillo, 1999) alternatively postulates that the neuronal enhancement can take place without taking into account the current sensory input. Instead single neurons receive a processing advantage dependent on the similarity of their encoded sensory features and the currently attended features.

These two concepts are difficult to tease apart, as their effects on the firing rates of single units are very similar. The following study deduces from human psychophysical performance that under presupposition of a canonical local normalization circuit (Carandini and Heeger, 2012), feature-based attention acts in both a stimulus dependent and independent way, further supporting the feature-similarity gain model of attention.

Author contributions:

PS and ST conceived the experimental paradigm, PS collected the data, analyzed the data and prepared all figures, PS and BSK developed the model and PS, BSK and ST wrote the manuscript.

An extended Normalization Model of Attention accounts for feature-based attentional enhancement of both response and coherence gain

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In revision

Abbreviated title: An extended NMoA

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Number of words:	Abstract (248) Significance Statement (118) Introduction (650) Discussion (1715)

Abstract

Paying attention to a sensory feature improves its perception and impairs that of others. Recent work has shown that a Normalization Model of Attention (NMoA) can account for a wide range of physiological findings and the influence of different attentional manipulations on visual performance. A key prediction of the NMoA is that attention to a visual feature like an orientation or a motion direction will increase the response of neurons preferring the attended feature (response gain) rather than by increasing the sensory input strength of the attended stimulus (input gain). This effect of feature-based attention on neuronal responses should translate to similar patterns of improvement in behavioral performance, with psychometric functions showing response gain rather than input gain when attention is directed to the task-relevant feature. In contrast, we report here that when human subjects are cued to attend to one of two motion directions in a transparent motion display, attentional effects manifest as a combination of input and response gain. Contradicting the NMoA's predictions, the impact on input gain is greater when attention is directed towards a narrow range of motion directions than when it is directed towards a broad range. These results are captured by an extended NMoA which either includes a stimulus-independent attentional contribution to normalization or utilizes direction-tuned normalization. The proposed extensions are consistent with the feature-similarity gain model of attention and the attentional modulation in extrastriate area MT, where neuronal responses are enhanced or suppressed by attention to preferred and non-preferred motion directions.

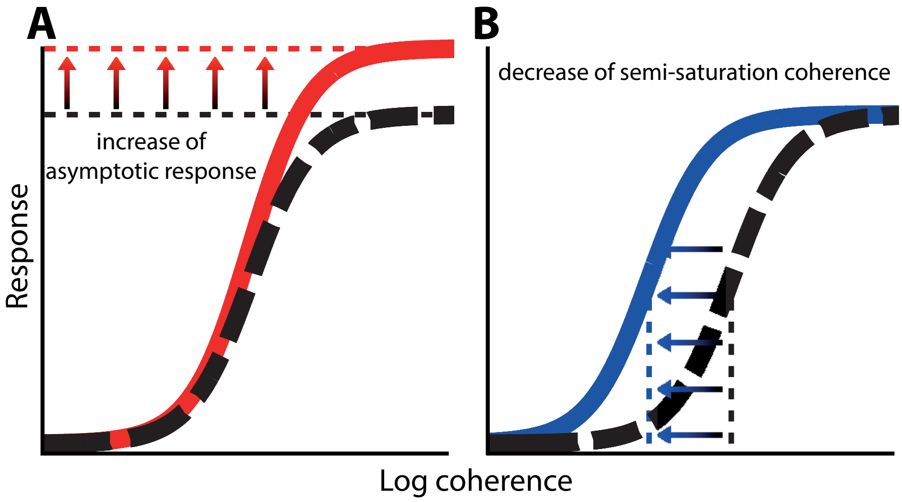
Significance statement

We report a pattern of feature-based attentional effects on human psychophysical performance, which cannot be accounted for by the Normalization Model of Attention using biologically plausible parameters. Specifically, the model predicts that attention to a visual feature like a specific motion direction will lead to a response gain in the input-response function, rather than the input gain that we actually observe. In our data, the input gain is greater when attention is directed towards a narrow range of motion directions, again contrary to the model's prediction. We propose two physiologically testable extensions of the model that include direction-tuned normalization mechanisms of attention. Both models account for our data without affecting the previously demonstrated successful performance of the NMoA.

Introduction

Attention to visual features like a specific orientation or motion direction has been shown to enhance visual responses to the attended feature across visual cortex in both monkey neurophysiology (Maunsell and Treue, 2006) and human fMRI data (O'Craven et al., 1997; Saenz et al., 2002; Stoppel et al., 2011). Prior studies have reported that feature-based attention enhances responses in neurons tuned to the attended feature (Martinez-Trujillo and Treue, 2004; Treue and Martinez-Trujillo, 1999), privileges responses to the attended feature under competitive conditions (Khayat et al., 2010) and induces shifts of the preferred feature (David et al., 2008). Similarly, visual attention to a particular spatial location affects neuronal responses and improves perceptual performance at the attended location (reviewed in Reynolds and Heeger, 2009). In particular, attention has been shown to enhance neuronal responses by increasing the effective sensory input strength (in our task: coherence gain: Figure 1A) and/or by scaling the responses of the neuron (Li and Basso, 2008; Martinez-Trujillo and Treue, 2002; response gain: Figure 1B; McAdams and Maunsell, 1999a; Reynolds et al., 2000; Thiele et al., 2009; Treue and Martinez-Trujillo, 1999; Williford and Maunsell, 2006).

Figure 1[iv]



[iv] Illustration of the effect of change in response gain (A) and coherence gain (B) on the coherence-response function.

The Normalization Model of Attention (NMoA: Reynolds and Heeger, 2009) attempts to capture this variety of attentional effects in a single model. It proposes that attention multiplicatively scales the driving input to a neuronal population, and the response to this driving input of each individual neuron in the population is divisively normalized by the responses of all the neurons in the normalizing pool. Depending on the size of the visual stimulus and the spread of visual attention, the relative effects of sensory stimulation and visual attention on the individual neuron and the normalizing pool differ, leading to input-gain and/or response-gain effects that reproduce many of the effects of spatial attention on neuronal responses (Lee and Maunsell, 2009; Reynolds and Heeger, 2009). Further, fMRI measurements of the spatial spread of visual attention in human subjects provide support for this critical assumption of the NMoA by verifying the model's predictions regarding the influence of the spatial spread of visual attention on behavioral performance (Herrmann et al., 2010). The NMoA also captures some of the reported effects of feature-based attention on neuronal responses (Reynolds and Heeger, 2009), using the same underlying mechanism of attentional scaling of sensory responses. Importantly, the NMoA predicts that under plausible parameter settings (Herrmann et al., 2012), attention to a visual feature will impact neuronal responses by increasing the effective response of neurons tuned to the attended feature (response gain) rather than by increasing the sensory input strength of the attended stimulus (input gain). This implies, given reasonable assumptions linking neuronal responses to behavioral output (Pestilli et al., 2009), that attention to a visual feature will not produce input-gain effects, but only response-gain effects on the input-response function. Herrmann et al. (2012) confirmed this prediction when they observed only response gain effects in an experiment where human subjects paid attention to either narrow or broad ranges of orientation.

In contrast, we report here that when human subjects are cued to attend to one of two motion directions in a transparent motion display, attentional effects manifest as a combination of input gain (in our task "coherence gain") and response gain. Further, contradicting the NMoA's predictions, we observed a larger impact on input gain for a narrow focus of attention in feature space than for a broad focus. These results require either a revision of the assumptions linking neuronal activity to behavior, or extensions of the NMoA that include direction-tuned influences on the normalization pool. We propose and compare two possible extensions, introducing either coherence-dependent or coherence-independent direction-tuned normalization. The extended normalization models are consistent with the feature-similarity gain model of attention (Treue and Martinez-Trujillo, 1999) and the attentional modulation in extrastriate cortical area MT, where neuronal responses are enhanced or suppressed by attention to preferred and non-preferred motion directions respectively (Martinez-Trujillo and Treue, 2004).

Materials & Methods

In this study, we measured human psychophysical performance in a direction discrimination task using transparent motion stimuli with varying motion coherence. We used exogenous cues of varying directional precision and validity to achieve two levels and two directional spreads of voluntary feature-based attention. The attentional effects on the coherence response function were estimated by comparing performance in validly and invalidly cued trials and the two attentional states.

Human Subjects

Eight subjects (ages 18-27 years) participated in the study, out of which 6 subjects (2 naive female, 3 naive male and 1 male lab member) reached a sufficient performance level for analysis (see section Data Analysis below). All subjects reported normal or corrected to normal vision. Prior to entering the main experiment four subjects participated in a pilot study to determine a suitable task timing (data not shown). All naive participants received monetary compensation for each session. Subjects were verbally instructed about the task demands and received individual training before entering the main experiment (see section Pre-Tests). All experiments were in accordance with institutional guidelines for experiments with humans and adhered to the principles of the Declaration of Helsinki. Each subject gave informed written consent prior to participating in the study.

Apparatus

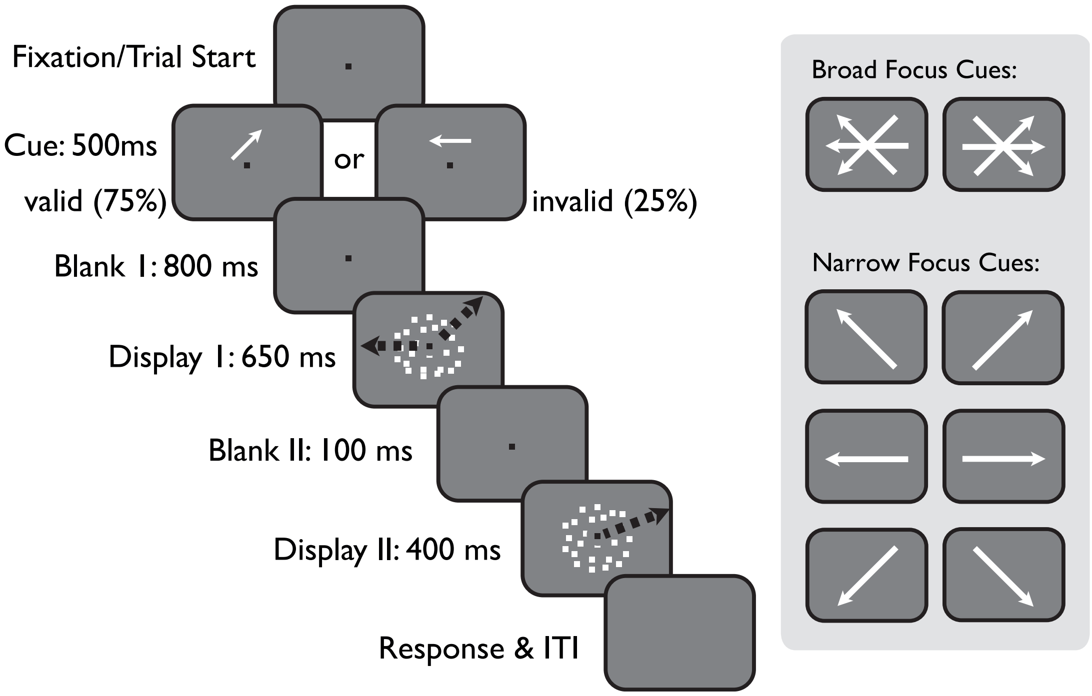
Stimuli were presented on a LCD screen (SyncMaster 2233, Samsung) with a refresh rate of 120Hz and a background luminance of 20 cd/m^2. The experiment was controlled by an Apple computer (MacPro 2010) running the open-source software MWorks version 0.5 (mworks-project.org). Subjects were seated in a dimly lit room at a viewing distance of 57cm from the screen, their head resting on a chin-rest. A gamepad (Precision, Logitech) was used for recording responses, such that a button press with the right index finger indicated a clockwise decision, and the left index finger a counter-clockwise decision. Each experimental trial was started by pressing a button with the right thumb. For three subjects, eye position was recorded monocularly (left eye) using a video-based eye tracker (IView X, SMI) sampling at 250Hz. For the remaining three subjects, eye position was recorded binocularly with a sampling frequency of 500Hz using an Eyelink-1000 system (SR Research). Both eye position systems were calibrated before each experimental session and the accuracy of the calibration confirmed by a custom calibration task (data not shown).

Stimuli and Procedure

Figure 2 depicts the experimental paradigm. Subjects viewed moving random dot patterns (RDPs) through a stationary annulus-shaped virtual aperture with an inner diameter of 5 degrees and an outer diameter of 17.8 degrees of visual angle. The RDPs contained 4 dots/deg^2, moving on individual linear paths at a speed of 15 deg/s. Each dot had a diameter of 0.252 degrees and a luminance of 70 cd/m^2. Subjects had to maintain their gaze on a fixation point central to the RDP and to initiate each experimental trial by a thumb-button press. Then an attentional cue was presented (see section "Attentional Cues") for 500ms on top of the fixation point.

Following the cue and a 800ms delay, a RDP was displayed for 650ms. This first presentation of the RDP contained two superimposed groups of coherently moving dots (‘direction components’), as well as an additional number of randomly moving dots. The two motion directions of this transparent motion display were always 135±20 degrees apart, with each direction being sampled randomly from a ±10 degree range around a reference direction. Reference directions were +45, 0 and -45 degrees from straight left or rightward motion. The presentation of this first RDP was followed by a short delay of 100ms with only the fixation point present on the screen. Then the second RDP was displayed for 400ms, with a slightly rotated version of one of the two previously shown motion directions, as well as the same proportion of noise dots as in the first RDP. Subjects had to indicate whether the single motion direction of the second RDP was rotated clockwise or counter-clockwise relative to the closest motion direction of the first RDP (2 alternative-forced choice, Figure 2). Subjects received auditory feedback indicating correct or wrong judgments. The magnitude of the direction change was individually set for each subject to be the pooled just noticeable difference of all reference directions (see section Pre-Tests).

Figure 2[v]



We varied the motion coherence on a trial-by-trial basis. Motion coherence was defined as the percentage of dots moving in signal directions. The remaining noise dots moved on linear paths in random directions. The coherence level was the same for both presentations of the RDP (i.e. regardless of how many motion directions were presented). We used 6 levels of coherences (1.6%, 6.4%, 12.8%, 25.6%, 51.2% and 100%) for each attentional condition. Throughout each session, all cue types and

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[v] Experimental protocol. Human observers performed a direction discrimination task and reported the rotational direction change between the motion direction shown in stimulus display 2 and the corresponding motion component of stimulus 1. Black arrows indicate two example direction components embedded in the transparent motion display 1, one of which is slightly rotated and shown again in display 2. Subjects are cued to which one of the two motion directions of the transparent motion display is likely to be the relevant direction. Cues indicate either a relatively small range of possible directions (right panel, narrow focus cues), or a wide range of possibly relevant motion directions (broad focus cues). The actually displayed motion is always jittered around the cued direction, such as the cue itself is non-informative about the precise direction of the relevant motion. In addition, cues indicate the correct motion component with a 75% validity, making it worthwhile for subjects to process both motion components of stimulus display 1.

coherence levels were pseudo-randomly interleaved. One session consisted of 576 properly terminated trials, excluding fixation errors and erroneous early responses. Each subject participated in 5 sessions for a total of 2880 analyzed trials per subject. Trials in which eye-positions occurred outside a radius of 2.5 degrees around the fixation point, or eye blinks were considered fixation breaks. They caused trials to be aborted with an auditory feedback to the subjects. On average across all trials the subject's eye positions during both stimulus presentations remained within a circular window with a radius of less than 0.6 degrees.

Attentional Cues

Previous studies aimed at developing or testing the NMoA have used spatially separated target and distractor stimuli, which could have been selected by spatial attention. We used a transparent motion display containing two spatially overlapping moving RDPs, leaving feature-based attentional mechanisms as the sole selection mechanism for behavioral enhancement. Two types of cues were used to direct subjects' attention to one of the two motion directions of the transparent motion display. The *narrow focus cue* was a single arrow pointing in one of the six reference directions, indicating that the relevant motion signal of the first stimulus presentation was likely to occur within a range of ±10 degrees around its heading. The *broad focus cue* consisted of three arrows, all pointing either towards the left or the right side, indicating that the relevant motion was likely to be right- or leftwards. Both cues were valid (i.e. the relevant motion occurred within ±10 degrees of the narrow focus cue and towards the side of the broad focus cue) in 75% of all trials and all subjects were verbally instructed and frequently reminded to also pay some attention to the uncued directions. The narrow focus cue was designed to enable subjects to direct their attention onto a narrow range (ca. 20 degrees) of possible target directions, while the broad focus cue was used to induce a much wider focus (ca. 110 degrees) of the feature-based attention field. In both cases, attention helped the subjects to preferentially focus on one of the two directions of the transparent motion stimulus for subsequent comparison with the single motion.

The frequency of occurrence for the different types of cues was balanced between cue directions and cue types, such that no cue direction or cue type was overrepresented. We determined the influence of feature-based attention on psychophysical performance by comparing validly and invalidly cued trials.

Pre-Tests

Pre-testing consisted of 2 to 6 sessions of 450 valid trials each. Pre-test trials were identical to regular trials, but contained no attentional cues. Furthermore, the coherence level of all stimuli was set to 51.2%. To measure each subject's individual just noticeable difference (JND), we varied the direction change magnitude in 15 discrete steps from -14 to 14 degrees. We then fitted a psychometric function (cumulative Gaussian) for each subject and each reference direction. Subjects started the main experiment once they reached a comparable performance for all six reference directions, with little to no bias in their discrimination thresholds. The subject JND was defined as the slope of the cumulative normal fit (Strasburger, 2001) to the pooled performance over all reference directions. Subjects were trained to perform the pre-task until they reached a JND smaller than 16 degrees in one complete session of testing, or until they aborted the experiment. Altogether, 23 subjects entered the pre-testing phase, out of which 8 subjects continued to the main experiment. Subjects aborting the experiment mostly reported that they found the task too demanding to commit to further training or testing. For subjects reaching the criterion, their JND from the last session of pre-testing was used throughout the main experiment (mean JND=12.86, standard-deviation=1.94).

Data Analysis

To test whether the two types of attentional cues led to measurable attentional effects, we compared each subject's mean performance over all levels of coherences between both attentional conditions. We calculated performance as

$$d' = zscore(p_{CW_{correct}}) - zscore(p_{CCW_{failure}})$$

where clockwise responses to clockwise changes were arbitrarily defined as hits, and counter-clockwise responses to clockwise changes as false-alarms. Using paired t-tests we determined whether performance differed between trials with narrow and broad focus cues and confirmed that attention was deployed in line with each cue type, as indicated by a significant difference between validly and invalidly cued trials.

In order to determine whether attention affected performance by response or coherence gain we investigated separately for each attentional condition, how each subject's performance changes with motion coherence. To obtain the coherence response function, we fitted a Naka-Rushton equation (Busse et al., 2009; Finn et al., 2007; Naka and Rushton, 1966)

$$d'(c) = d'_{max} \frac{c^n}{c^n + {c_{50}}^n}$$

to each experimental condition using a non-linear least-squares procedure. Using this equation, psychophysical performance d' for each level of coherence c can be described by the asymptotic performance at high levels of coherence d'_{max}, the coherence level at half asymptotic performance c_{50} and the slope of the function n. We tested with one-tailed, paired t-tests whether changes in c_{50} and d'_{max} occurred from invalidly to validly cued trials for each attentional condition. Significant increases in d'_{max} represent response gain effects and significant decreases in c_{50} represent coherence gain effects. The slopes of the corresponding coherence response functions for each attentional condition were constrained to be equal in all four fits per subject to minimize the number of free parameters. We validated this choice by comparing this reduced model (with a single exponent per subject) to those with two exponents per subject (one for each attentional condition) and to those with four exponents per subject (one for each attentional condition and cue validity). The reduced model with a single exponent per subject produced almost identical fits and was clearly preferred (due to its lower number of parameters) by AIC and BIC measures. We evaluated further-reduced models with shared parameters (d'_{max} or c_{50}) either across or within attentional conditions, but found that no simpler model was superior to the one described above. A robust fit of the coherence response functions requires that the asymptotic performance saturates at high levels of coherence. We therefore excluded two subjects with performance increases of $\Delta d' \geq 1$ between the two highest coherence levels, leaving a total of 6 subjects for the final analysis.

To determine the coherence gain and response gain changes between attentional conditions, we computed a modulation index for each of the gain enhancements:

$$MI_{\zeta} = \frac{\zeta_{valid} - \zeta_{invalid}}{\zeta_{valid} + \zeta_{invalid}}$$

where ζ corresponds to one of the two fitted coefficients c_{50} or d'_{max}. We calculated the differences in modulation magnitude between conditions and tested with 2-sample t-tests if the effect sizes of coherence and response gain varied significantly between the two attentional conditions. All statistical tests were Bonferroni corrected for multiple comparisons. Data analysis was done using custom scripts in Matlab R2014a (MathWorks). We used the Palamedes routines (Prins and Kingdom, 2009) for fitting psychometric functions and the Matlab Curve Fitting toolbox (MathWorks) for the non-linear fitting.

Model Simulations

The NMoA computes the response of a single neuron to a given set of stimuli as:

$$R(x, \theta; c) = \frac{A_i(x,\theta)E(x,\theta;c^n)}{S(x,\theta;c)+\sigma^n} \qquad \text{(Equation 1)}$$

where $R(x, \theta; c)$ is the response of a neuron with its receptive field centered at x and its feature tuning centered at θ, receiving stimulus input with contrast c. $A_i(x, \theta)E(x, \theta; c^n)$ is a term composed of the net excitatory input drive to the neuron $E(x, \theta; c^n)$ scaled by the attentional gain $A_i(x, \theta) \geq 1$: the attentional gain varies with cue validity and attentional condition (ie. narrow or broad focus). Further, $E(x, \theta; c^n)$ also depends on the stimulus contrast raised to an exponent (c^n) while both $E(x, \theta; c^n)$ and $A_i(x, \theta)$ depend on the location of the corresponding stimuli with respect to the neuron's receptive field and tuning properties. $S(x, \theta; c)$ is the effect of the normalizing pool and represents the excitatory drive convolved by the suppressive surround:

$$S(x, \theta; c) = s(x, \theta) * [A_i(x, \theta) E(x, \theta; c^n)] \qquad \text{(Equation 2)}$$

where $s(x, \theta)$ is the suppressive filter (e.g. the amount of surround suppression) and $*$ indicates a convolution.

To simulate our empirical data with the NMoA, we used custom Matlab scripts, based on the code of Reynolds and Heeger (2009). We changed the original code to use a circular von Mises distribution for both the stimulation and the attention fields' theta dimension. Therefore we express the width of the feature-attention spotlight in terms of parameter κ, which is the concentration of the distribution around it's mean ($1/\kappa$ is roughly equivalent to σ^2 of a gaussian). We confirmed that this modified model produces similar results to the original NMoA by comparing our results with the outcome of the Matlab scripts available on the authors' website.

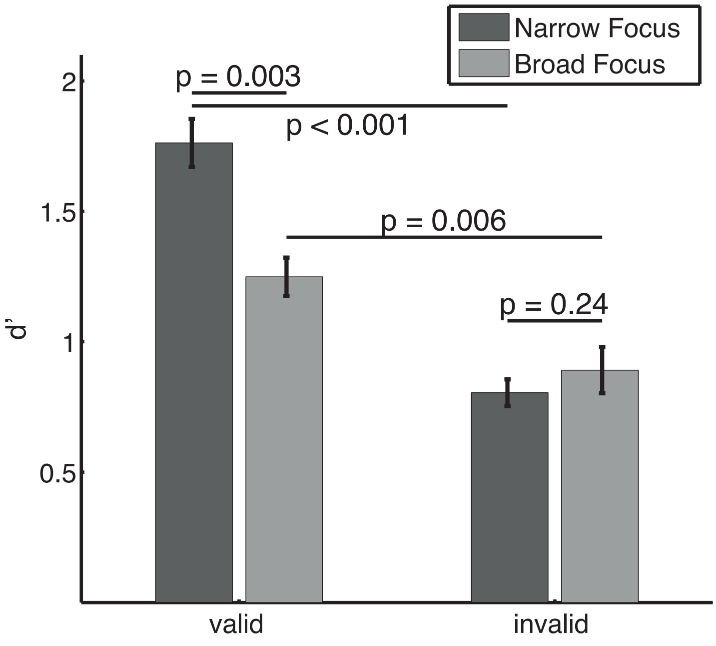
We modeled our empirical results by defining a stimulus that is infinite in space, since no spatial position inside the annulus carried more relevant signal than any other and thus spatial attention could not have impacted psychophysical performance. Consequently we assumed that for modeling purposes, spatial attention was evenly distributed across all spatial locations. The two directions of the transparent motion display were modeled as two narrow bands in the theta dimension, each with a concentration of $\kappa = 33$, corresponding to roughly 10 degrees σ. The means of the two signals were 135 degrees apart from each other, corresponding to the mean difference in motion directions of the transparent motion display.

We then simulated an attentional field with either a narrow or a broad focus of feature-based attention. The narrow focus was an enhancement with a concentration (angular extent) of $\kappa = 15$ around one of the signals. The broad focus was centered on the same direction (i.e. as if it were a horizontal movement), but enhanced a much broader range of directions around it ($\kappa = 0.5$, which corresponds roughly to 90 degrees σ). Our model MT population was defined to have Gaussian receptive fields with a spatial extend of $\sigma = 5$ degrees and a tuning width of $\sigma = 37$ degrees. The suppressive field was defined to have a spatial kernel width of $\sigma = 20$ degrees and a feature tuning width of $\sigma = 180$ degrees. The latter parameter was used since it is known that in motion-selective area MT, surround tuning is present, but is generally very broad (Hunter and Born, 2011). Overall, this biologically plausible set of parameters is very similar to the one used in previous simulations by Herrmann et al. (2012) or Reynolds & Heeger (2009).

We modeled increasing levels of coherence by increasing the value of the sensory input strength parameter c. In the NMoA, this essentially equates increases in coherence to increases in contrast. This choice (also made by Jazayeri and Movshon (2006) in a related context) can be justified by the physiological finding that MT units display constant tuning bandwidth with changes in coherence (Britten and Newsome, 1998). It also simplifies linking neuronal activity to behavioral performance, since the noise amplitude is constant in all simulations. In order to convert the modeled population activity into a prediction of behavioral performance, we assumed that task performance is dominated by the quality of decoding of the two motion directions of stimulus display 1. Consequently, we selected two units of the simulated population with their tuning centered on the corresponding directions of stimulus display 1 (out of which one was previously cued and thus in the focus of attention). We assumed that task performance on validly and invalidly cued trials is proportional to the values of the neurometric function for the attended and unattended unit respectively. A large value of the neurometric function translates to a greater signal-to-noise ratio for the neural representation and a better identification of the stimulus directions. Since the direction-difference between the sample and test directions was small, units tuned to the sample directions also responded strongly to test directions and received levels of attentional enhancement similar to units tuned to the test directions. Therefore, their neurometric functions would also be proportional to detection performance for presented test stimuli.

In order to obtain the neurometric functions for relevant units, we repeated the simulation for varying values of c (i.e. signal to noise ratios of the two bands in theta). Through appropriate rescaling with just one additional parameter, we converted the neuronal activity of the relevant unit (depending on cue validity) into psychophysical performance. Importantly, as shown by Pestilli et al. (2009), such a readout which equates attentional effects on neuronal response functions with those on behavioral psychometric functions (after a rescaling) leads to the same conclusions as those given by a more detailed implementation of an ideal likelihood-based observer (Jazayeri and Movshon, 2006). Even when using this ideal observer to predict behavioral psychometric functions from the underlying modeled neuronal representation, the attentional effect on the behavioral psychometric function mimics the attentional effect on the underlying neuronal functions.

Figure 3[vi]



Results

We determined human perceptual performance for strongly and weakly attended stimuli, using cues that were valid in 75% of all trials. In addition to these two validity conditions we employed two attentional conditions to generate narrow and wide feature-based attentional distributions to specifically test the critical role that the width of the attentional focus plays in the NMoA. For each of the four task constellations of the two cueing validities and the two widths of the attentional focus (valid-narrow, invalid-narrow, valid-broad and invalid-broad) we determined performance as a function of stimulus signal strength (coherence) and evaluated the effects of feature-based attention on the coherence response function.

Cue validity affects performance, especially when attention is focused

To validate whether our cueing paradigm was effective in causing differential attentional deployments, we computed each subject's mean performance across coherences for each of the four task constellations and performed four pair-wise comparisons (Bonferroni corrected $\alpha = 0.0125$, paired t-tests, n=6 subjects). Figure 3 shows the average of these mean performances across the subjects. For both attentional conditions, subjects performed significantly better when the cue was valid than when it was invalid (narrow focus: mean $\Delta d' = 0.958$, p<0.001, broad focus: mean $\Delta d' = 0.358$, p=0.006). Further, the performance for the validly cued direction was significantly better in the narrow focus condition compared to the broad focus condition (mean $\Delta d' = 0.513$, p=0.003). The performance in the invalidly cued direction was not significantly different between the two attentional conditions (mean $\Delta d' = -0.087$, p=0.24).

[vi] Discrimination performance of all six observers, pooled across all levels of coherence. Colors indicate cue type. For each cue type, there is a significant difference between validly and invalidly cued trials, indicating that the cue lead to deployment of feature-based attention. In addition, the two types of cues (narrow and broad focus cues) lead to a significant difference in discrimination performance for validly, but not invalidly cued trials. Error bars indicate standard errors. P values correspond to paired t-tests.

A wide feature-focus causes pure response gain, while a narrow focus causes both coherence and response gain

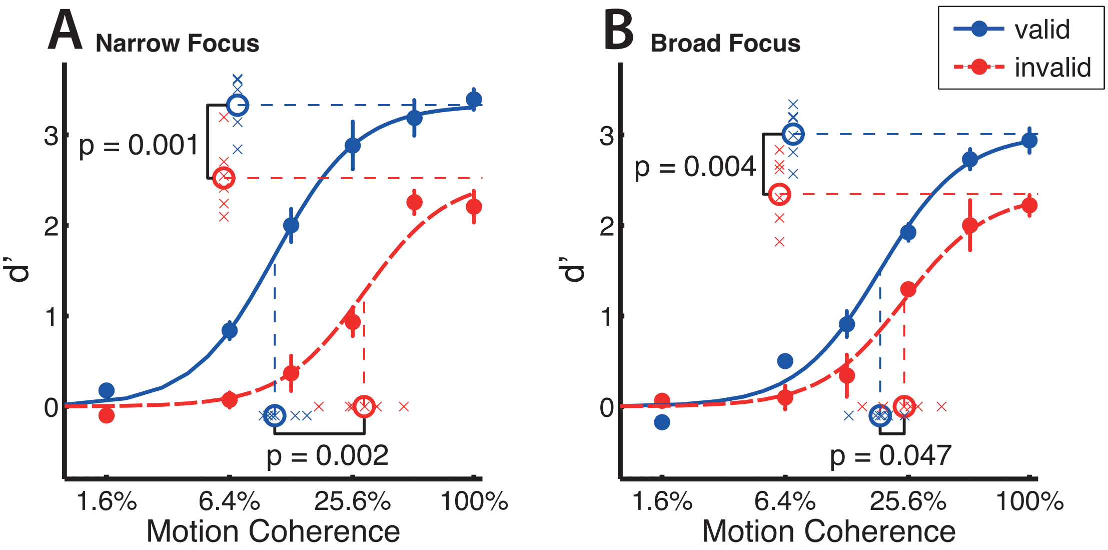
The core aim of our study was to determine whether feature-based attention enhances performance by coherence or response gain and match our findings to the predictions of the NMoA. This was done by determining each subject's coherence response function in each of our four task constellations by fitting Naka-Rushton equations (Figure 4). We then compared the fitted Naka-Rushton coefficients for validly and invalidly cued trials, to test if attention induced a reduction in c_{50} and/or an increase in d'_{max}. A decrease in c_{50} indicates an increase in coherence gain and an increase in d'_{max} indicates an increase in response gain. We performed four pair-wise comparisons (Bonferroni corrected $\alpha = 0.0125$, paired, one-tailed t-tests, n=6 subjects, we also performed this analysis with paired, two-tailed t-tests, which did not change our conclusions).

For the narrow focus condition (Figure 4A), we find a significant cue-induced increase in coherence gain (mean $\Delta c_{50} = -0.179$, p=0.002, Figure 5A) as well as in response gain (mean $\Delta d'_{max} = 0.895$, p=0.001, Figure 5B). In the broad focus condition (Figure 4B), the response gain enhancement is of similar magnitude and also significant (mean $\Delta d'_{max} = 0.628$, p=0.004, Figure 5B) while the coherence gain enhancement is much smaller and narrowly misses significance (mean $\Delta c_{50} = -0.062$, p=0.047, Figure 5A). As plotting performance as d' might amplify differences at high coherences, we also performed the same analysis based on the proportion of correct responses. This did not change the pattern of results (i.e. response gain in the broad focus condition and a combination of coherence and response gain in the narrow focus condition).

We then tested whether the magnitude of coherence (c_{50}) and response gain (d'_{max}) changes with attentional condition (i.e. with an increasing width of the feature-based attentional focus). We calculated a modulation index MI_{ζ} ($(a-b)/(a+b)$, see section Data Analysis) for each coefficient-condition pair. We find that the magnitude of coherence gain is significantly different between the attentional conditions (mean $\Delta MI_{c_{50}} = 0.293 \triangleq 82.9\%$, p=0.002, 2-sample t-test), while there is no significant change in response gain (mean $\Delta MI_{d'_{max}} = 0.033 \triangleq$

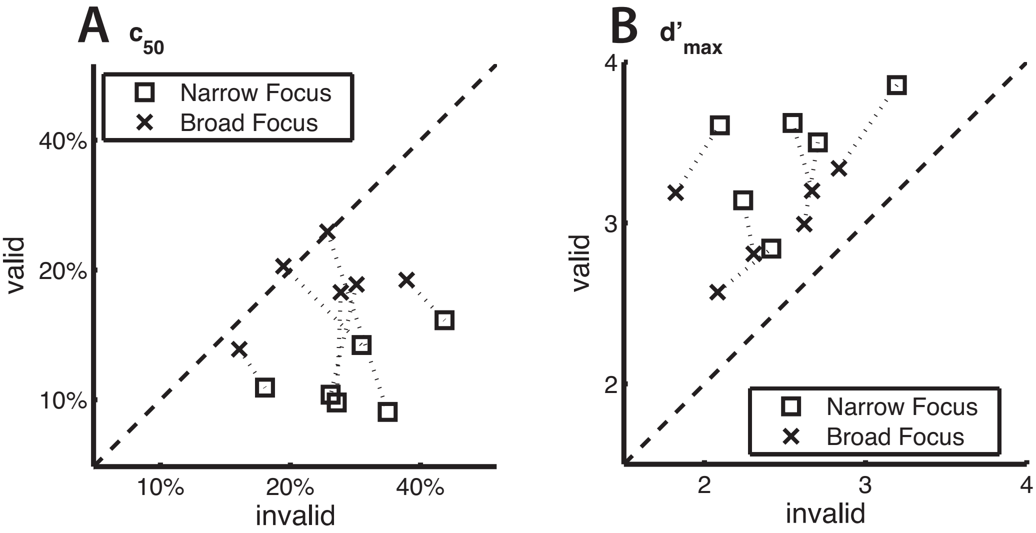
6.8%, p=0.451, 2-sample t-test, Bonferroni corrected $\alpha = 0.025$). For the above-performed statistical tests, we repeated all comparisons with two-sided Wilcoxon tests. This did not qualitatively change our results (i.e. all statistically significant results remained significant and all non-significant results remained non-significant). We further addressed a potentially confounding ceiling effect of performances at high coherences by repeating the above analysis, leaving out the two highest coherences (i.e. the highest performances we measured in our task) of the valid condition in narrow focus trials, thereby disregarding data points that might have been affected by a ceiling effect of performance. With this reduced dataset, the increase in response gain narrowly misses significance in the narrow focus condition, however, a coherence gain change was still highly significant.

Figure 4[vii]



[vii] Coherence response functions for pooled performance across 6 subjects. Data points are the mean discrimination performance across subjects for each tested attentional condition, cue validity and coherence level. Panel A corresponds to the narrow focus cue type (single headed arrow) and panel B to the broad focus cue type (three headed arrow). Significance values indicate differences in Naka-Rushton fit coefficients of per-subject fits (see Figure 5). When comparing invalidly and validly cued trials, increases in the asymptotic performance at high levels of coherence indicate response gain effects, while decreases in coherence level at half maximum indicate coherence gain effects. Error bars of data points indicate standard errors, crosses around coefficient indicators represent individual coefficients obtained from per-subject fittings of the coherence response function.

Figure 5[viii]



The current NMoA cannot plausibly account for these results

Our experimental results reveal a mixture of coherence and response gain enhancements when attention is focused on a narrow range of directions (narrow focus condition), and a pure response-gain enhancement when attention is focused on a broad range of directions (broad focus condition). As pointed out by Herrmann et al. (2010; 2012), the NMoA predicts that the behavioral output will mimic the underlying change in neuronal response functions, and therefore only a pure response gain for attention to motion direction will be visible in the psychometric function, as long as certain assumptions (Pestilli et al., 2009) about the relationship between changes in the sensory neuronal representation of the motion stimulus and the behavioral output hold. Further, even if any coherence gain effects were to arise, they would be found in the broad focus condition, which is the opposite of what our

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[viii] Per subject fit coefficients c_{50} and d'_{max}, corresponding to contrast level at half maximum performance and asymptotic performance, respectively. For each subject, two Naka-Rushton equations per cue type were fit to the psychophysical data, revealing four informative coefficients. A decrease in c_{50} between validly and invalidly cued trials indicates a contrast gain effect and an increase in d'_{max} a response gain effect.

empirical results show. The intuition behind these statements has been presented in detail by Herrmann et al. (2012) as well as Reynolds and Heeger (2009), but we summarize it briefly here. For the transparent motion stimuli with two component motion directions that we used, the response of a neuron with preferred direction centered at one of the component directions (from Equation 1) can be re-written as:

$$R(c) = \frac{\alpha c^n}{S + \sigma^n} \qquad \text{(Equation 3)}$$

where S represents the net normalizing effect of the neurons in the population and is regulated by the width of $s(x, \theta)$ (see equation 2). When $s(x, \theta)$ is narrow (strongly tuned normalization), attention (γ) acts equally on the driving input and the normalizing factor S and this leads to a coherence-gain effect (Reynolds and Heeger 2009):

$$R(c) = \frac{\gamma \alpha c^n}{\gamma S + \sigma^n} = \frac{\alpha c^n}{S + \frac{\sigma^n}{\gamma}} \qquad \text{(Equation 4)}$$

More explicitly, this happens because the normalizing pool is dominated by the inputs that excite the neuron and attention to the non-preferred feature is essentially invisible to the neuron since it lies outside both the excitatory and suppressive filters. In contrast, when $s(x, \theta)$ is broad, the impact of attention on the denominator $S + \sigma^n$ is minimal (even if the attentional spread is broad) since the normalizing pool includes almost equal contributions from the neurons centered at the preferred and non-preferred directions. Under these conditions,

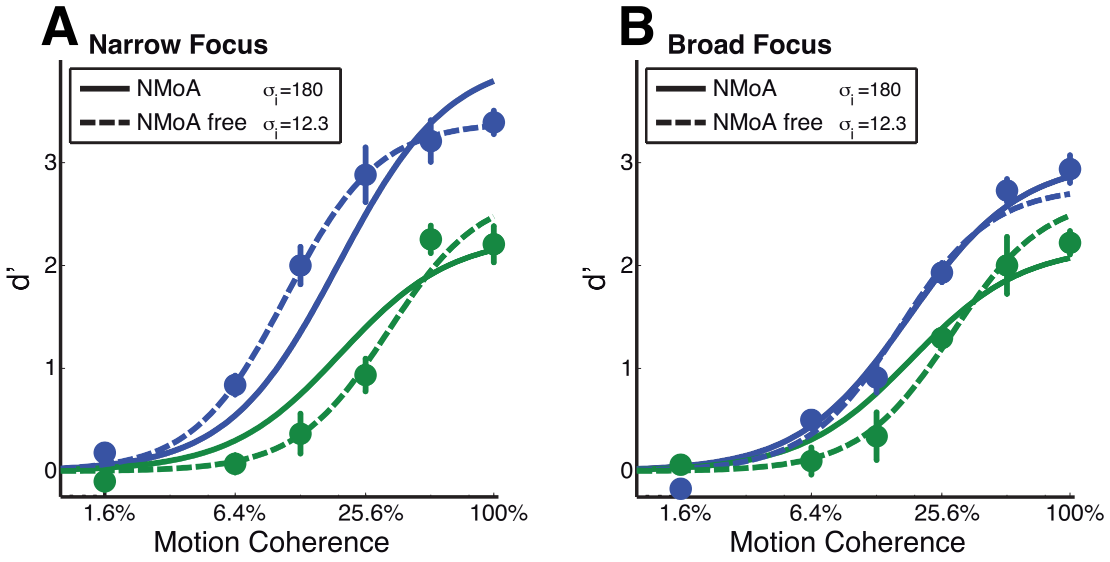
$$R(c) = \frac{\gamma \alpha c^n}{S + \sigma^n} \qquad \text{(Equation 5)}$$

which represents a response gain for the validly cued condition compared to the invalidly cued one. As a result, for the NMoA to predict a coherence-gain effect of attention, the normalizing pool (or suppressive surround) would have to be so narrow (see below) as to be physiologically implausible. Further, since the coherence-gain effect is facilitated when attention has a greater impact on the normalizing pool (by acting more broadly), it is the broad focus condition that should show a stronger coherence-gain effect of attention.

We confirm these statements by explicitly fitting the NMoA to our data. Free parameters, shared among attentional conditions, were the gain of A_i, separately for each attentional condition, the normalization constant σ, the exponent n and a scaling parameter to convert simulated values to d' (for the values of the fixed parameters, see Methods). The best fitting NMoA model showed a clear lack of fit to the empirical data (Figure 6), especially in the narrow focus condition, which is expected because that is where the coherence-gain effects manifest. The NMoA model's best fit resembles a response gain in both attentional conditions, as expected. The observed lack of fit is not a result of our chosen fixed parameters: varying all but one of those parameters over a large range did not change our conclusions. The only critical parameter, as mentioned above, was the width of the suppressive filter in the feature dimension. We therefore redid the fits, but with the featural width of the suppressive filter as an additional free parameter (NMoA free model). This resulted in an optimal, yet biologically implausible, inhibitory tuning width of $\sigma=12.3$ degrees and a model producing clear effects of coherence gain in both attentional conditions (Figure 6). This model accounts for the reduction of coherence gain in the broad-focus condition by proposing that the broader width of the attentional field is accompanied by a reduced attentional gain. While this is not an unreasonable assumption, it compromises the ability of the model to account for the observed response-gain changes in the broad-focus condition (Figure 6B).

[ix] Model predictions of coherence response functions for individual fittings to the empirical performance of 6 subjects. Data points with standard errors are the mean discrimination performance across subjects for each tested attentional condition, cue validity and coherence level. Panel A corresponds to the narrow focus cue type (single headed arrow) and panel B to the broad focus cue type (three headed arrow). The two evaluated models are the original NMoA with 5 free parameters and a NMoA with optimal, yet biologically implausible suppressive tuning width (NMoA free, 6 free parameters).

Figure 6[ix]



Adding tuned normalization accounts for the empirical data

Since the NMoA fails to capture the observed effects of feature-based attention, we attempted to extend the NMoA in the simplest, yet most plausible manner in order to do so. The empirical data indicate that the coherence-gain effect of feature-based attention emerges for the validly-cued feature and is greater in the narrow focus condition. One way to incorporate a coherence-gain effect is to postulate that in addition to enhancing the input drive to the attended feature, feature-based attention reduces the coherence-independent normalization term σ^n (NMoA+ciN model) and that this reduction is greater when attention is more focused (as in the narrow focus condition). This reduction is independent of stimulus strength (coherence) and direction, but tuned to the attended direction such that attention to a particular motion direction reduces the normalizing effect on neurons tuned to that direction and potentially enhances the normalizing effect on neurons tuned to far-away directions. In other words, Equation 1 (see Methods) can be rewritten in an extended form as:

$$R(x,\theta;c) = \frac{A_i(x,\theta)E(x,\theta;c^n)}{S(x,\theta;c)+\frac{\sigma^n}{N(\theta)}}$$ (Equation 6, NMoA+ciN model)

where 1≤$N(\theta)$ represents the direction-tuned effect of attention that is maximal for motion directions close to the attended feature.

Another way to incorporate a coherence-gain effect is to unify the NMoA with models utilizing previously proposed ideas of neuronal self-normalization (Ni et al., 2012; e.g. Rust et al., 2006). Here, each neuron is normalized not only by its suppressive surround, but also by its own net-excitatory input. Such a coherence-dependent extension of the NMoA (NMoA+cdN model) can be written as:

$$R(x,\theta;c)=\frac{A_i(x,\theta)E(x,\theta;c^n)}{N*A_i(x,\theta)E(x,\theta;c^n)+(1-N)*S(x,\theta;c)+\sigma^n}\qquad\text{(Equation 7, NMoA+cdN model)}$$

where 0≤N≤1 is a single free parameter determining the balance between pure self-normalization ($N=1$), predicting only coherence-gain, and the original NMoA ($N=0$), predicting mainly response gain.

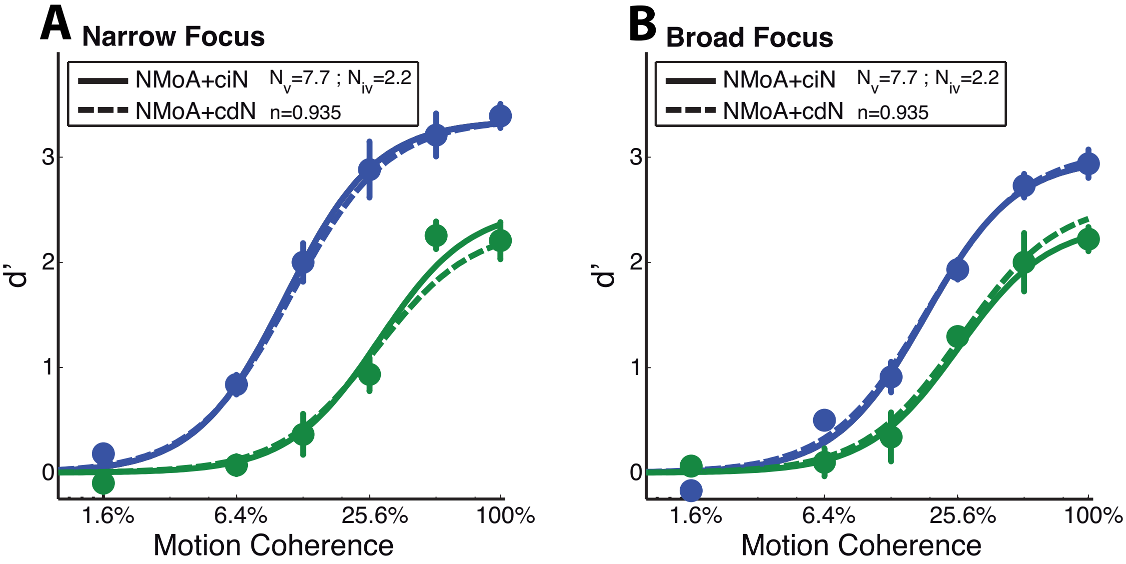
We examine the potential physiological bases of both extended versions of the NMoA in the Discussion section. In terms of capturing the coherence-gain effects of attention, both models effectively capture both the response-gain and coherence-gain effects evident in our empirical data (Table 1 and Figure 7).

We fit both extended NMoAs (with one and two additional free parameters for the NMoA+cdN and NMoA+ciN model, respectively) and compared them to the previously computed best fits from the original NMoAs (fixed and free suppressive width, Figure 6). Table 1 summarizes the results. Both extensions fit the data significantly better than the original NMoA (F=59.29, p<0.001, between NMoA and NMoA+cdN; F=33.20, p<0.001, between NMoA and NMoA+ciN). Compared to the NMoA free model, only the NMoA+ciN model shows a significant advantage (F=0.98, p=0.56, between NMoA free and NMoA+cdN; F=8.60, p=0.004, between NMoA free and NMoA+ciN). However, both AIC and BIC measures indicate both extended NMoAs as superior to the original NMoAs. Between extended models, we find that the NMoA+ciN model performs marginally better than the NMoA+cdN model (F=5.23, p=0.024) with both lower AIC and BIC metrics for the NMoA+ciN model, confirming that the use of one extra parameter was justified and the model with a coherence-independent influence of attention on normalization described the data better than the model incorporating neuronal self-normalization.

Table 1. Model comparison

	NMoA	NMoA free	NMoA+cdN	NMoA+ciN
Free param.	5	6	6	7
Adj. R^2	0.8626	0.9017	0.9040	0.9070
AIC	-229.32	-275.59	-278.98	-282.42
BIC	-214.57	-257.89	-261.28	-261.78

Figure 7[x]



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[x] Model predictions of coherence response functions for two extended Normalization Models. The NMoA+ciN model (7 free parameters) includes a coherence independent contribution of feature-based attention to normalization while the NMoA+cdN model (6 free parameters) includes a weighted contribution of tuned-normalization. Panel and data points like in Figure 6.

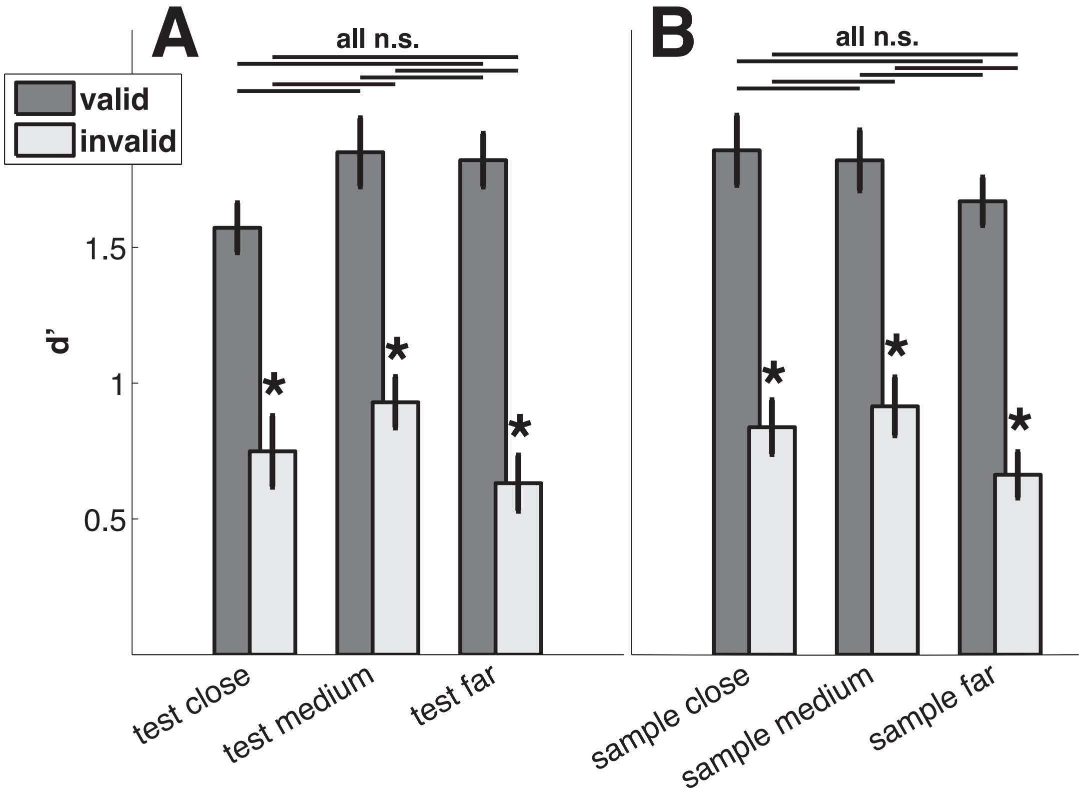
Subjects used the sample, not the cue direction

The narrow focus cue did not signal the precise direction of the sample stimuli, but rather indicated that the relevant sample was likely to occur within a range of ±10 degree around the cued direction (heading of the arrow). Nonetheless, we tested whether subjects used the cued direction as sample and simply ignored the subsequently presented sample direction. If this were true, direction discrimination performance should increase once the test direction was far off from the cued direction. Figure 8A shows the performance across coherences for three groups of trials that differ in how far off the cued direction the test direction occurred. Groups were defined individually for each subject based on their JND's and divide the possible range of absolute cue-test differences in three evenly spaced parts (close, medium and far). Since upcoming invalidly cued directions could also be inferred from the cue (since the uncued direction range centered ±135 degrees from the cued direction), we were able to define the same three groups for invalidly cued trials.

For each group we find significant effects of cue validity (paired t-tests, $p<0.001$, $p=0.002$, $p<0.001$ for close, medium and far, respectively) but pairwise comparisons indicated that none of the three groups of validly cued trials was significantly different from the others. The same was true for the invalidly cued trials (all $p>0.027$, Bonferroni corrected $\alpha = 0.0083,\ n = 6$ comparisons). We thus find no evidence pointing towards subjects using the cued direction as a reference for the direction discrimination task in the narrow focus condition.

We also tested whether sample presentations occurring far off the cued direction resulted in improved task performance. For this purpose trial groups were defined as sample directions close (0-2 degrees), medium (3-6 degrees), and far (7-10 degrees) from the cued direction (or the inferred uncued direction). Figure 8B shows the performance across coherences for those three trial groups. Similar to the trial grouping by sample-test difference, we find significant effects of cue validity (paired t-tests, $p=0.001$, $p<0.001$, $p=0.001$, for close, medium and far, respectively). Again, no pairwise comparison between groups was significant for either valid or invalid trials (all $p>0.02$, Bonferroni corrected $\alpha = 0.0083,\ n = 6$ comparisons). This suggests that in the narrow focus condition, the featural extent of attention covered at least a range of 20 degrees, centered on the attentional cue, which we also assumed in all model simulations.

Figure 8[xi]



[xi] (A) Task performance across coherences for groups of trials that differ in how far off the cued direction the test direction occurred. The possible range of test-cue differences was divided in three evenly spaced groups (close, medium, far). Lines above bars represent pairwise comparisons and stars indicate significant differences of adjacent bars. (B) Like A, but groups were defined based on the differences between cue and sample.

Discussion

The Normalization Model of Attention (Reynolds and Heeger, 2009) has become the central model for capturing the known variety of attentional effects on neuronal responses, fMRI signals and behavioral performance. While the NMoA is powerful enough to explain a wide range of response patterns under reasonable assumptions, it also predicts that there are response patterns that will not be found. Since the assumptions underlying the NMoA's parameters are not easily verified, such predictions of "impossible results" are critical because they allow the model to be stringently tested against empirical data. Here, we report that human subjects show behavioral performance patterns that go against a prediction of the NMoA and suggest and compare two simple and testable extensions to the NMoA that can account for the findings.

As pointed out by Herrmann et al. (2012), the NMoA predicts that under plausible parameter settings, attention to a visual feature like orientation or motion direction will not produce input-gain effects, but only response-gain effects in neuronal response functions. Under reasonable assumptions regarding how the behavioral response emerges from the neuronal representation (Pestilli et al., 2009), these effects imply that similarly, only response-gain effects will be found when comparing psychometric functions measuring performance on tasks involving attended and unattended features. Herrmann et al. (2012) went on to confirm this prediction by showing only response gain effects in psychometric functions when subjects paid attention to either narrow or broad ranges of orientation. Here, we tested this prediction by measuring the performance of human subjects on a task requiring them to discriminate a direction change in one of the two directions of a transparent motion display. Performance increased with motion coherence and was greater for validly cued stimuli. Importantly and contrary to the predictions of the NMoA, attentional effects manifest as a combination of input gain and response gain on the psychometric function. In addition, when we compared the results when subjects were cued to direct attention towards either a narrow or broad range of motion directions, we found a significant decrease of input gain for the broad focus.

Our results using a motion direction discrimination task differ from those of Herrmann et al.'s (2012) task using orientation discrimination, despite the fact that the two tasks are conceptually very similar. One difference is that we varied coherence rather than contrast to manipulate signal strength in order to obtain a sufficiently large dynamic range. It is not obvious why this should cause the different results. However, we show that adding either a coherence-independent contribution of attention to normalization or a coherence-dependent mechanism of self-normalization to the NMoA is sufficient to fully account for our data. This points to differences between the strengths of the attentional contribution to normalization between our results and Herrmann et al. (2012). Further research is needed to determine how different stimulus properties and task demands might lead to different amounts of stimulus-dependent and stimulus-independent, feature-based attentional contributions to neuronal normalization.

We suggest two possible extensions of the NMoA both including direction-tuned influences on the normalization pool. The first model (NMoA+ciN) implements a coherence-independent, attentional contribution to normalization. Here, attention not only modulates the input drive to a neuronal population, but also reduces the impact of the normalization on the responses of neurons tuned for the attended direction. Further, the data indicate that such a tuned normalizing effect of attention would have to be greater when attention is more narrowly focused than when it is broadly distributed. To implement such a specific rescaling of the coherence-independent normalizing input in the brain, we suggest that since the NMoA can be considered a steady-state version of an unspecified network model with mutual competition, a stimulus at the preferred direction of the neuron could suppress the local population that is tuned to non-preferred directions and thereby reduce their contribution to the normalizing pool.

Alternatively, we propose in the second model (NMoA+cdN) that each neuron preferentially weights its own contribution to the normalization pool (self-normalization) in comparison to the contribution of all suppressive neurons. Such a mechanism was previously shown to be a vital component in a model capturing the response properties of direction-selective neurons in extrastriate cortex (Rust et al., 2006). The tuned normalization in another recent report (Ni et al., 2012) is also conceptually similar: here, the authors showed that MT neuronal responses to a pair of stimuli within the receptive field (one moving in the preferred direction and the other in the anti-preferred direction) were well explained by direction-tuned divisive normalization. The majority of neurons in their data showed a greater normalizing influence of the preferred stimulus. We show here, that extending the NMoA with an explicit tuned-normalization component also captures our results in an attention task, despite the fact that this coherence-dependent mechanism is independent of the spread of attention. However, the difference between both extensions is significant and the NMoA+cdN model described the data worse than the NMoA+ciN model.

The proposed NMoA+ciN model modifies the normalization mechanism to include a reduction by feature-based attention of the normalizing influence for neurons tuned to the attended direction. There are a variety of ways in which this modification could be implemented. For example, if feature-based attention suppresses the responses of neurons tuned to non-preferred directions, their contribution to the normalization pool could be reduced thereby reducing the coherence gain for neurons tuned to the attended direction (but increasing it for neurons tuned to the unattended direction, where the normalization pool will be enhanced). Alternatively, feature-based attention may enhance both the "stimulus drive" as well as the "normalization" for neurons tuned to the attended direction, and this effect may manifest as a reduction in sigma. Importantly, here the direction selectivity of the normalization pool is not critical, but instead, attention has a selective effect on neurons tuned to the attended direction (Martinez-Trujillo and Treue, 2002). Thus, the mechanism works even if the normalization pool is untuned, but critically, it may also work when the normalization pool is tuned.

In a related framework, Boynton (2009) proposed a normalization model with a stimulus independent contribution of attention to the normalization pool. This untuned normalization can account for attentional effects of input gain when attention is directed inside versus outside of a neuron's receptive field. For non-spatial forms of attention, as described here, a feature-tuned input to normalization is necessary since attention does not shift out of the receptive field. It should be pointed out, however, that the proposed extension with a coherence-independent, tuned input to normalization (NMoA+ciN) can similarly be applied to this or other previously proposed models of attentional normalization (Boynton, 2009; Ghose, 2009; Ghose and Maunsell, 2008; Lee and Maunsell, 2009).

In addition to the extended normalization models considered above, one can imagine an important alternative to account for our empirical results. The hypothesized modifications all assume, that the behavioral effects of attention and its spread emerge from its effects on the neuronal representations of the stimulus (i.e. the perceptual representation). However, attention may also act by modifying the decisional mechanism, for example, through enhanced weighting of the cued stimuli (Borji and Itti, 2014; Dosher and Lu, 2000; Eckstein et al., 2009; 2013; Palmer, 1994; Palmer et al., 1993; Pestilli et al., 2011; Zénon and Krauzlis, 2012). Specifically, the change in performance between validly and invalidly cued features could result from the differential weighting of inputs from the two motion directions, with greater weight given to the validly cued feature. With a lower weight to the unattended motion direction, the performance may only rise above chance once the coherence becomes sufficiently large. Similarly, the change in performance for validly cued motion directions between trials with focused or dispersed feature-based attention may be due to improved weighting of the same perceptual representation, rather than an effect of attention on the perceptual representation itself (as we assume here). Differentiating between these two alternatives may require physiological recordings that examine the effects of feature-based attention under our conditions in the dorsal motion-processing pathway in order to measure the underlying neuronal coherence-response functions.

Spatial attention has been shown to affect correlations within neuronal populations encoding visual features (Cohen and Maunsell, 2009; Ruff and Cohen, 2014) and to reduce single-neuron variability (Mitchell et al., 2007; Niebergall et al., 2011a). Such effects can cause improvements in psychophysical performance even without increases in neuronal responses. The NMoA does not consider such attentional effects and thus aims to account for changes in psychophysical performance by changes in mean spiking activity. Consequently, we have assumed that the attentional modulation of psychophysical performance is independent of changes in correlations between neuronal firing of individual neurons. Additional experiments are needed to clarify to which degree feature-based attention causes changes in both neuronal correlations and neuronal variability and how those potential effects translate into changes in psychophysical performance.

Attention to an anti-preferred motion direction suppresses the responses of MT neurons across the visual field in a multiplicative manner (Treue and Martinez-Trujillo, 1999). This finding inspired the feature-similarity gain model of attention which postulates that attending to a particular motion direction (or more generally, visual feature) enhances the responses of neurons tuned to the attended motion direction and suppresses the responses of neurons tuned to the opposite motion direction (Martinez-Trujillo and Treue, 2004). The NMoA can account for these findings by postulating that feature-based attention to the non-preferred direction increases its contrast or coherence-dependent contribution to the normalizing pool. Both of the proposed extensions to the NMoA do not compromise these previous predictions made by the NMoA, since they both contain the original model as a special case. However, the NMoA+ciN model has an additional mechanism whereby feature-based attention to the preferred direction has a coherence-independent “pure attentional” effect on the normalizing pool. This attentional influence can release a neuron from the suppressive effect of normalization when its preferred direction is attended. Measuring the extent to which these two effects contribute to the enhancing and suppressive effects of feature-based attention will require experiments specifically designed to tease apart these two effects.

In summary, our results support the notion that the NMoA needs extensions that will allow this and similar models of attention to cover an even wider set of conditions.

As the extensions generate testable predictions, they are well suited to guide further research into the mechanisms and phenomenology of feature-based attention.

2.3 Attention to features modulates MT units in a delayed match-to-sample task: feature-based enhancement precedes object-based attention

As outlined previously (Chapters 2.1 and 1.4.2), visual feature-based enhancement is the selective propagation of a specific image feature (like the color red) for neuronal processing due to a behavioral demand of the organism. This enhances both speed and accuracy of decisions made based on that feature. In the following study, the effects of feature-based attention were quantified for macaque MT single units, while the animal was performing a match-to-sample task.

However, attentional effects on feature-processing modules, like motion-selective area MT are similarly predicted by the deployment of feature-based and object-based attention. Consistent with previous reports showing attentional enhancements of motion-selective area MT while monkeys attended to colors, we found that a task-irrelevant motion feature of a stimulus was also enhanced, when the stimulus matched the attended color. This argues for a deployment of object-based attention, spreading to all features of the attended object and it predicts a limit for the attentional selection mechanism when conjunctions of features have to be attended (see also Chapter 1.4.3).

We specifically addressed this prediction by recording MT units while monkeys selected target stimuli based on a unique conjunction of their color and motion features and found that attention enhanced neuronal responses for all target stimuli matching either of the attended features. This is consistent with the deployment of object-based attention. However, we also show that attention directed to motion enhanced MT faster than when it was directed to color or a conjunction of color and motion. This argues that feature-based attention precedes object-based attentional enhancement.

Author contributions:

PS and ST conceived the experiment, PS collected the data, analyzed the data and prepared all figures, PS and ST wrote the manuscript.

Attention to features modulates MT units in a delayed match-to-sample task: feature-based enhancement precedes object-based attention

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Abstract

A rapid and accurate identification of behaviorally relevant stimuli is often mediated by the deployment of attention. If target stimuli requiring a behavioral response can be identified based on their stimulus features (e.g. their specific color or motion direction), feature-based attention enhancing searched-for features constitutes an efficient mechanism to quickly separate targets from distractors.

We measured feature-based enhancements of single units in motion-selective area MT of rhesus monkeys while animals performed a delayed match-to-sample task. Target stimuli matching the attended motion feature were enhanced by attention, but we also found significant modulation of firing rates when the task required animals to attend only to the color of the stimuli. This result is consistent with a theory of a unified, object-based attention system and is in line with previous studies of color-based attention in MT. Further, the time-courses of the observed modulation suggest a sequential activation of feature-processing modules, with feature-based attention to motion preceding object-based attention in area MT.

However, when monkeys identified target stimuli based on a unique conjunction of color and motion, the observed modulation was not the sum of color- and motion-based matching tasks. Instead, we found the largest effects for stimuli matching either of the searched-for features, consistent with a role of area MT to highlight all potential targets, rather than only the actual targets.

Introduction

During visual search, target stimuli have to be selected based on their features, like their color or motion direction. If searched-for features are unique and highly discriminable among distractor stimuli, targets tend to ‘pop-out’ for selection (Treisman and Gelade, 1980; Wolfe et al., 1989). A particularly effective neuronal tool to facilitate such a rapid and accurate detection of targets is feature-based attention (Maunsell and Treue, 2006). In essence, target features can be enhanced to maximize the saliency (Treue, 2003) of targets either among simultaneously presented distractors or when single stimuli need to be discriminated between target and distractor categories. The former case was investigated by Zhou and Desimone (2011) in a task requiring monkeys to saccade to a target stimulus contained in a stimulus array. The authors showed that single-units in area V4 were significantly modulated by target features, indicating that feature-based attention was deployed to enhance potentially matching stimuli among distractors.

Feature-based attention is known to affect extrastriate visual cortex, with particularly rich evidence for areas V4 and MT (Bichot et al., 2005; Chelazzi et al., 2001; Hayden and Gallant, 2005; Martinez-Trujillo and Treue, 2004; Maunsell and Treue, 2006; McAdams and Maunsell, 2000; Motter, 1994; Treue and Martinez-Trujillo, 1999). At least for the case of MT, the attended feature-dimension does not necessarily have to match the primarily encoded feature-dimension (in MT: motion). Instead, when monkeys attend to the color of a stimulus, MT single units show enhancements reminiscent of attention directed to motion (Chen et al., 2012; Katzner et al., 2009). It was hypothesized that in those cases, attention spreads to behaviorally irrelevant features of the stimulus, since single neurons in MT were modulated according to the similarity between their motion direction preferences and the task-irrelevant motion feature, consistent with predictions made by the feature-similarity gain model (Katzner et al., 2009; Treue and Martinez-Trujillo, 1999).

This matches theories of a more unified attentional system, with single features of a stimulus bound together by the stimulus object. Such an object-based enhancement then enhances all stimulus features, regardless of their behavioral relevance (Blaser et al., 2000; Duncan, 1984; Treisman and Kanwisher, 1998). It was recently shown using MEG recordings in humans, that the deployment of object-based enhancement relies on the sequential activation of feature-processing cortical modules (Schoenfeld et al., 2014). In essence, this requires cortical areas tuned to a specific feature to be first modulated by attention directed to the primarily encoded feature, and only later by attention to other, non-preferentially encoded features.

We report electrophysiological evidence from macaque area MT supporting this hypothesis. When monkeys performed a delayed match-to-sample task, we found MT single units to be modulated by attention both when targets were defined by their motion direction and when they were defined by their color. In the former case, however, the modulation onset occurred synchronized to test stimulus onset while modulations based on a matching color became significant with a marked delay relative to the modulation onset evoked by a matching direction. Since MT predominantly encodes the motion direction of the stimulus, this is consistent with a feature-based attentional deployment followed by object-based attention.

However, such a spread of modulation to all features of the stimulus can be detrimental to task performance when multiple features have to be attended simultaneously. In this case, an independent assessment of two features within one object is necessary for target identification. To our knowledge, no studies exist investigating how attention enhances single neurons when multiple feature dimensions have to be attended simultaneously. Here we show that when monkeys identified target stimuli based on a unique conjunction of color and motion, attention modulates area MT as soon as the stimulus contains at least one of the searched-for features. This is again consistent with an object-based attentional deployment, but also indicates a potential limitation of the attentional system, as in those cases attention does not enhance only behaviorally relevant targets among distractors, but rather also affects distractors with only one of the searched for features. Here, attention cannot directly subserve the creation of a saliency map for targets (Treue, 2003), but rather helps to identify all potentially matching stimuli for a subsequent decision process.

Materials and Methods

Subjects

We recorded single unit activity from two adult male macaque monkeys (*macaca mulatta*, both 13 years old, weights 13kg and 8kg) out of which one monkey did not reach a sufficient task performance to be included in the data analysis. As such, the results and their interpretation should be considered preliminary until data collection can be finalized. Prior to entering the experiment, we implanted custom-made titanium headposts and custom made recording chambers (TECAPEEK, USA) centered over the left superior temporal sulcus. Surgeries were performed under aseptical conditions and Propofol (12.5-25mg/h) and Isoflurane (0.8-1.5%) anesthesia. We confirmed the location of the recording chamber with structural MR images and estimated access to area MT based on its anatomical location relative to the chamber positions.

All experiments and procedures were in accordance with institutional guidelines and approved by the regional governmental office.

Apparatus

Monkeys were seated in a primate chair at a viewing distance of 102cm from a back projection screen (dnp Black Bead, Denmark, 171.5x107.2cm image size). Two projectors (Projection Design F22, Norway) were used to display stereoscopic stimuli with a 60Hz refresh rate and a resolution of 1920x1200 pixels. We used two sets of linear polarizing filters (SX42-HD) to deliver separate images to the monkeys' eyes. Projectors were separately calibrated with a spectrally-based luminance photometer/colorimeter (SpectraScan PR-650, Photo Research, USA) which was also used to estimate the binocular crosstalk of the system to be around 3%. Stimuli were presented perimetrically on a virtual spherical bowl with the desired binocular disparity.

Eye position was recorded binocularly with an Eyelink 1000 system (SR-Research, Canada) at a sample rate of 500 Hz. The eye position system was calibrated with a custom 3D calibration routine prior to each experimental session. Monkeys responded by depressing a mechanical lever and received liquid reward for each correct answer. The experiment was controlled by an Apple computer (Mac Pro 2010) running the open-source software MWorks 0.5 (mworks-project.org).

Stimuli and Procedure

A red fixation point central to a random dot stereogram (3x3 degrees, displayed at 0° disparity) instructed the monkeys to maintain fixation within a sphere with a radius of 1.2 degrees around the fixation point and to depress and release the lever to start an experimental trial. We then presented colored random dot patterns (RDP) with a dot luminance of 19 cd/deg^2, a radius of 3 degrees and a dot-density of 0.5 dots/deg^2 on a grey background (13 cd/deg^2). The first presentation of the RDP (*sample*) always occurred at 0° disparity, centered 4.7° left of the fixation point and lasted 1 second. The sample dots were either light grey, or had one of four isoluminant colors (orange, cyan, green, magenta)[xii] and they either moved coherently in one of the cardinal directions, or moved incoherently on individual linear paths.

The sample composition instructed the monkeys which out of four possible task rules they had to follow and which stimulus feature to attend (Figure 1): either only the direction, only the color, or the presented conjunction of direction and color was relevant for subsequent target identification. The fourth task rule (grey, randomly moving RDP) occurred together with a fixation point color change and instructed the monkeys to attend to the fixation point and report the reversal of the fixation point change, which occurred on 50% of all trials simultaneously with the test RDP onset.

After a variable memory period (800-1600ms) following the sample offset, a second RDP (*test*) was displayed for 250ms at a location optimal for the current recording site and at a disparity most preferred by the single units currently under study (see next section). Throughout a daily session, the test location stayed constant. Test RDPs were always colored and always moved coherently in a cardinal direction,

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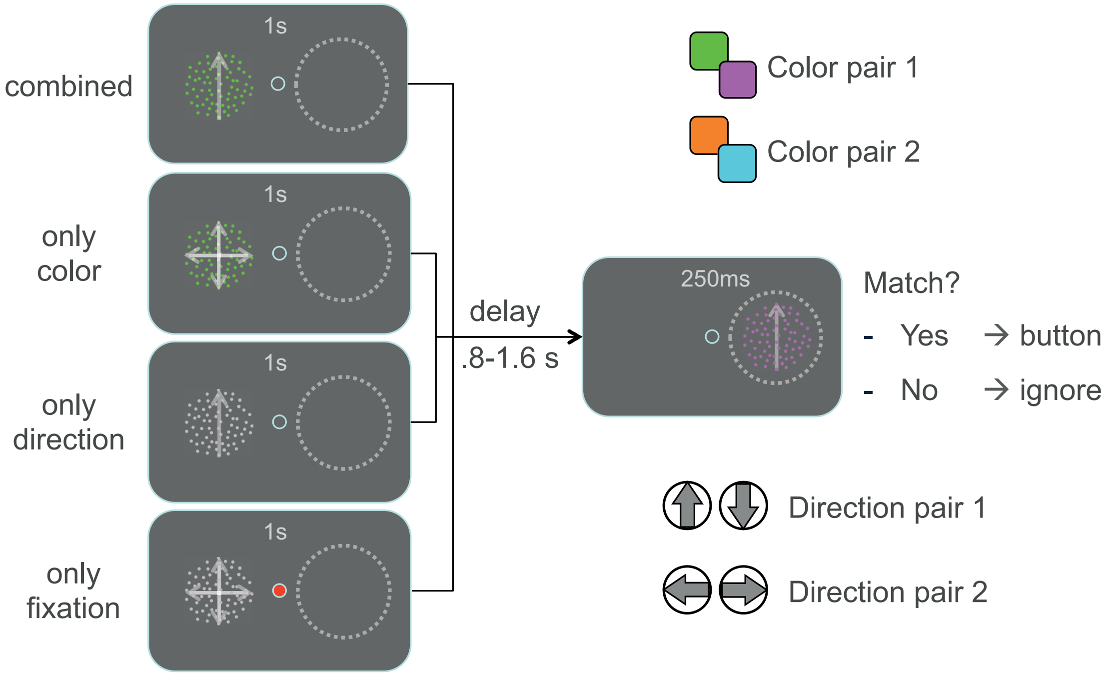
[xii] CIE-L*ab color values for used colors (measured with SpectraScan PR-650):

orange:	L=50.73	A=16.87	B=57.89
cyan:	L=50.83	A=-35.27	B=-0.11
green:	L=50.89	A=-55.09	B=51.22
magenta:	L=50.69	A=39.47	B=-21.95
grey:	L=50.69	A=-1.56	B=2.61
background:	L=42.76	A=-1.37	B=2.35

except in fixation trials, in which we also used the four diagonal directions to estimate neuronal tuning based on a total of eight directions. In trials in which the sample contained a direction, the test moved either in this, or the opposite motion direction. Similarly, when a color was cued, the test was either colored with the same color, or with the 'opposite' color (Figure 1). Each test stimulus presentation was equally likely to be a target or distractor (with distractors having the opposite of the cued feature in the color and direction tasks and only one or none of the cued features in the combined task). For all matching tasks (color, direction and combined task) the set of possible test stimuli was identical (always moving and always colored).

Figure 1[xiii]



[xiii] Task flow: Monkeys were required to keep fixation on the central fixation dot throughout the whole duration of a trial. After initiating a trial by button press, a sample was presented, cueing the monkeys both in the type of trial and the relevant feature(s). Following a variable memory period (800-1600ms) a test stimulus was presented in the RF of the unit(s) currently under study. Monkeys ignored distractors and responded to matches by pressing a button. Matches were stimuli matching both the cued direction and color (combined task), only the color (color task) or only the direction (direction task). In fixation trials, the fixation point changed color with sample onset and either changed color again with test onset, or stayed colored. In those cases, monkeys reported the color change.

Following test stimulus onset, monkeys were allowed to respond to targets within a time window from 80ms to 600ms relative to test stimulus onset. If no response was given within this time, the test stimulus was counted as rejected. Both hits (correct identification of targets) and correct rejections of distractors were rewarded with equal volumes of liquid. Wrong answers (either false alarms or target misses) led to a penalty epoch of 1s and the restart of the reward scheme (maximum reward factored by 0.3 (1st), 0.5 (2nd), 0.75 (3rd) and 1.0 (≥4 correct in a row)). Auditory feedback indicating correct and wrong judgments was given to the monkeys after each trial. Trials in which monkeys' gaze deviated from the fixation sphere at any point in time were immediately aborted with auditory feedback and repeated later during the session. The same was true for trials resulting in wrong answers; they were repeated at a later point during the session.

During each experimental session, we typically recorded 480 correctly-terminated trials. All task types were presented pseudo-randomly interleaved with a slight over-representation of conjunction trials, since those required more repetitions for data analysis.

Single unit recordings

On each recording day, we advanced up to three single electrodes or one electrode and two tetrodes (Thomas Recording, Germany, all impedances between 1-2MΩ) into the bank of the superior temporal sulcus, targeting area MT. We used a Mini Matrix system (Thomas Recording, Germany) to position the electrodes, with stainless steel guide tubes just penetrating the dura. Signals were amplified and recorded using an Omniplex acquisition system (Plexon, USA, sampling at 40kHz, 16bit).

Once we isolated one or more single units from the recordings, we began mapping each unit's RF with an automated mapping procedure while the monkey maintained its gaze on a central fixation dot. We determined the size and location of each RF and placed a mapping stimulus with the same size used in our experimental paradigm (see previous section) at a location inside the RF of one unit, or in the overlap of multiple units' RFs, if possible. We then presented 9 directions of motion on 6 disparity planes to determine each cell's tuning to linear motion and disparity. For this purpose we fitted a von Mises function for each set of directions presented at different disparities and then interpolated with a spline-based method across disparities. We began recording the main task once we identified a suitable recording site based on the qualitative assessment of the properties of at least one single unit. Here, MT units were defined as having RF sizes of ~3-10 degrees diameter (Dubner and Zeki, 1971), circular and approximately symmetric tuning to linear motion and being located at an electrode depth corresponding to our estimation of MT (based on structural MRI). We then recorded any single units isolated in the vicinity of this recording site.

After collecting neuronal data for each session, we used OfflineSorterV3 (Plexon, USA) to filter the raw signal with a 6-pole Bessel high-pass at a cut-off of 250Hz. We defined a suitable threshold for spike waveform detection by their threshold crossing (including some of the noise). We then sorted single units with an adaptive template matching method. Only time-epochs in which a unit was clearly separable from noise (i.e. its waveform's PCA cluster did not overlap with the noise cluster) and its negative spike deflection was sufficiently far from the threshold were used in the subsequent analysis.

Single unit inclusion criteria

For each recorded single unit, we used the fixation task data to estimate the tuning to linear motion. For this purpose we averaged test stimulus responses in an analysis window 80-320ms relative to test onset. If less than 4 directions with 4 repetitions each were available for data analysis we substituted the analysis pool with tuning stimulus presentations used for the online tuning analysis (see previous section). We then fitted a circular von Mises function using a non-linear least-squares procedure:

$$y = b + a * \exp\left(\kappa * \cos\left((x - \mu) * \frac{\pi}{180}\right)\right)$$

where μ is the preferred direction, κ is the concentration of the distribution around the preferred direction and a and b define baseline and peak activity levels. We evaluated how well this parametric model explained the responses to different test directions by calculating an adjusted R^2 goodness of fit for each unit. We excluded any unit with adjusted R^2 values of less than 0.3, biologically implausibly narrow tuning widths of $\kappa > 7$, or an activity of less than 10sp/s for the fitted preferred direction. This reduced our population of 129 recorded single units to 58 units tuned to linear motion (Figure 2A). In order to constrain our analysis on single units originating from area MT, we further calculated each unit's directional index:

$$DI = \frac{y(\mu) - y(\mu + 180)}{y(\mu) + y(\mu + 180)}$$

which can be converted to % signal change from null to preferred direction by:

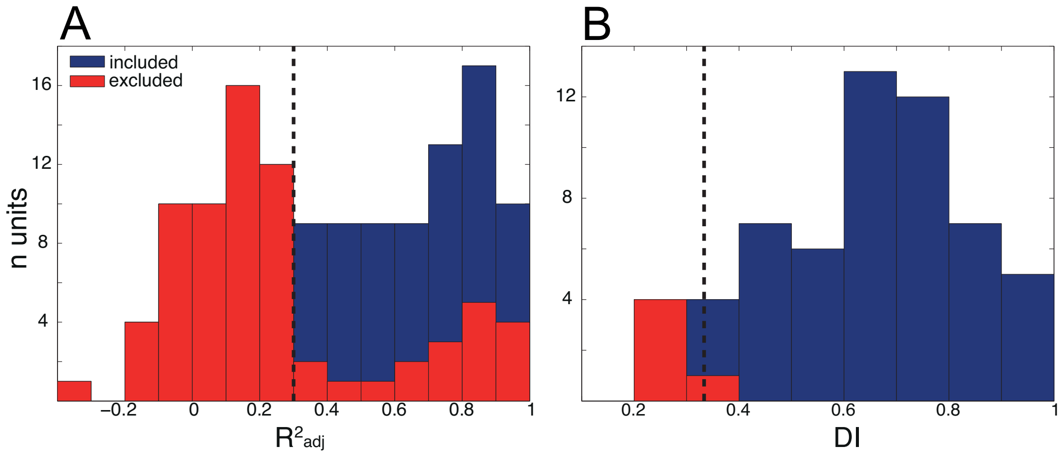
$$\%change = \frac{2DI}{1 - DI} * 100$$

Since we opted to analyze only well-tuned MT units, we defined a DI-cutoff of $DI > {}^{1}\!/_{3}$, i.e. a 100% response increase from the null to the preferred direction. This reduced our population of 58 well-fitted units to 53 units (Figure 2B).

We then calculated for the direction task and color task separately each sessions behavioral performance $d' = zscore(p_{hit}) - zscore(p_{false\ alarm})$. We only analyzed recording sessions in which monkeys reached $d' > 1$ for both the direction and color tasks. This excluded 6 more units (two sessions) and thus left 47 units for the final analysis. For those units we tested for the individual analysis steps if enough repetitions were collected and excluded further units, if necessary (see next section).

[xiv] (A) goodness of fit (von Mises distribution) for 129 recorded single units. Units were included in the analysis if they had adjusted R^2 values of more than 0.3, biologically plausible tuning widths of $\kappa < 7$, and activities of more than 10sp/s for the fitted preferred direction. Blue portions of the histogram indicate included, red portions excluded units. (B) The remaining 58 tuned units were evaluated based on their fitted directionality and excluded if they showed activity increases of less than 100% between null and preferred directions. Colors as in A.

Figure 2[xiii]



Data Analysis

The data analysis was performed with MATLAB 2014a (Mathworks, USA) using custom scripts. First, we defined three analysis periods in which we averaged and analyzed neuronal firing rates: *sample period* (80-1000ms relative to sample onset), *memory period* (300-800ms relative to sample offset) and *test period* (80-320ms relative to test onset). For the data analysis we used only correct trials (hits and correct rejections).

We first determined each neuron's stimulus preferences with a separate 3-way ANOVA for each of the three analysis periods. We tested for main effects of presented stimulus (sample or test) direction and color, as well as for an interaction of the two across all four task types.

In order to quantify differences in firing rate elicited by a test stimulus when it was presented as target vs. distractor, we constructed an attentional index:

$$AI = \frac{R_{target} - R_{distractor}}{R_{target} + R_{distractor}}$$

This index normalizes spike rate differences for each unit and thus its distribution reflects the normalized attentional modulation between targets and distractors. Positive indices reflect an increase in firing rate for targets compared to distractors and a significant shift of the distribution of indices relative to the 0-value reflects population activity differences. For each unit, we used only stimulus directions closer than 55° to the individually fitted preferred direction of each unit. We then equalized trial groups for targets and distractors regarding their color frequencies by excluding trials from either group until they contained the same number of measurements for each color. We averaged responses across colors and calculated the AI when each group contained at least 5 repetitions. Statistical tests (t-tests, evaluated at $\alpha = 0.05$) were used to determine if the distribution of AIs was significantly different from zero.

To estimate the time-course of modulation during the test epoch, we calculated each unit's spike density function with a sliding boxcar method (50ms width, 1ms steps) in the time period from -30ms to 430ms relative to test stimulus onset. We then normalized groups of averaged trials to the peak of the target presentations and calculated normalized activity differences for each unit. For this difference (modulation) function we bootstrapped 95% confidence intervals by sampling randomly with replacement from the averaged group of units and re-calculating the difference function. We repeated this procedure 10000 times and determined the confidence intervals with a bias corrected accelerated method.

We then fitted the difference function with a parametric model making two assumptions: (1) the onset of modulation has a Gaussian distribution across neurons and (2) at least a fraction of the modulation dissipates exponentially (Roelfsema et al., 2003). The model then equates to:

$$M(t; a, b, \mu, \sigma, \lambda) = a * exG(t, \mu, \sigma, \lambda) + b * G(t, \mu, \sigma)$$

where the modulation M over time is given by the weighted sum of an exponential Gaussian (Luce, 1986):

$$exG(t, \mu, \sigma, \lambda) = \lambda * \exp\left(\frac{(\lambda\sigma)^2}{2} - \lambda * (t - \mu)\right) * G(t, \mu + \sigma^2\lambda, \sigma)$$

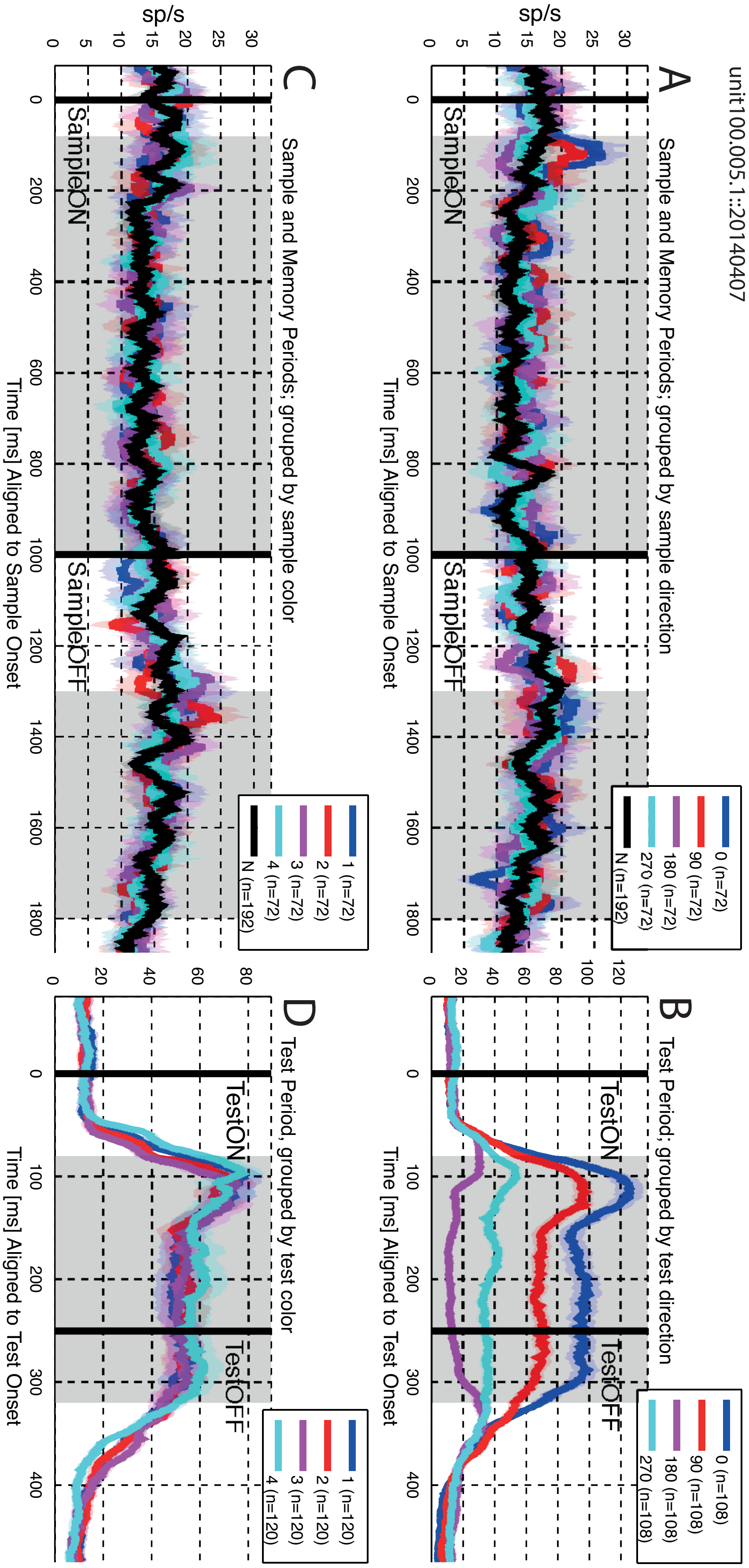
and a cumulative Gaussian $G(t, \mu, \sigma)$. Both components (dissipating and non-dissipating) are weighted by parameters a and b, respectively. Parameters μ and σ determine the location of the modulatory peak and the rate of build-up, respectively, while λ determines the rate of decay towards a plateau b. Variations of the function M were previously used by a number of studies to characterize response onsets and attentional modulation time-courses (Khayat et al., 2006; 2009; Roelfsema et al., 2003; Thompson et al., 1996).

The model was fitted to the normalized activity differences between 0 and 320ms relative to test stimulus onset using a non-linear least squares procedure. We then determined the time-point of 50% modulation and defined this time as modulation onset, since it is least affected by the temporal smoothing inherent to the approach. The 68.3% confidence intervals on the estimated parameters were bootstrapped by resampling (with replacement) from the pool of units and refitting the function. This procedure was repeated 10000 times and the confidence interval determined with a biased corrected accelerated method.

The function M was also used to determine the stimulus evoked activity onset. For this purpose we averaged the spike-density functions for targets and distractors and fitted function M with an additional free parameter defining the baseline activity. We then determined the activity onset and bootstrapped 95% confidence intervals, as described above.

[xv] Response of an example unit: (A) Spike density functions grouped by sample direction and time aligned to sample onset. Colors indicate the 5 possible directions (4 cardinal directions and incoherent noise). Grey, shaded epochs indicate the sample and memory epoch, respectively. Black bars indicate sample onset and offset. Error bars indicate 95% confidence intervals. Number of trials contributing to the function is given in the legend. (B) Spike density functions for four possible test directions and time aligned to test onset. Shaded area indicates test analysis epoch and black bars test onset and offset. (C) as A but grouped by sample color (from 1-4: orange, cyan, green, magenta. N reflects grey ‘null’ color). (D) as B but grouped by the four possible test colors

Figure 3[xiv]


unit100.005.1::20140407
A
Sample and Memory Periods; grouped by sample direction
sp/s
0
5
10
15
20
25
30
SampleON
SampleOFF
0 (n=72)
90 (n=72)
180 (n=72)
270 (n=72)
N (n=192)
0
200
400
600
800
1000
1200
1400
1600
1800
Time [ms] Aligned to Sample Onset
B
Test Period; grouped by test direction
0
20
40
60
80
100
120
TestON
TestOFF
0 (n=108)
90 (n=108)
180 (n=108)
270 (n=108)
0
100
200
300
400
Time [ms] Aligned to Test Onset
C
Sample and Memory Periods; grouped by sample color
sp/s
0
5
10
15
20
25
30
SampleON
SampleOFF
1 (n=72)
2 (n=72)
3 (n=72)
4 (n=72)
N (n=192)
0
200
400
600
800
1000
1200
1400
1600
1800
Time [ms] Aligned to Sample Onset
D
Test Period; grouped by test color
0
20
40
60
80
TestON
TestOFF
1 (n=120)
2 (n=120)
3 (n=120)
4 (n=120)
0
100
200
300
400
Time [ms] Aligned to Test Onset

Results

We recorded the responses of single units from extrastriate cortical area MT during a delayed match-to-sample task that required monkeys to identify target stimuli either based on their color, motion direction, or a unique conjunction of color and motion. Only test stimuli were presented in the neuron's RFs. Figure 3 shows the spike density functions of a typical example unit during three analysis periods (sample, memory and test).

Even though this unit is not significantly selective for color, it shows different latencies in the response for different colors (Figure 3D). Those differences are likely attributable to presentation asynchronies due to the projection hardware (DLP color wheel technology). This unit also responds to preferred directions during the sample presentation with a very short impulse (Figure 3A). As this brief increase in activity is tuned, it renders the unit 'direction-selective' for the sample direction (even though the sample was presented contralateral to the neuron's RF).

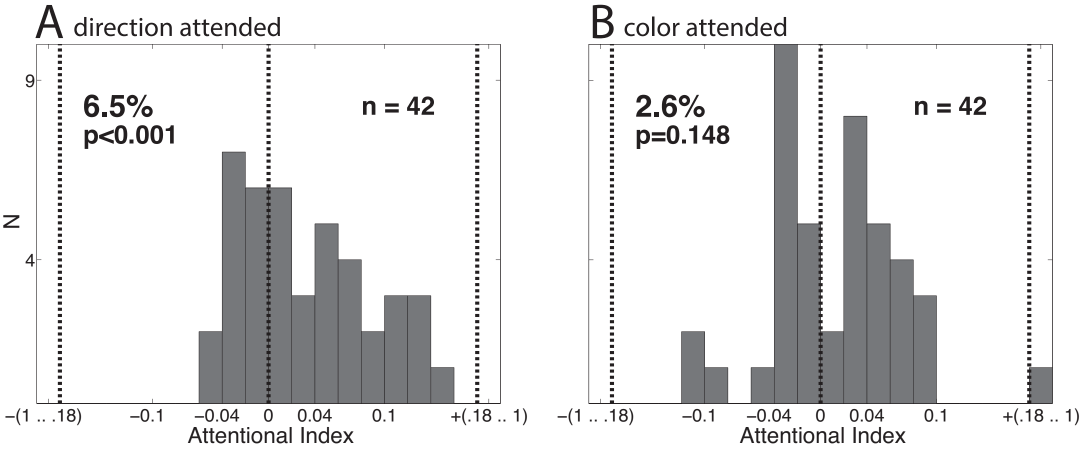
For all units, we then determined the selectivity of our neuronal population by calculating a 3-way ANOVA for each analysis period, testing for main effects of stimulus direction and color, as well as for an interaction of the two. We evaluated the results of the ANOVA at an $\alpha = 0.001$ confidence boundary. Table 1 summarizes the results. About half of all MT units (which were selected by their tuning for motion) are additionally selective for the stimulus color. Surprisingly, we also find strong selectivity for the sample direction in our population, even though the sample was presented contralateral to the neurons' RFs. This sample-induced activity, however, does not extend into the memory period for any of the units under study.

Table 1[xv]	Sample Epoch	Memory Epoch	Test Epoch
Color	0/47 (0.0%)	0/47 (0.0%)	20/47 (42.6%)
Direction	23/47 (48.9%)	0/47 (0.0%)	47/47 (100%)
Color*Direction	1/47 (2.1%)	0/47 (0.0%)	11/47 (23.4%)

MT units increase their firing rates for target stimuli when motion is attended

We selected our population of MT units based on their directionality and tuning for linear motion (see Methods section) and only analyzed trials in which the test direction was within 55° of the neuron's preferred direction. For each of the single feature tasks (only-direction or only-color task) trials with preferred targets and preferred distractors were pooled separately. To counterbalance potential color selectivity, the proportion of individual stimulus colors was equated between target and distractor groups by excluding trials from either group. Responses in the test epoch were averaged across colors and units included in the analysis if all groups contained sufficient repetitions (see Methods section). This reduced the population of 47 MT units to 42 units used in the following analysis.

Figure 4[xvii]



To compare neuronal responses to target and distractor stimuli we calculated an attentional index (AI=(T-D)/(T+D)) for each unit. The AI distribution is significantly

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[xvi] ANOVA results for 47 MT units: columns indicate which analysis period was used for the tests and rows indicate explanatory variables and whether they reached significance evaluated at $\alpha = 0.001$. Percentages indicate the proportion of units in the population of 47 tested neurons that showed significant effects of a given explanatory variable.

[xvii] Distribution of attentional indices for 42 units in the only-direction task (A) and only-color task (B). Percentage values indicate the mean activity difference for targets relative to physically identical distractors. Significant p-values (t-test) indicate significant average differences in neuronal activity between targets and distractors.

shifted to positive values in the only-direction task (mean AI=0.031, or 6.5%; t-test p<0.001, n=42, Figure 4A), indicating a significant increase in firing rates for stimuli with the searched-for direction relative to physically identical stimuli in cases in which the opposite motion was attended. In the only-color task targets do not lead to significantly higher responses than distractors (mean AI=0.013, or 2.6%; t-test p=0.148, n=42, Figure 4B).

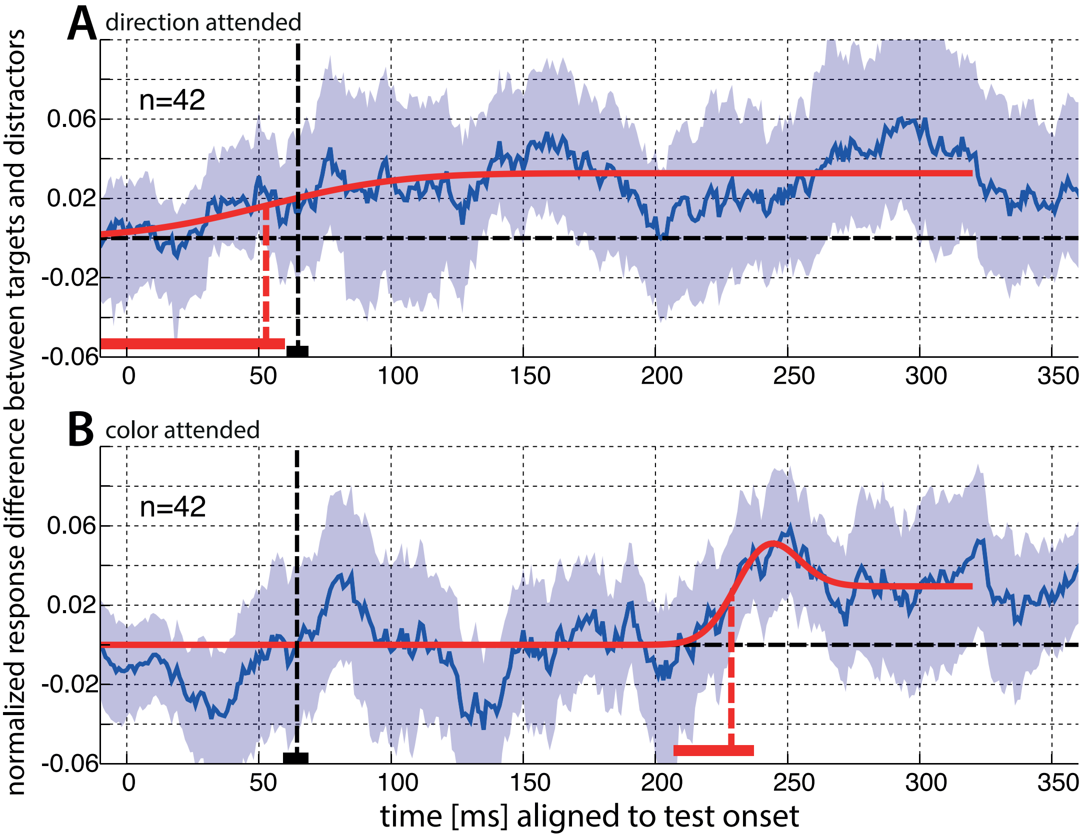
The attentional modulation begins with response onset when targets are defined by a specific direction

We determined the time-course of modulation separately for the only-direction task and only-color task by normalizing each unit's mean spike-density functions for targets and distractors to the peak target response, separately for each task type. Figure 5 plots the average difference in spike-rates between targets and distractors across units. A fitted modulation function M (see Methods section) was used to determine the time of modulation onset for the population as well as the time of visual activity onset (by fitting a similar function to the averaged activities of target and distractor trials).

When the monkeys identified targets based on their direction (only direction task, Figure 5A), the modulation onset occurred together with the visual activity onset, followed by a sustained modulation for targets relative to distractors. Figure 5B shows that targets defined by their color (only-color task) are also modulated relative to distractors with a subsequent sustained phase. In this case, however, the onset of modulation occurs much later during the test presentation.

[xviii] Time courses of normalized firing-rate differences between targets and physically identical distractors when targets were defined by stimulus direction (only-direction task; A) or by stimulus color (only-color task; B). Red lines indicate the best fitting parametric model for the time-course of modulation (weighted sum of exponential Gaussian and cumulative Gaussian, see Methods section), with the 50% modulation onset indicated by dashed red lines and 68.3% confidence intervals for the modulation onset estimate indicated by thick red bars. Black dashed lines indicate visual activity onset (50% point) and thick black bars the 95% confidence interval. Blue shaded areas correspond to 95% bootstrapped confidence intervals for the mean time-course of modulation.

Figure 5[xvii]

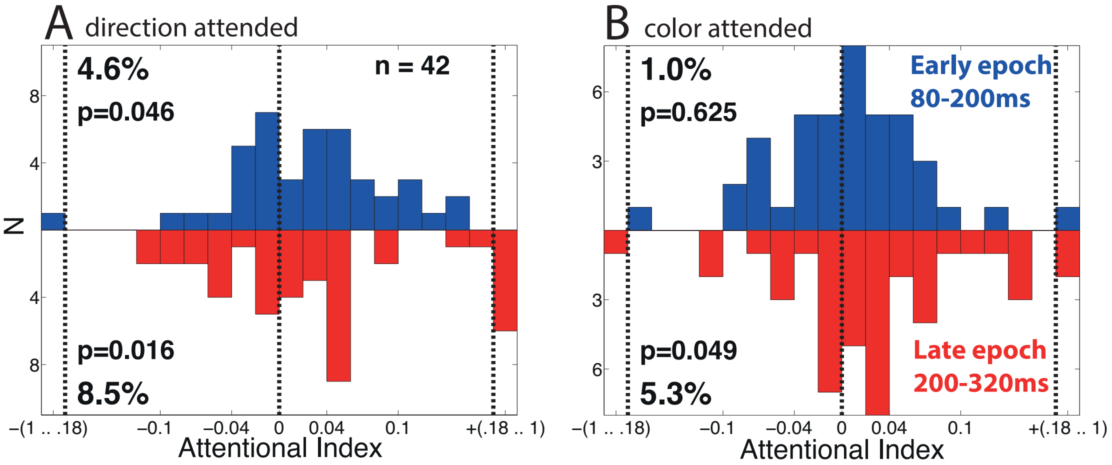


Attentional modulation for targets defined by colors begins late during stimulus presentation

Next, we split the test analysis period into two even parts – early (80-200ms) and late (200-320ms) epochs. Attentional indices were recalculated for the two periods and the distribution of indices tested with t-tests for shift away from the 0-point. Confirming our previously outlined results, we found that when targets were defined by a specific direction (only-direction task) both epochs' AI-distributions were significantly shifted from zero (early epoch: mean AI=0.023, or 4.6%; t-test p=0.046, n=42; late epoch: mean AI=0.041, or 8.5%; t-test p=0.016, n=42; Figure 6A). In contrast, when targets were defined by a specific color and the direction of the test was irrelevant (only-color task), the attentional modulation was not significant during the early epoch, but reached significance in the late epoch (early epoch: mean AI=0.005, or 1%; t-test p=0.625, n=42; late epoch: mean AI=0.026, or 5.3%; t-test p=0.049, n=42; Figure 6B).

Those results confirm what the time-courses of modulation also indicate: the attentional modulation onset for our population of directionally selective MT units occurs early in the test epoch when direction is attended and occurs later during the test epoch when color is attended.

Figure 6[xviii]



MT signals single feature matches rather than targets

In the combined task, targets were defined by a unique conjunction of a specific motion and color. Consequently, stimuli with only one matching feature (motion or color) were distractors and had to be ignored. We first reduced our original population of 47 MT units by excluding units that were recorded in sessions in which the monkeys had a biased performance for one of the two relevant feature dimensions. For this purpose we determined the behavioral performance for the two types of distractors that matched either of the searched-for features (motion/~~color~~, ~~motion~~/color). We excluded recording session in which the difference in probabilities

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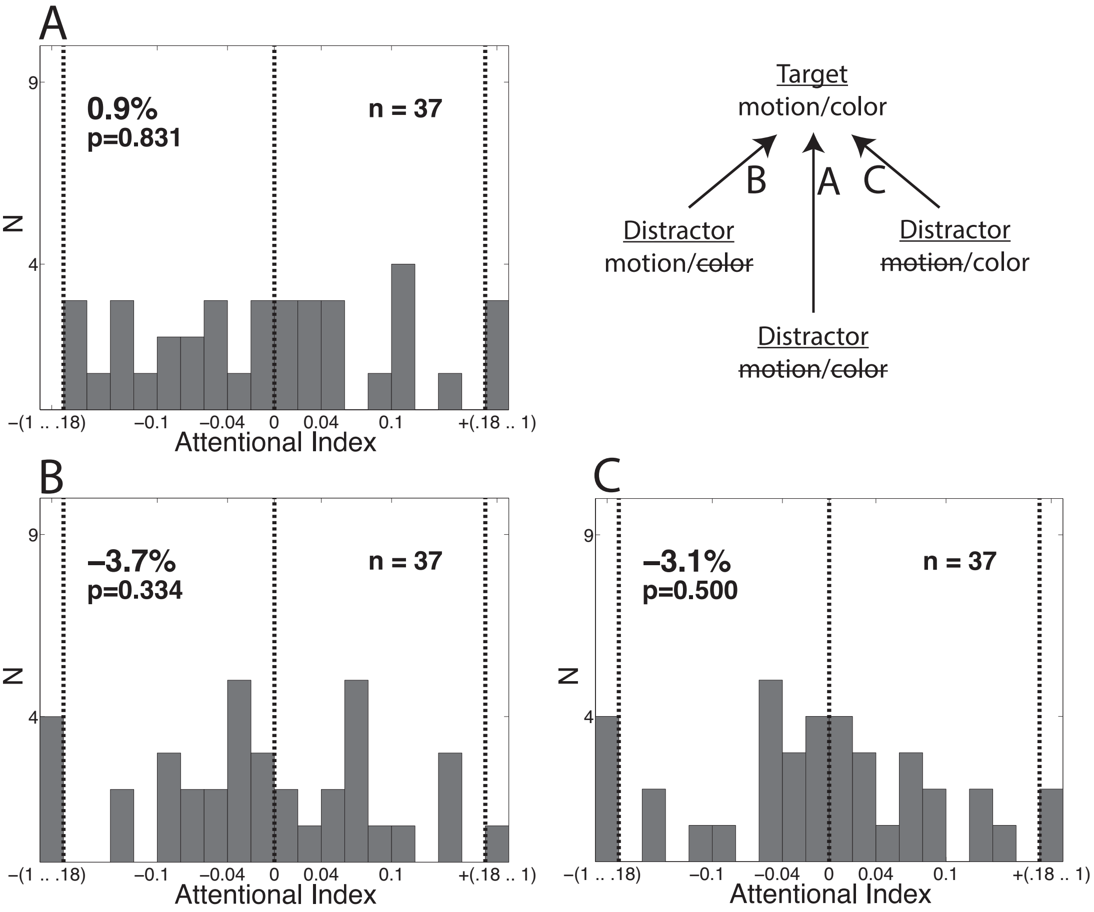
[xix] Distribution of attentional indices for 42 units in the only-direction task (A) and only-color task (B). Percentage values indicate the mean activity difference for targets relative to physically identical distractors in two consecutive analysis windows: blue histograms correspond to an early (80-200ms relative to test onset) epoch and red histograms to a late epoch (200-320ms). Significant p-values (t-test) indicate significant differences in neuronal activity between targets and distractors (AI distribution shifted from 0-point) within a given epoch.

for false-alarms and correct-rejections for either of the two distractor types was less than 15%. This excluded two more recording sessions and two units. We then determined for each unit, similar to the two single tasks, if enough (color balanced) repetitions for each of the test stimulus types were recorded (see Methods section). This left 37 units, which were used for the subsequent attentional analysis.

Figure 7[xx]



A comparison of target stimuli with matching motion and color features (motion/color) to the three possible distractor types (motion/~~color~~, ~~motion~~/color,

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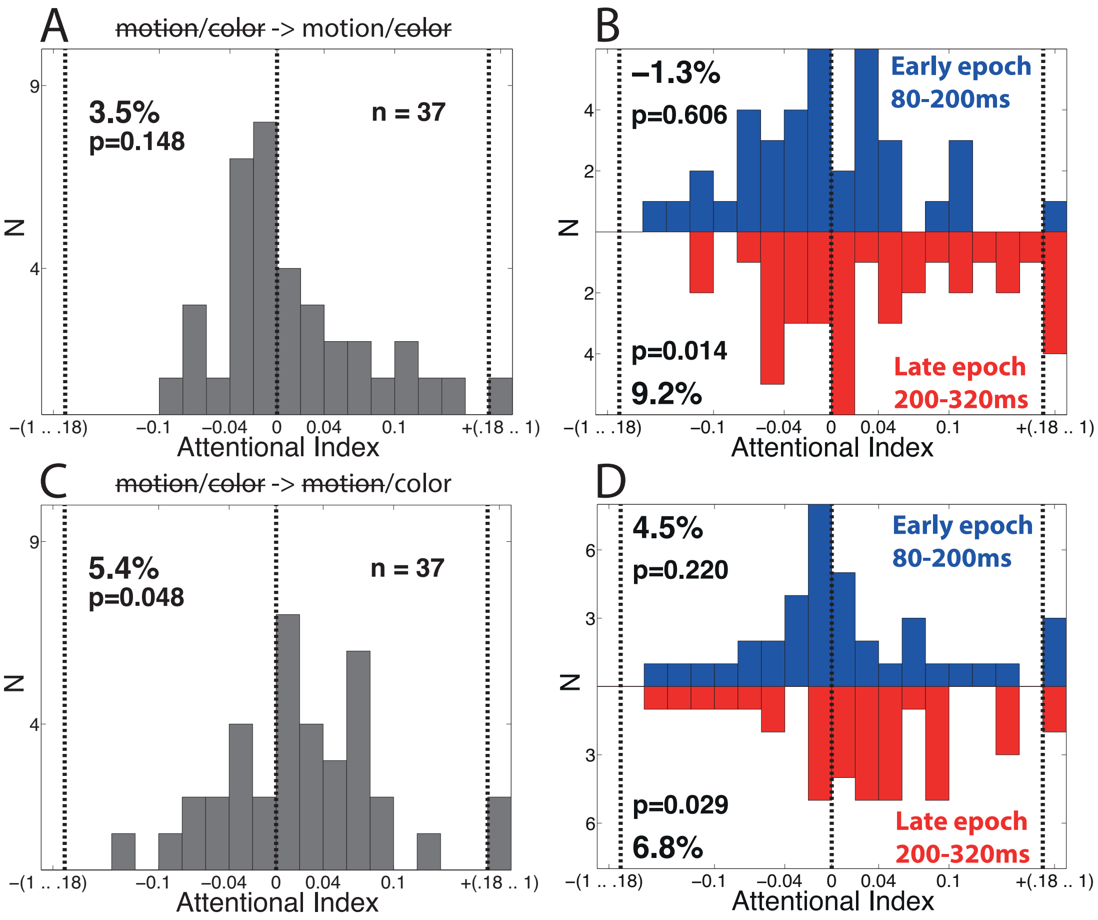
[xx] Distribution of attentional indices for 37 units in the combined task. (A) Attentional indices between targets and ~~motion~~/~~color~~ distractors. Percentage values indicate the mean activity difference for targets relative to physically identical distractors. Significant p-values (t-test) indicate significant differences in neuronal activity between targets and distractors. (B) as A but for targets and motion/~~color~~ distractors. (C) as A but for targets and ~~motion~~/color distractors.

~~motion~~/~~color~~) did not reach significance in any of the three comparisons. This indicates that targets did not elicit stronger responses than any of the three types of distractors (Figure 7A-C: ~~motion~~/~~color~~ distractor: mean AI=0.005, or 0.9%; t-test p=0.831, n=37; motion/~~color~~ distractor: mean AI=-0.019, or -3.7%; t-test p=0.334, n=37; ~~motion~~/color distractor: mean AI=-0.016, or -3.1%; t-test p=0.5, n=37).

We then calculated AIs between the two half-matching distractors (motion/~~color~~ and ~~motion~~/color) and complete distractors (~~motion~~/~~color~~). This comparison is similar to comparisons made earlier for the two single feature tasks, as the difference between complete distractors and half-matching distractors is the presence of one (of the two) searched-for features. Surprisingly, MT units were significantly modulated by the presence of the searched-for color, but not direction (Figure 8A,C: motion/~~color~~ distractor: mean AI=0.017, or 3.5%; t-test p=0.148, n=37; ~~motion~~/color distractor: mean AI=0.027, or 5.4%; t-test p=0.048, n=37). However, when the analysis period was divided into early and late epochs, both features led to significantly shifted distributions of AIs in the late epoch and not significantly shifted distributions in the early epoch (Figures 8B,D: motion/~~color~~ distractor: mean AI=-0.007 and 0.044, or -1.3% and 9.2%; t-test p=0.606 and 0.014, for early and late periods, respectively, n=37; ~~motion~~/color distractor: mean AI=0.022 and 0.033, or 4.5% and 6.8%; t-test p=0.22 and 0.029, for early and late periods, respectively, n=37).

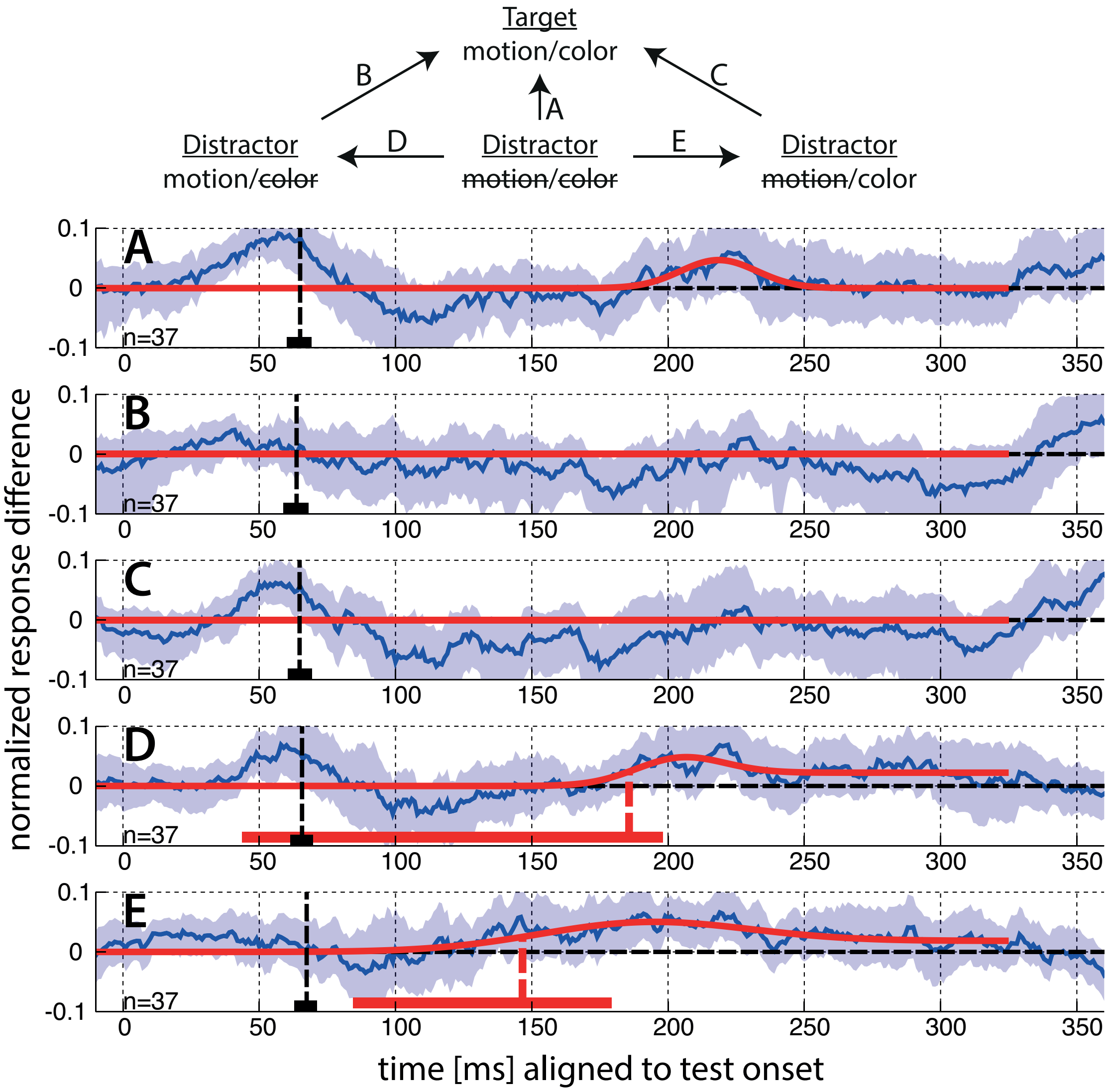
[xxi] Distribution of attentional indices for 37 units in the combined task. (A) Attentional indices between motion/~~color~~ distractors and ~~motion~~/~~color~~ distractors. Percentage values indicate the mean activity difference for targets relative to physically identical distractors. Significant p-values (t-test) indicate significant differences in neuronal activity between targets and distractors. (B) like A but analysis period split in two even epochs. (C,D) like A,B but between ~~motion~~/color distractors and ~~motion~~/~~color~~ distractors.

Figure 8[xx]



An analysis of the time-course of normalized response differences between trial groups revealed that both color and motion half-matching distractors (motion/~~color~~ and ~~motion~~/color) were modulated relative to complete distractors (~~motion~~/~~color~~) with modulation onsets during the sustained phase of test presentation (Figure 9D-E). Targets were somewhat suppressed relative to the two half-matching distractors during test presentation (Figure 9B-C), confirming the (not significantly) negatively shifted AI distributions between those stimuli (Figure 7B-C). This indicates that the presence of a single target feature is sufficient to cause attentional top-down modulation in area MT, even when the detection of the behaviorally relevant target requires attention to be directed to a conjunction of two features.

Figure 9[xxii]



[xxii] Time courses of normalized firing-rate differences for groups of physically identical stimuli presented in the combined task: (A) difference between targets and ~~motion~~/~~color~~ distractors. (B) difference between targets and motion/~~color~~ distractors. (C) difference between targets and ~~motion~~/color distractors. (D) difference between motion/~~color~~ distractors and ~~motion~~/~~color~~ distractors. (E) difference between ~~motion~~/color distractors and ~~motion~~/~~color~~ distractors. (A-E): Red lines indicate the best fitting parametric model for the time-course of modulation (weighted sum of exponential Gaussian and cumulative Gaussian, see Methods section), with the 50% modulation onset indicated by dashed red lines and 68.3% confidence intervals for the modulation onset indicated by thick red bars (where applicable). Black dashed lines indicate visual activity onset (50% point) and thick black bars the 95% confidence interval. Blue shaded areas correspond to 95% bootstrapped confidence intervals for the mean time-course of modulation.

In addition, we observed significant deviations of spike-rate differences around the onset of visual response for comparisons made between test stimuli matching and not matching the attended direction (Figure 9A,C-D). This pattern of results visually suggests a decreased response latency for stimuli matching the attended direction, relative to stimuli not matching the attended direction. However, we estimated the time of visual activity onset separately for each unit and condition and tested with paired t-tests whether the visual response onset occurred earlier for stimuli matching attended features. None of the comparisons were statistically significant (paired t-tests, all p>0.2), ikely due to the high variability between neurons and the limited number of repetitions.

Discussion

We recorded single-unit activity from extrastriate area MT while monkeys performed a delayed match-to-sample task with three randomly interleaved task rules: targets were defined either by their motion direction, their color, or a unique conjunction of motion and color. We compared neuronal responses between target stimuli and physically identical distractors and found that when targets were defined by their motion direction, motion-selective MT units increased their firing rates significantly for targets compared to distractors. The modulation started together with visual response onset and persisted throughout the test stimulus presentation. Although we find that about 50% of the recorded units also encoded the motion direction of the sample (see also Zaksas and Pasternak, 2005), we cannot detect any significant trace of such selectivity in the memory period. This argues for the involvement of a top-down modulatory input to MT, effectively priming single units tuned to the searched-for motion to contribute to a fast and reliable detection of target stimuli.

Such a modulation for specific features of a stimulus was previously measured in macaque area MT when monkeys attended to motion directions (Martinez-Trujillo and Treue, 2004; Treue and Martinez-Trujillo, 1999) and was attributed to the deployment of feature-based attention. In fact, the strength of modulation we found for targets relative to distractors is very similar to previously reported magnitudes of feature-based attentional modulation in MT (Treue and Martinez-Trujillo, 1999). Further, since attention enhances behaviorally relevant stimuli among irrelevant ones, we argue that in the match-to-sample paradigm used in this study, targets (which required a behavioral response) were enhanced by feature-based attention relative to distractors (which did not require a response).

Consistent with at least two previous reports of color-based modulation in MT (Chen et al., 2012; Katzner et al., 2009), we also found target-evoked attentional modulations in our population of motion-selective MT units when the test color was the decision-defining feature dimension. Although MT units can show some selectivity to color (Seidemann et al., 1999), and we also detect significant selectivity for tested colors in about half of our recorded neurons, MT predominantly encodes stimulus motion. Katzner et al. (2009) argued, that when effects of feature-based attention to color emerge in MT, attention spreads to irrelevant features of the stimulus, effectively enhancing also the motion component. This view is consistent with theories of a more unified, object-based attentional system in which single features of one object (stimulus) are bound and enhanced together. In addition, we show here that although single units in MT are modulated by attention to color, this modulation appears delayed as compared to the attentional modulation for motion. This pattern of results is consistent with a recent report of modulatory time-courses of object-based attention in humans (Schoenfeld et al., 2014), showing that attention to color first modulates color-selective cortical areas and only later emerges in the human MT+ complex. We estimated the onset of modulation in macaque MT to be 52.7 and 228.7 ms, respectively for motion and color attention, which corresponds to Schoenfeld et al.'s (2014) estimations of 155 and 225 ms for motion and color based modulations of the human MT+ complex.

This challenges theories of 'pure' feature-based and also of 'pure' object-based attention. If feature-based attention were to enhance multiple independent features, a spread of modulation within objects creates a modulation dependency, which can be detrimental to a fast and simple read-out of decision variables when the detection of a conjunction of features is behaviorally relevant. On the other hand, if the spread of modulation to all features of an object is delayed relative to a ‘reflexive’ modulation specific to the tuning properties of a visual area, such a delay could leave enough time for a reliable detection of specific feature-conjunctions.

However, our data indicate that attending to motion/color-conjunctions does not produce a neuronal modulation that is the sum of the modulation observed in trials where monkeys attended only to motion and only to color. Although we cannot exclude the possibility that our recorded population of MT units was not large enough to detect a significant modulation between conjunction targets and distractors not matching either of the attended features, we clearly show that the presence of just one of the relevant features is sufficient to cause strong modulation in MT when monkeys attended a conjunction of features. Further, the data also indicate that during the conjunction search, both modulatory strength and time-course of attention are similar for color and motion matches of the test stimulus. This is consistent with a role of area MT in which neuronal populations signal unspecific feature matches, rather than detecting targets. As a consequence, the detection of target matches then has to be made elsewhere in the brain, for example in area LIP, which receives strong input from MT and is known to accumulate evidence for decisions based on visual stimulation (de Lafuente et al., 2015; Ibos and Freedman, 2014; Roitman and Shadlen, 2002; Shadlen and Newsome, 2001).

An important alternative interpretation of the data relies on the fast (‘reflexive’) modulation of target-direction matches we detect when targets are defined by their motion direction, but also when they are defined by a conjunction of motion and color. In the latter case, however, attention to the displayed direction first increases and then decreases the firing rate of single units. This is reminiscent of a decrease in neuronal latency for target directions relative to distractor directions, without a subsequent attentional modulation of firing rates. Latency differences in visual response onset can be caused by increases in stimulus contrast (Gawne, 2000; Gawne et al., 1996), but the effects of spatial attention (in area V4) do not include significant changes in response latency, whilst changes in contrast do (Lee et al., 2007). Other studies investigating the time-course of neuronal modulation caused by spatial attention also did not reveal effects on response latencies in macaque MT (Busse et al., 2008; Seidemann and Newsome, 1999). For feature-based attention it was shown that during a visual search task, V4 units are not modulated by target features in the response transient but that this effect becomes significant 100-130ms after stimulus onset (Zhou and Desimone, 2011). In addition, Schoenfeld et al. (2007) detected significant modulations for the motion feature dimension in human MT+ no earlier than 110-120ms after stimulus onset. However, consistent with our data, it has been shown that exogenous spatial attention can cause modulations that effect early visual onset transients in macaque MT (Busse et al., 2008). Yet, how exogenous, bottom-up attention would have been able to selectively enhance searched-for motion features in a match-to-sample task can only be speculated upon. One possibility would be a variant of a recently reported type of bottom-up feature-based attention (Lin et al., 2011), possibly controlled by subcortical structures (e.g. McAlonan et al., 2008).

We observed modulations around the time of visual onset only for matching motion features of the stimulus, not color. This signature of activity may therefore provide viable evidence for the detection of not only potentially matching stimuli, but stimuli specifically matching the searched-for motion feature. However, due to limitations in the temporal accuracy of our measurements, further research is needed to target the role of visual latency changes in match-to-sample paradigms.

In summary, our results show that extrastriate, motion-selective area MT is modulated by target features when monkeys perform a delayed match-to-sample task. In contrast to previous studies showing firing-rate enhancements for targets relative to distractors, we demonstrate here that this enhancement is not exclusive to the searched-for motion but also occurs when monkeys attend to features not preferentially encoded by the cortical area under study. Further, in cases in which targets are defined by a unique conjunction of features, area MT appears to be modulated by all potential target stimuli, not only targets. This is consistent with theories of a unified attentional system, enhancing all features of a stimulus, regardless of their relevance.

Summary and Outlook

We have come a long way in our understanding of the brain networks subserving visual attention. However, the source of top-down visual attention has yet to be identified. The search for a neuronal circuit controlling the deployment of feature-based attention must rest on prior knowledge of the properties of the attentional signal itself. First of all, it has to be known in what form top-down information enters feature-coding populations and how different behavioral demands shape the signal. Only then do more ambitious attempts to identify the brain areas involved in the generation of such an attentional signal seem practicable. This work contributes to our understanding of the attentional signal and guides such a search.

First, I outlined in this work that feature-based attention, in contrast to spatial attention, modulates feature-coding populations of neurons by means of a stimulus-independent influence on the putative internal normalization circuitry of a local neuronal population. In practice, such an influence might release specific single units in a neuronal population from their suppressive surrounds, thereby enhancing their individual firing rates. This finding (see Chapter 2.2), is consistent with the feature-similarity gain model of attention (Treue and Martinez-Trujillo, 1999) and previous reports of feature-based attention in macaque MT, where neurons are enhanced or suppressed based on the similarity of their tuning preferences to the currently attended feature (Martinez-Trujillo and Treue, 2004). Further, releasing single units from the suppressive (or excitatory) influence of surrounding units leads to an increase in variability between neurons in a feature-coding population. Recent evidence from macaque visual cortex also supports this prediction (Cohen and Maunsell, 2009; Ruff and Cohen, 2014).

Further, I outlined that the attentional signal acts independently of stimulus input, again consistent with predictions made by the feature-similarity gain model (Chapters 2.1 and 2.2). In practice, this suggests that the modulatory top-down signal enters the visual processing stream on the level of area MT, and is not inherited from upstream areas. Such a prediction is important in guiding the search for the origin of the attentional signal: there should exist a modulatory projection from at least one other cortical or subcortical brain region projecting to area MT. This hypothetical control region should encode currently attended features and selectively synchronize with similarly tuned neurons in visual cortex (see Chapter 1.4.4). In fact, recent evidence suggests such a candidate region for the deployment of feature-based attention: prefrontal area 8AV (Paxinos et al., 1999) contains neurons encoding both the attended direction and color (Lennert and Martinez-Trujillo, 2011; 2013; Zaksas and Pasternak, 2006) and projects directly to area MT (Petrides and Pandya, 2006). Area 8AV is also located directly adjacent to (or even overlaps with) the frontal eye field, which was previously indicated to be heavily involved in the guidance of visual attention (see Chapter 1.4.4). My ongoing experiments aim at showing that this area indeed synchronizes to area MT while attention is directed to a motion feature.

Here, the physiological results from macaque area MT (Chapter 2.3) provide an important foundation in establishing such a guidance of attentional selection by the prefrontal cortex (Chapter 1.4.4). In the framework of a behavioral task requiring monkeys to attend to the color and/or the motion feature of a stimulus, the results indicate that feature-based attention precedes object-based selection when a single feature is attended, but not when a conjunction of features is attended. This provides important insights regarding the processing capacity available to the attentional system. In particular, the data indicate that feature-based attention cannot be deployed independently to both color and motion features (Chapter 2.3). Such a limitation should be reflected in the activity of a putative control area for the deployment of feature-based attention and thus provides a testable prediction for the activity of single units in area 8AV.

In summary, this work provides novel insights into the properties of the feature-based attention system of monkeys and humans. I described a stimulus-independent influence of attention on neuronal normalization and a potential resource limitation of feature-based attentional deployment. Both results will guide further research aiming at characterizing the brain networks subserving the deployment of top-down feature-based attention.

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HONORS AND AWARDS

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PUBLICATIONS

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- Schwedhelm, P., & Treue, S. (2014). *Attentional Top-Down Modulation, Models of.* Encyclopedia of Computational Neuroscience *(pp. 1–5). New York, NY: Springer New York. doi:10.1007/978-1-4614-7320-6_566-1*
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POSTERS & TALKS

- Schwedhelm, P., & Treue, S. (2014). *Feature-based attentional modulation of macaque area MT in a match-to-sample task.* Poster presented at SfN, Washington, DC
- Schwedhelm, P., & Treue, S. (2014). *Interactions of color and motion directed feature-based attention in macaque area MT.* Poster presented at BCCN, Göttingen
- Schwedhelm, P. (2014). *Feature-based attention enhances performance by a combination of response and contrast gain.* Talk given at Networks! Symposium, Tübingen
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