UNIVERSITY
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Center for Mind/Brain Sciences

Neural mechanisms of attention to motion

PhD Dissertation

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Chapter 1

Introduction

Natural scenes contain more information than the visual system can process all at once. Only a fraction of the available information appears to reach visual awareness. Visual attention is the perceptual mechanism by which observers select important aspects of a scene for further processing, for example by biasing processing of attended as compared with ignored stimuli (Desimone & Duncan, 1995). Attention can be allocated to locations, which then receive enhanced processing, for example when a hunter perceives a slight movement behind a bush. But it can also be allocated to features such as the color, orientation or movement direction of a stimulus (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990), for example when we have to search for police officers amongst a group of people.

While the term "attention" is an everyday usage, it has been difficult to define what attention is and how it operates when it comes to neural mechanisms. The most prominent definition of attention states that "*Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others*" (James, 1890, pp. 381–382).

James' account of attention contains core elements that are still being investigated today. Attention is selective, it comes into play when many, maybe too many, stimuli are available for visual processing, such that some have to be chosen while others have to be ignored. The last

part of James' description may be taken as a speculation about how attention might actually operate when it comes to neural processing of attended and ignored stimuli.

Attention alters appearance: Attention and the Psychometric Function

A currently debated account of what attention actually does (Carrasco, Ling, & Read, 2004) can be traced back to the early work of James and von Helmholtz. This account postulates that "attention alters appearance"; in other words, attention intensifies the sensory impression of selected or to be selected stimuli while it reduces the sensory impression of stimuli that are not or will not be selected for further processing.

A current debate in attention research is how this increase and reduction of sensory impressions might operate. Behavioral research uses psychophysical methods that relate subjective experience to different levels of stimulus intensity. For example, participants can be asked to detect a stimulus ("yes, I see the stimulus", "no, I don't see the stimulus") at varying levels of *contrast* (the difference of highest stimulus intensity and lowest stimulus intensity divided by its sum). Such experiments yield psychometric functions, which show the probability of the participant reporting "yes" as a function of stimulus intensity (here, contrast intensity).

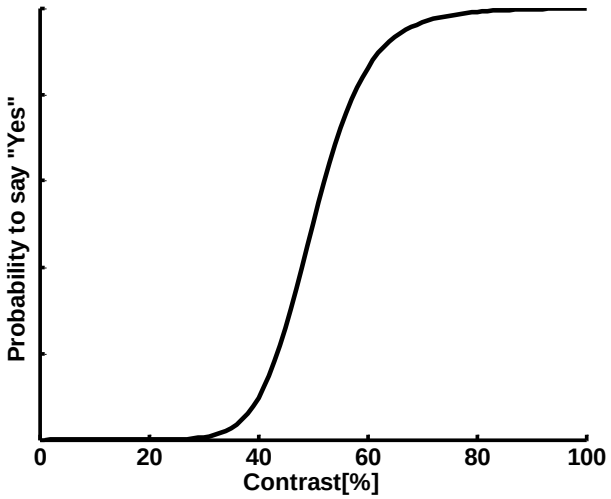

Figure 1. Hypothetical psychometric function. This psychometric function relates subjective experience (e.g. the probability of reporting "yes, I saw the stimulus"), to stimulus intensity, here, luminance contrast. Typically, the probability that observers will respond "yes" increases with stimulus intensity.

This psychometric function, hereafter termed the contrast response function (CRF) can now be assessed under two conditions, a) when participants do not attend to the stimulus, and b) when participants attend to the stimulus. If attention alters stimulus appearance, then the psychometric functions for attended and ignored stimuli should differ. In principle, we can hypothesize three different ways in which CRFs for attended and non-attended, or ignored, stimuli can differ. A) Attention may make a stimulus appear to have a slightly stronger contrast compared with when it is not attended. For example, a stimulus of 5% contrast may appear to have a 10% contrast, a stimulus of 10% contrast may appear to have a 15% contrast and so on. Such a mechanism, called *contrast gain*, would lead to a leftward shift of the entire CRF (see Figure 2A). B) Alternatively, attention might operate as a multiplicator of stimulus strength, for example doubling it. A stimulus with 5% contrast may appear to have 10% contrast, a stimulus of 10% contrast may appear to have 20% contrast and so forth. This mechanism is called *response gain*,

and it would effectively lead to the CRF for attended stimuli deviating more and more from the CRF for unattended stimuli as contrast increases (see Figure 2B). C) Finally, one could imagine that an observer simply changes her or his criterion for responding "yes", responding 10% more often with "yes" when attending to stimuli, irrespective of stimulus strength. This is called *baseline shift*, and it leads to a constant upward shift of the entire CRF with attention (see Figure 2C).

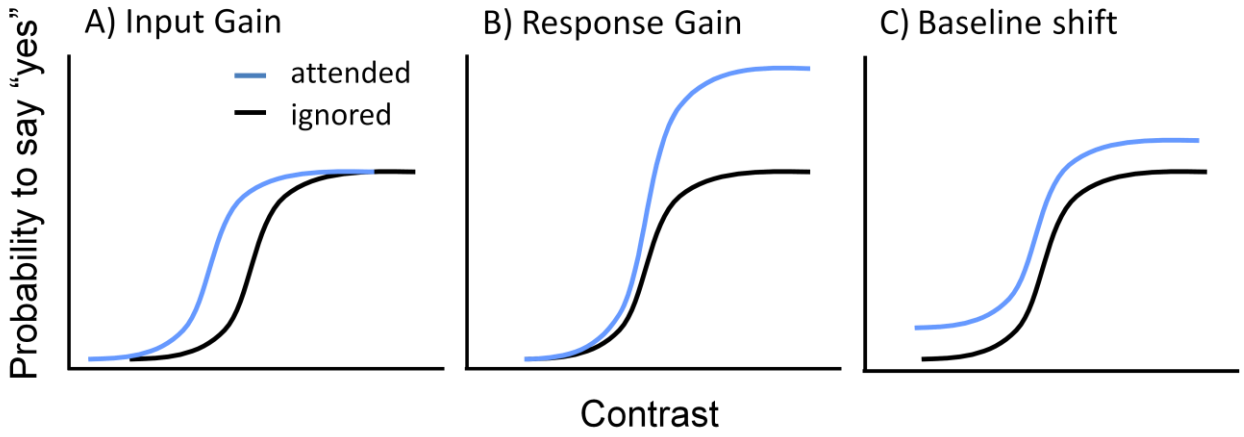

Figure 2. Three putative mechanisms of attention. Subjective report is shown as a function of contrast when stimuli are ignored (black lines) or attended (blue lines). In passive viewing, performance increases in a sigmoidal fashion as a function of contrast. When stimuli are attended, performance may be modulated differently according to the proposed mechanisms of input gain (A), response gain (B) or baseline shift (C).

It has to be noted here that in our example we have ignored the problem of saturation. Take for example a high contrast stimulus to which a participant would always respond with "yes, I have seen it" even when attending elsewhere. In such conditions, attention cannot change anything. To illustrate using the same strengths for attentional effects as before, input gain cannot make the stimulus appear to have 110% contrast, response gain cannot make the stimulus appear to have 200% contrast and baseline shift cannot make the participant respond "yes" in 110% of the trials. Thus, saturation has to be taken into account when making inferences from the shape of CRFs to

underlying mechanisms when drawing conclusions from either psychometric data or (as later in this text) neural data.

In the cognitive Neurosciences we try to relate behavior and experience to brain activity. In my thesis, I will use a measure of brain activity, the Blood Oxygenation Level Dependent (BOLD) response (Ogawa, Lee, Nayak, & Glynn, 1990), as the dependent measure instead of behavioral responses to look at changes of BOLD amplitude as a function of stimulus intensity and attention. In this way I can find, for example, BOLD-CRFs with and without attention. First, however, I would like to review a selection of the neurophysiological literature which reports a link between stimulus intensity and spiking of neurons for single unit recordings in cat and monkey when animals attended to or ignored visual stimuli. In these studies, CRFs no longer represent psychometric functions, but rather neural response functions. Since the publication of seminal papers on the relation between neural spiking and subjective experience (Shadlen, Britten, Newsome, & Movshon, 1996; Sheinberg & Logothetis, 2001), the assertion is that neural firing can be translated into subjective experience and vice versa.

Review of input gain, response gain and baseline shift

The contrast response function in single unit recordings and fMRI

Low level visual processing has been widely studied using experiments in which stimulus contrast is parametrically varied. In a seminal paper, Albrecht & Hamilton (Albrecht & Hamilton, 1982) studied the response of neurons in cat primary visual cortex to stimuli of different luminance contrast. They observed a sigmoidal increase of firing rate with contrast (Figure 3) which is very similar to the above mentioned psychometric function. (Figure 1).

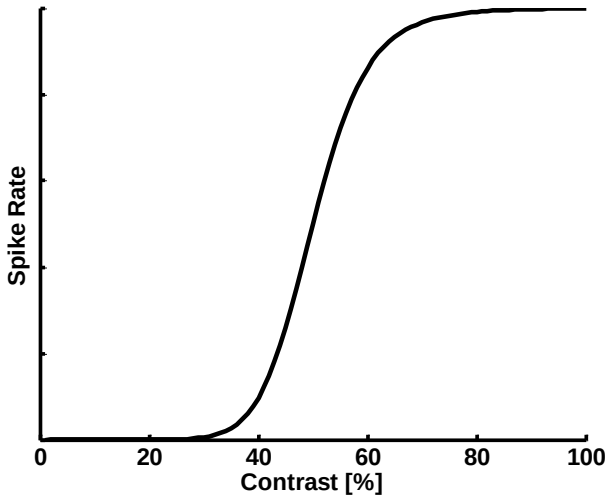

Figure 3: Hypothetical neural response is shown as a function of feature strength, e.g. stimulus contrast. Neural activity increases as a function of stimulus strength.

They mathematically described the neural contrast response function with the Naka – Rushton function (Naka & Rushton, 1966) taking the following form:

$$R(c) = \frac{R_{max} C^n}{C^n + {C_{50}}^n} + B \tag{1}$$

In this equation *R(c)* represents the predicted neural response as a function of contrast. R_{max} is the maximum attainable response. *C* is the contrast level. C_{50} is the semi-saturation contrast, namely the stimulus intensity at which half of the maximum response is obtained. *n* is the exponent that specifies the slope or steepness of the function. *B* represents the baseline neural activity.

Similar findings have been reported in monkey neurophysiology and monkey fMRI (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001) as well as in human fMRI (Boynton, Engel,

Glover, & Heeger, 1996) with CRFs relating increases in stimulus contrast to increases in brain activity, i.e. spike rates and BOLD amplitude, respectively.

Attentional modulation of stimulus representations

Several neurophysiological studies in monkey V4 (Reynolds, Pasternak, & Desimone, 2000) and MT (Martinez-Truijllo, 2002) have reported a leftward shift of the neural CRF when animals were attending a stimulus compared to when this stimulus was ignored. These data have been interpreted as evidence for the assumption that attention alters appearance by effectively changing stimulus contrast, i.e. contrast gain. In humans, fMRI results have been mixed. Two studies (Li, Lu, Tjan, Dosher, & Chu, 2008; Schwarzbach & De Weerd, 2006) report evidence for contrast gain combined with an unspecific upward or baseline shift of the BOLD CRF. Pure baseline shift has been reported in one monkey-physiology (Williford & Maunsell, 2006) and in one human imaging (Buracas & Boynton, 2007) study.

Other studies (Lee & Maunsell, 2010) find that attention enhances neural responses more as contrast increases, indicating a response gain mechanism. Much of the research in feature-based attention, i.e. the ability to enhance the representation of image components *throughout the visual field* that are related to a particular feature, is concerned with the change of tuning curves by attention. Tuning curves depict the response strength (neural response, hemodynamic response or average performance of an observer) as a function of the value of a particular stimulus parameter. For instance, a direction tuning curve describes the sensitivity to visual motion in various directions (Albright, 1984; Dubner & Zeki, 1971). A typical finding for orientation tuning in V1 and V4 (Maunsell et al., 1999) and for tuning to direction of motion in MT (Cook & Maunsell, 2004; Treue & Maunsell, 1999) is that attention acts by multiplying the

neuronal firing rate by a constant factor, a phenomenon known as response gain (Figure 2B) or feature similarity gain.

Despite the variability of these findings, there is a growing consensus that contrast gain may be particularly linked to spatial attention, while response gain may pertain to feature-based attention (Boynton, 2009). The role of baseline shift is rarely discussed beyond the speculation that baseline shift might reflect changes in overall arousal.

Using Random Dot Motion patterns in attention research

Random dot motion (RDM) patterns allow for the study of both space-based and feature-based attention. RDM patterns comprise signal dots moving coherently with the same speed in the same direction and noise dots that move randomly.

Random dot displays are one of the standard displays used to investigate motion processing in behavioral, neurophysiological and neuroimaging studies. They consist of a sequence of several frames in which dots move through space and time to evoke direction and speed percepts at some level of coherence (Figure 4). RDM stimuli allow relative motion energy in a given direction to be manipulated with respect to direction, speed, colour, contrast, coherence, size, and density of dots as well as by the position and size of the aperture in which dots are displayed, making RDMs an excellent candidate for studying the effects of attention on parametrically varied feature strength.

A B C

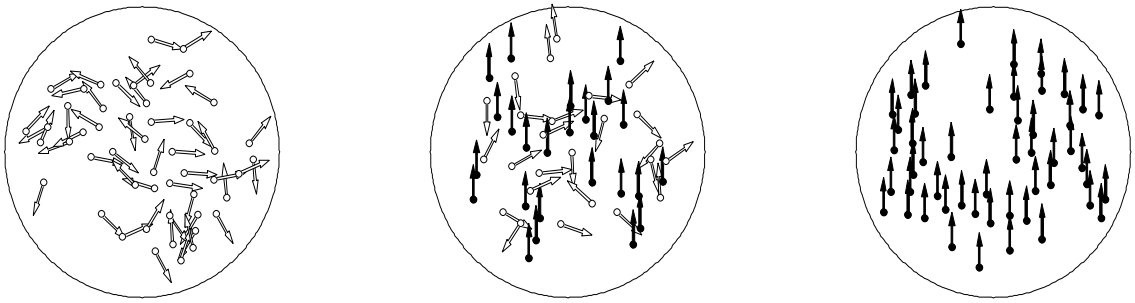

Figure 4: RDM displays. At 0% coherence, all dots move in a random direction on successive frames (A). At 100% coherence, all dots move in a fully coherent fashion in one direction (C). For intermediate levels of coherence, the dots fall into two populations: signal dots (black) that move coherently and noise dots (white) that move randomly (B).

RDMs allow us to determine another type of psychometric function, namely the coherence response function (Britten, Shadlen, Newsome, & Movshon, 1992), which depicts the strength of subjective experience of dots moving in the same direction as a function of coherence (see Figure 4 and Figure 5).

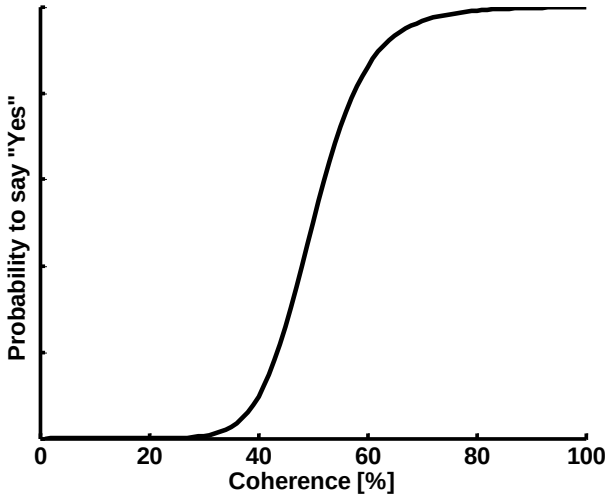

Figure 5. Hypothetical Coherence Response Function. The probability of reporting "yes, dots are moving in the same direction" is shown as a function of motion coherence. Typically, the probability that observers will respond "yes" increases with coherence.

Behavioral studies have demonstrated that attention alters the perception of coherence, leading to a leftward shift of the coherence response function similar to what would be expected for input gain (Liu, Fuller, & Carrasco, 2006).

Goals of this thesis

We rarely have the opportunity to perform single unit recordings in humans (with the notable exception of Engel, Moll, Fried, & Ojemann, 2005; Quiroga, Reddy, Kreiman, Koch, & Fried, 2005; Slotnick, Moo, Kraut, Lesser, & Hart, 2002). However, the recent development of noninvasive methods for assessing brain activity, such as fMRI, have led to the attempt to identify brain mechanisms underlying cognitive processing in humans. While fMRI holds great promise, its limits have recently been pointed out (Bartels, Logothetis, & Moutoussis, 2008; Logothetis, 2008). The main conclusion to be drawn from these papers is that fMRI is not a low-resolution (in terms of space and time) surrogate for measuring spiking activity by means of single unit recordings, but a technique in its own right. One of the possible strengths of fMRI may lie in the fact that it is highly sensitive to neuromodulation of synaptic activity (Logothetis et al., 2001), which is the level on which attention is thought to operate (Logothetis, 2008).

Here I want to investigate by means of fMRI how attention alters appearance of coherently moving dots. As laid out above, three possible mechanisms have been proposed to account for the modulation of appearance through the modulation of underlying brain activity. Contrast gain, response gain, or baseline shift. Each of these would lead to a distinct pattern when comparing the coherence response functions for attended and unattended RDMs. Below, I will report two fMRI experiments. The first experiment assesses coherence response functions for RDMs of different contrast levels when participants ignore the RDMs. This experiment will show what

kind of response pattern should be expected with fMRI if attention alters appearance by means of a contrast gain mechanism. In the second experiment I assess coherence response functions when physical contrast is kept constant, but participants either attend or ignore the stimulus. In the General Discussion a synthesis of the two experiments will be attempted.

Chapter 2

Experiment 1: The Effect of Contrast on Coherence Response Functions

Introduction

Many studies in neurophysiology report a significant increase in the response of MT neurons when dots are moving coherently compared with randomly moving dots (Newsome & Pare, 1988). In the past few years these findings have been replicated in humans using neuroimaging (Braddick et al., 2001; Tootell et al., 1995; Zeki et al., 1991). The relation between motion coherence and neural responses has been described as log-linear in both monkey (Heuer & Britten, 2007) and human brain (Rees, Friston, & Koch, 2000).

The motion processing complex is sensitive to contrast as well, as it was shown in neurophysiology (Heuer & Britten, 2002) and neuroimaging studies (Tootell et al., 1995). The relation between contrast and neural activity has been described to be log – linear both in monkey brains (Martinez-Truijllo, 2002) and in human brains (Gardner et al., 2005).

It is has been reported that contrast could affect some motion features such as speed (Thompson, 1982), but nothing is known about the possible effect of contrast on motion coherence. This interaction has never been explored with the fMRI before, so this study can provide important information about the relationship between these two visual dimensions.

The effect of contrast level on BOLD coherence response functions is an important step towards understanding how attention might modulate the processing of coherence. Several authors argue that attention alters appearance by increasing stimulus contrast (Carrasco et al., 2004). Thus,

assessing coherence response functions under different contrast levels serves as an emulation of what one would expect in an attention experiment on processing of coherence.

The aim of this paper is to assess (a) whether we are able to measure with BOLD changes in contrast and coherence, (b) whether a parametric modulation of contrast leads to a modulation of the coherence response function. Our predictions are that (a) the hemodynamic response increases as a function of both contrast and coherence and that (b) an increase of contrast leads to a leftward shift of the coherence response function.

To this aim we conducted two independent experiments. The purpose of the first experiment was to localize individually the human motion complex (hMT+) allowing us also to determine middle temporal (hMT) and medial superior temporal (hMST) cortex individually for each participant. The purpose of the second experiment was to test whether we can measure variations in the feature dimensions with BOLD.

hMT/hMST localizer

Methods

Participants

Five participants took part in this experiment (2 females and 3 males, mean age 27.3). All of them had normal or corrected-to-normal vision. None of the participants had any prior psychiatric or neurological history, and all were medically screened. Informed consent was obtained after the explanation of the experiment. Participants were paid for the time spent doing the experiment. The study protocol was approved by the ethics committee of the University of Trento.

Visual stimulation

Visual stimuli were generated using inhouse software (ASF, available from JS) which builds upon the psychophysics toolbox (Brainard, 1997; Pelli, 1997) for MATLAB 7.7 (Mathworks Inc, Natick, MA, USA). Images were presented with a liquid crystal display projector EPSON EMP 9000 to a screen at the head end of the scanner bore and they were viewed via a mirror mounted on the head coil. Stimulus presentation was synchronized with MR data acquisition by triggering the stimulus program with the first MR pulse. Stimulus timing was controlled by synchronization to the vertical refresh signal of the projector which ran at 60Hz. Stimuli were composed as one patch of white moving dots presented on gray background. Each dot subtended 0.25° and moved at a speed of 8°/s, with a density of 10 dots/degree^2 and a luminance of 72 cd/m^2. All the dots were moving coherently, i.e. moving in the same direction for two or more frames. Dots had a lifetime of 10 frames with an initial random age between 1 and 10 frames at the onset of the stimulus. Moving dots moved in one of eight directions (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°) with two levels of speed (0°, 8°/sec) and a contrast of 35%. Electrophysiological studies in monkey MT (Sclar, Maunsell, & Lennie, 1990; Thiele, Dobkins, & Albright, 2000) have shown that this contrast level leads to saturation in spike rate and BOLD in the respective motion-sensitive areas. Dots leaving the border of the aperture were replaced by dots entering in the aperture from the opposite side. The patch of dots was shown inside a circular aperture of 6° diameter, placed at the right side of the center of the screen with its center at an eccentricity of 10°. We presented moving dots or stationary dots to the left or right of fixation in a 2 by 2 block design. Stimulation blocks of 16s alternated with 16s of fixation. Each combination of conditions

was repeated 4 times leading to 16 stimulation blocks and an overall length of the experiment of 9 minutes

Procedure

Each block started with the presentation of a central fixation point, which remained on the screen throughout the block. After 16 seconds a circular aperture appeared to the left of the central fixation point in which the moving dots were presented. The direction of moving dots and the color of the central fixation point changed every 500 ms in order to avoid habituation. The direction of moving dots changed randomly to one of the eight directions while the color of the fixation changed randomly to one of four colors (red, blue, green, yellow). The speed of dots changed between blocks in a factorial design. There was a 16s period between stimulation blocks in which only the fixation point was shown. To ensure that participants kept their eyes at fixation throughout the entire experiment, they were instructed to pay attention to the color of the fixation dot and to press the response button whenever the fixation cross turned red (See Figure 6).

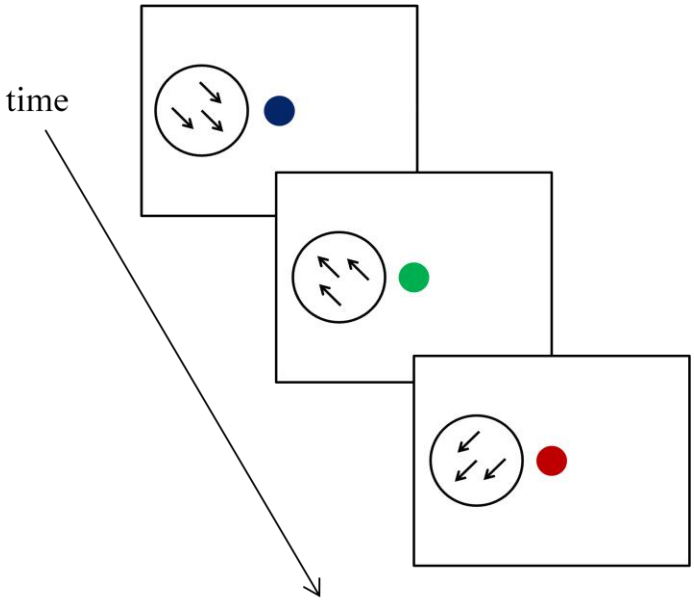

Figure 6. Procedure. A colored central fixation point was shown for 16 seconds (rest condition). Then a circular aperture was presented to the left of the point for other 16 seconds (stimulation condition). Black arrows represent the motion direction and velocity of coherently moving dots. During the stimulation the fixation color and the motion direction changed every 500 ms. Participants had to signal by button press whenever the central fixation point turned red.

Data acquisition

Magnetic resonance images were obtained with a 4-Tesla Bruker MedSpec scanner with an eight-channel array head coil. Functional data were acquired during 1 scanning run of 256 volumes using an Echo Planar Imaging sequence (EPI, 34 slices, even-odd ascending interleaved acquisition order, field of view 192mm x 192mm, slice thickness 3mm, voxel size 3x3mm, gap size = 0.45mm, TR = 2000ms, TE = 33ms, flip angle = 74°). Functional slices were aligned to a high – resolution anatomical (T1-weighted) data set acquired in the middle of each scanning session (i.e., after 4 functional runs) using a Magnetization-Prepared Rapid Gradient Echo sequence (MP-RAGE, 176 axial slices, field of view 256mm x 224mm, 1-mm isotropic voxels, Generalized autocalibrating partially parallel acquisition (GRAPPA) with acceleration factor = 2, TR = 2700ms, TE = 4.180ms, TI = 1020ms, flip angle= 7°). An additional Point Spread Function

scan (PSF) was acquired at the beginning of the run in order to (a) reduce distortion in regions of high-field inhomogeneity and (b) to correct geometric and intensity distortions whether the voxels overlap in the distorted image (Zaitsev, Hennig, & Speck, 2004; Zeng & Constable, 2002).

Data analysis

Data analysis was performed using Brain Voyager QX (version 1.10.4, Brain Innovation, Maastricht, The Netherlands) in combination with Matlab 7.7.

Preprocessing

The functional scan was corrected for slice scan time (using trilinear interpolation) and for 3D head motion by aligning them to the first volume of the respective run using rigid body transformation and trilinear interpolation. Linear trends and low frequency drift were removed from the data using a temporal high-pass filter of 3 cycles/scan. The first three volumes of were discarded in order to remove T1-saturated images from the time series data. The first of the removed volumes was used as a reference to which all the functional data from the same run were coregistered. Then the data were spatially smoothed with an 8 mm kernel (FWHM) and spatially normalized across participants by transforming each data set to standard Talairach space (Talairach & Tournoux, 1988).

Definition of regions of interest (ROI)

We localized the human motion complex following a standard procedure for fMRI (Huk, Dougherty, & Heeger, 2002) that labels hMT as an area that is sensitive to contralateral motion only, while labeling those voxels that are sensitive to ipsi- and contralateral motion as hMST.

Regions of interest were functionally defined separately for each participant. Human MT+ was defined by comparing contralateral moving dots with contralateral stationary dots. Then hMT+ was divided in two sub-regions. Human MST was defined as the sub-region activated both by contralateral and ipsilateral stimulation, while hMT was defined as the sub-region activated by contralateral stimulation only. We defined hMT as that set of voxels in hMT+ that had no overlap with hMST.

Results

Since the stimulation was presented in the left visual field, from now on we will focus on one region of interest only, namely hMT+ in the right hemisphere. We were able to define this area in all the participants. Table 3 and 4 in the appendix depict the average and individual locations.

Main Experiment

Methods

Participants

The same 5 participants for whom we collected the localizer-data took part in the main experiment.

Visual stimulation

Visual stimuli were generated using inhouse software (ASF, available from JS) which builds upon the psychophysics toolbox (Brainard, 1997; Pelli, 1997) for MATLAB 7.7 (Mathworks Inc, Natick, MA, USA). Images were presented with a liquid crystal display projector EPSON EMP 9000 to a screen at the head end of the scanner bore and they were viewed via a mirror mounted on the head coil. Stimulus presentation was synchronized with MR data acquisition by triggering the stimulus program with the first MR pulse. Stimulus timing was controlled by synchronization to the vertical refresh signal of the projector which ran at 60Hz. Stimuli were composed as one patch of white moving dots presented on gray background. Each dot subtended 0.25° and moved at a speed of 8°/s, with a density of 10 dots/degree^2 and a luminance of 72 cd/m^2. A defined percentage of dots were moving coherently (i.e., moving in the same direction for two or more frames) while the remaining dots were moving randomly (i.e., changing direction on each frame). All dots had a lifetime of 10 frames with an initial random age between 1 and 10 frames at the onset of the stimulus. Coherently moving dots moved in one of four directions (45°, 135°, 225° or 315°) with one of six levels of motion coherence (0, 6.25, 12.5, 25, 50, 100%) and one of six levels of luminance contrast (2.188, 4.375, 8.750, 17.5, 35, 70%). Dots leaving the border of the aperture were replaced by dots entering in the aperture from the opposite side. The patch of dots was shown inside a circular aperture of 6° diameter, placed at the right side of the center of the screen with its center at an eccentricity of 10°. Six levels of motion coherence and six levels of contrast were used in a block design that was fully factorial leading to 36 conditions. Each condition was replicated 3 times, in random order, for a total of 108 blocks presented in a single run that lasted 60 minutes

Procedure

Each block started with the presentation of a central fixation point, which remained on the screen throughout the block. After 16 seconds a circular aperture appeared to the left of the central fixation point in which the moving dots were presented. The direction of moving dots and the color of the central fixation point changed every 500 ms in order to avoid habituation. The direction of moving dots changed randomly to one of the four directions while the color of the fixation changed randomly to one of four colors (red, blue, green, yellow). The respective levels of motion coherence and luminance contrast were kept constant throughout a block, but changed between blocks in a factorial design. There was a 16s period between stimulation blocks in which only the fixation point was shown. To ensure that participants kept their eyes at fixation throughout the entire experiment, they were instructed to pay attention to the color of the fixation dot and to press the response button whenever the fixation cross turned red (See Figure 6).

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Statistical analysis

Each event type was modeled by convolving the event timing with a canonical hemodynamic impulse response function ($\delta = 2.5$, $\tau = 1.25$, Boynton et al., 1996). The resulting reference time-courses were used to fit the percent-signal-change (PSC) transformed time course of each voxel within each region of interest (i.e., hMT and hMST) by means of the general linear model. The output of the general linear model provided us with beta values representing the mean estimate in PSC across participants. Data were submitted to a two – way analysis of variance (ANOVA) for repeated measures with contrast (6) and coherence (6) as within-subject factors, and to *post hoc* testing with polynomial contrasts on the same factors. Data were then fit (via maximum likelihood) to the Naka – Rushton function (Equation 1). To fit the data to each condition (coherence x contrast), we allowed threshold (C_{50}) and slope (n) to vary freely. In fitting the contrast response function, the asymptote was preset with the maximum response at the respective coherence level. In fitting the coherence response function, the asymptote was preset with the maximum response at the respective contrast level.

Results

In area hMT+ the BOLD response increased linearly with coherence (main effect coherence: $F_{(5, 15)} = 10.922$, $p<0.001$; linear trend coherence: $F_{(1, 3)} = 33.496$, $p=0.01$) and contrast (main effect contrast: $F_{(5, 15)} = 22.428$, $p < 0.001$; linear trend contrast: $F_{(1, 3)} = 152.125$, $p < 0.001$). Contrast modulated the BOLD response with the same strength irrespective of the coherence (interaction Contrast x Coherence: $F_{(25, 75)} = 1.375$, $p = 0.147$) (Figure 7). Figure 8 depicts the average BOLD amplitude (ordinate) estimated from the GLM for different contrast levels (abscissa) by stimulus coherence (different panels).

A B

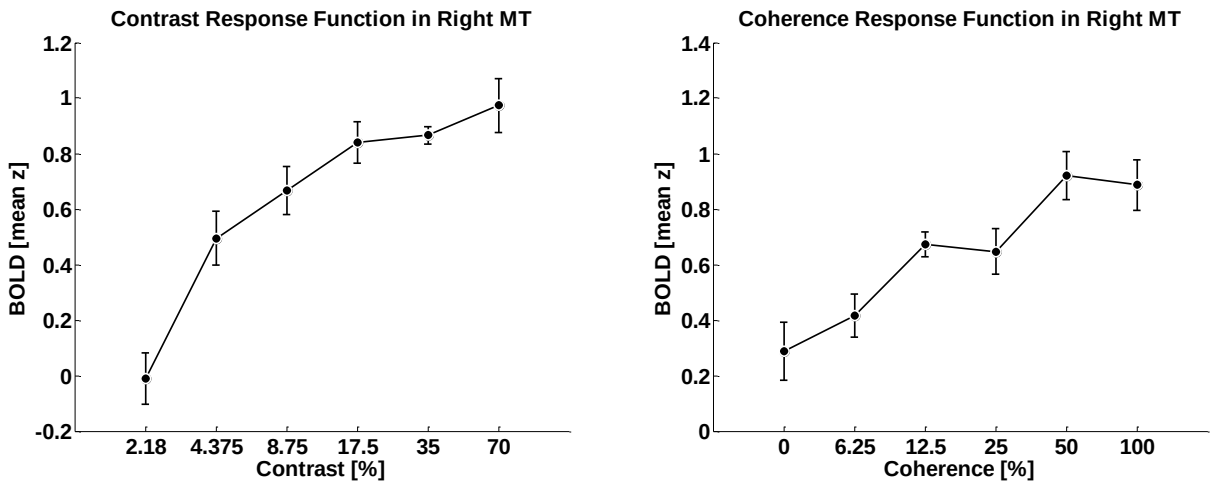

Figure 7. Contrast and coherence response functions in right hMT+. The BOLD response is plotted as a function of stimulus contrast after being averaged across coherence (A) and for each coherence level separately (C). The BOLD response is plotted as a function of stimulus coherence after being averaged across contrast (B) and for each contrast level separately (D). Error bars depict ±SEM.

Contrast response functions reach asymptotic amplitudes for coherence levels of 12.5% and above. Further increase of coherence produced a leftward shift of the contrast response function, i.e. a decrease in the C50, or semi-saturation parameter. See Table 1 for a listing of the fitted parameters.

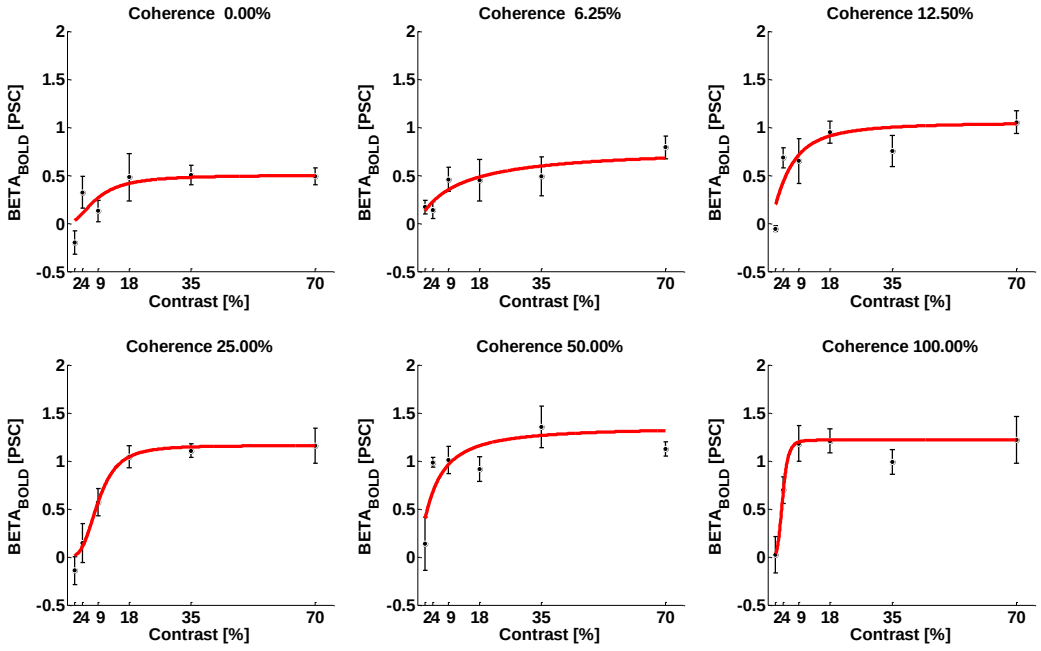

Figure 8. Fitted contrast response functions for different coherence levels. The decrease in the C_{50} (semi saturation parameter) produces a leftward shift of the response function. The asymptotic response (R_{max}) increases with coherence, and reaches the peak at 1.218 PSC. Error bars depict ±SEM.

Coherence	C_{50}	N	R_{max}	R^2
0.00	8.315	2.097	0.503	0.230
6.25	11.097	0.982	0.791	0.527
12.50	5.465	1.586	1.053	0.821
25.00	8.826	3.176	1.160	0.863
50.00	4.311	1.262	1.356	0.717
100.00	4.153	5.455	1.218	0.953

Table 1. Parameters for fitted contrast response functions. Contrast response functions reach asymptotic amplitudes for coherence levels of 12.5% and above. Further increase of coherence produced a leftward shift of the contrast response function, i.e. a decrease in the C50, or semi-saturation parameter.

Coherence response functions reach asymptotic amplitudes for contrast levels of 8.75% and above. Further increase of contrast produced a leftward shift of the coherence response function, i.e. a decrease in the C50, or semi-saturation parameter. See Table 2 for a listing of the fitted parameters.

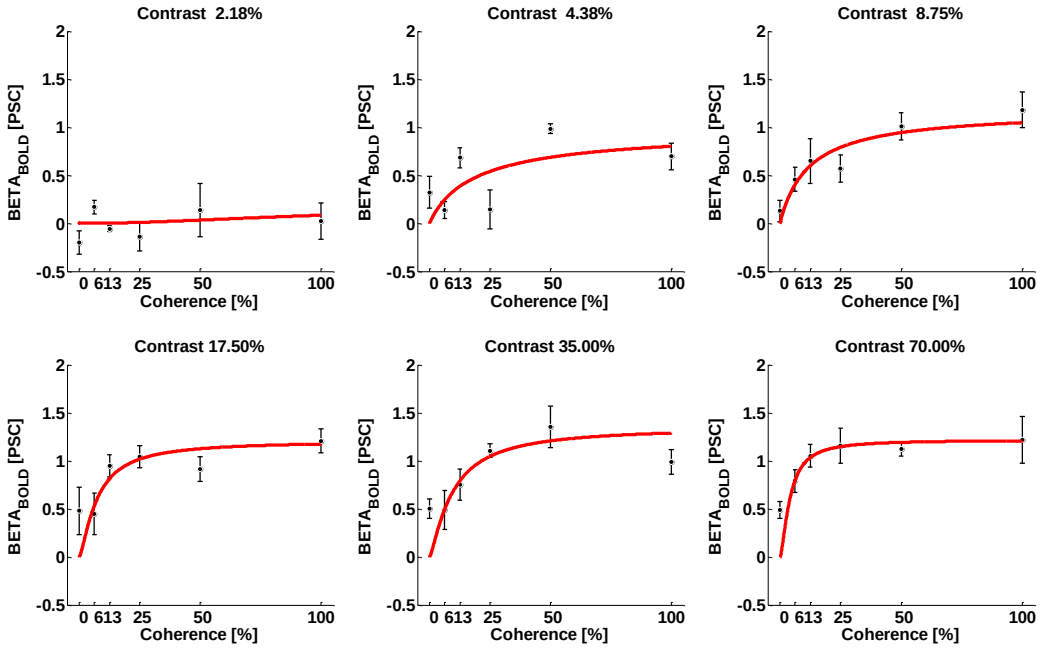

Figure 9. Fitted coherence response functions for different contrast levels. The decrease in the C_{50} (semi saturation parameter) produces a leftward shift of the response function. The asymptotic response (R_{max}) increases with coherence, and reaches the peak at 1.218 PSC. Error bars depict ±SEM.

Contrast	C_{50}	n	R_{max}	R^2
2.180	100.000	1.984	0.169	0.076
4.375	20.281	0.929	0.985	0.331
8.750	12.187	0.978	1.182	0.887
17.500	7.401	1.376	1.208	0.754
35.000	9.588	1.275	1.356	0.732
70.000	4.126	1.557	1.218	0.940

Table 2. Parameters for fitted coherence response functions. Coherence response functions reach asymptotic amplitudes for contrast levels of 8.75% and above. Further increase of contrast produced a leftward shift of the coherence response function, i.e. a decrease in the C50, or semi-saturation parameter.

Discussion

The aim of this experiment was to assess (a) whether we are able to measure with BOLD changes in contrast and coherence in the human motion complex, and (b) whether a parametric modulation of contrast leads to a modulation of the coherence response function.

To this aim we localized the motion complex hMT+ in five participants. Using hMT+ as a region of interest we estimated the amplitude of the BOLD response in a factorial experiment that varied coherence and contrast. We found coherence response functions for all contrast levels. This is consistent with previous neurophysiological (Newsome & Pare, 1988) and neuroimaging studies (Braddick et al., 2001; Tootell et al., 1995; Zeki et al., 1991) that report both higher spike rate and higher BOLD signal when the visual system is processing coherent motion than when it is processing noise.

Fitting the estimated amplitudes to the Naka-Rushton equation separately for each contrast level we found that the strength of coherence response functions increased with contrast. In particular, at low contrast levels an increase of contrast changed the asymptote and C50. At higher contrast levels we observed that the coherence response functions started to saturate (constant asymptote), and only C50 decreased with increase of contrast. In other words, at higher contrast the entire coherence response function shifted leftwards when contrast was increased. This finding is the typical finding to be expected for contrast gain. In terms of the underlying neural activity this is not surprising, however it is important to establish such a finding in fMRI, since as has been argued before (Bartels et al., 2008; Logothetis, 2008) "*... fMRI is highly compelling in its own right – comparisons with spiking data can be interesting, but they can hardly be*

deduced on the basis of fMRI signals" and vice versa. To our knowledge this is the first study to show that contrast gain, in principle, is detectable by means of fMRI.

It has to be noted, though, that what may look like contrast gain here, i.e. a leftward shift of the coherence response function, leaves open the possibility that the underlying mechanism is response gain. As has been pointed out in the introduction, the range of the neural signal as well as the BOLD signal has its upper limit after which any increase of stimulus intensity leads to saturation. Any study that wants to distinguish between contrast gain and response gain, thus has to ensure that stimulus intensity levels are chosen such that saturation is avoided, see e.g. Reynolds (Reynolds et al., 2000), who used nonoptimal stimuli when studying gain in V4 neurons to avoid saturation. Our strategy for the next experiment is therefore to avoid saturation when probing the effects of attention on the coherence response function by using suboptimal, that is low to medium contrast, stimuli.

Chapter 3

The following chapter reports the original submitted manuscript of our second experiment. In this experiment we measured the effect of motion coherence by comparing the BOLD response of attended with the BOLD response unattended condition.

Experiment 2: The effect of attention on motion coherence

Introduction

Natural scenes contain more information than the visual system can process at once. Visual attention is the perceptual mechanism by which observers select important aspects of a scene for further processing, for example by biasing processing of the attended with respect to the ignored stimulus (Desimone & Duncan, 1995). In line with this view, there exists a growing body of electrophysiological (Martinez-Truijllo, 2002; Reynolds & Chelazzi, 2004; Reynolds et al., 2000; Williford & Maunsell, 2006), behavioural (Carrasco et al., 2004) and imaging (Buracas & Boynton, 2007; Li et al., 2008; Schwarzbach & De Weerd, 2006) data that suggest that attention enhances processing of stimulus contrast (see Boynton, 2009 for a review). Recently, three mechanisms for attentional modulation of contrast-processing (input-gain, response-gain, baseline shift) have been debated, based on experiments which parametrically varied the luminance-contrast of stimuli that were either attended or ignored (see Figure 10). Several electrophysiological recordings from monkey V4 (Reynolds et al., 2000) and MT (Martinez-Truijllo, 2002) found a leftward shift of the neuronal contrast response function (CRF), which indicates that attention acts by increasing the effective strength of the attended stimulus (i.e., the perceived contrast), a phenomenon known as input gain (Figure 10A). Other studies exploring

the same question in visual areas V1 and V4 reported an increase of neuronal firing with attention particularly with higher contrast levels, indicating that attention acted by multiplying the neuronal firing rate by a constant factor (McAdams & Maunsell, 1999), a phenomenon known as response gain (Figure 10B). Finally, it has been suggested that attention can increase the firing rate of neurons irrespective of variations in the stimulus strength (Williford & Maunsell, 2006), a phenomenon known as baseline shift (Figure 10C).

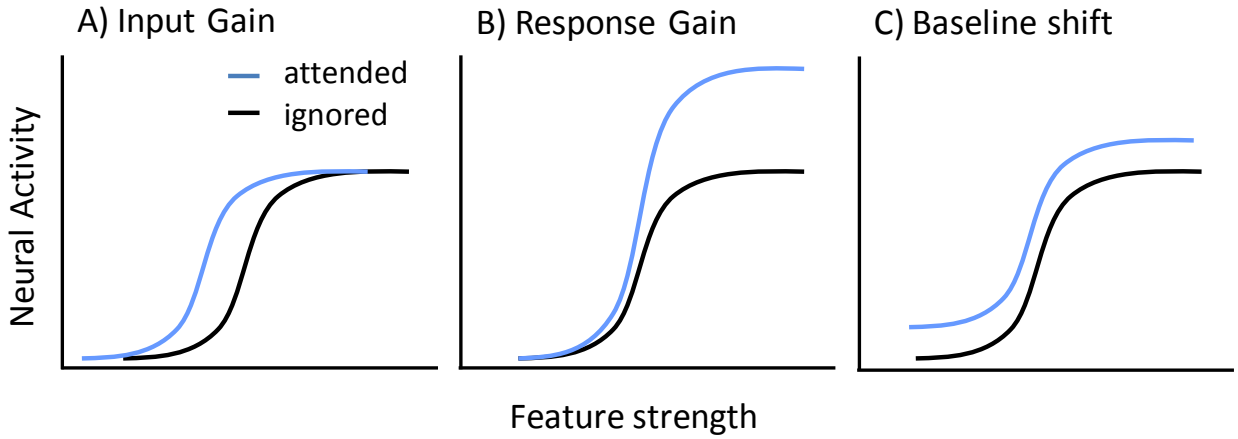

Figure 10. Three putative mechanisms of attention. Neural activity or its hemodynamic correlate is shown as a function of feature strength (e.g., contrast or motion coherence) when stimuli are ignored (black lines) or attended (blue lines). In passive viewing, neural activity increase in a sigmoidal fashion as a function of stimulus strength. When stimuli are attended, neural activity may be modulated differently according to the proposed mechanisms of input gain (A), response gain (B) or baseline shift (C).

Several human fMRI studies which have investigated the effect of attention on contrast processing in visual cortex reported either only baseline shift for the BOLD-CRF (Buracas & Boynton, 2007) or a mixture of input-gain and baseline shift (Li et al., 2008; Schwarzbach & De Weerd, 2006). Here, we want to test the applicability of gain- and baseline shift mechanisms to other stimulus features than contrast, namely motion coherence whose parametric variation is also known to lead to a parametric change in the BOLD signal (Rees et al., 2000). Since motion

coherence, i.e. the percentage of dots moving together in a random dot kinematic display, has been intensively studied in neurophysiological experiments with non-human primates, it provides excellent opportunities to link human imaging studies of attention with monkey electrophysiology (Bartels et al., 2008; Rees et al., 2000). We have focused our investigation on the middle temporal and on the medial superior temporal areas. Together, these areas form the human motion complex (hMT+), that is the human homologue of macaque area V5 (Allman & Kaas, 1971; Dubner & Zeki, 1971). Both hMT+ and V5 share the same functional properties, namely they are strongly driven by motion (Tootell & Taylor, 1995; Zeki et al., 1991), and they are sensitive to motion coherence (Heuer & Britten, 2007; Newsome & Pare, 1988). Furthermore neurons in the motion complex are substantially modulated by attention (Beauchamp, Cox, & DeYoe, 1997; Martinez-Truijllo, 2002; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Treue & Maunsell, 1996, 1999; Williford & Maunsell, 2006). The purpose of this study was to measure the effect of attention on the BOLD signal in hMT and hMST cortex for a range of different levels of motion coherence while participants had to judge the predominant direction of moving dots. Attention was either directed to or withdrawn from the stimulus. Our predictions were the following. First, in the absence of attentional modulation, we expected to find a modulation of the BOLD signal as a function of motion coherence, i.e. a Coherence Response Function (CohRF). Second, attention should modulate the CohRF similar to what has been reported above for contrast response functions. Using the BOLD signal to unattended stimuli as our reference, attention should either shift the CohRF to the left (input gain, Figure 10A), particularly increase the signal for high coherence levels (response gain, Figure 10B) or by shifting the entire CohRF upward by a constant amount (baseline shift, Figure 10C).

Methods

We conducted two independent experiments. The purpose of the first experiment was to localize individually the human motion complex (hMT+) allowing us also to determine for each participant areas hMT and hMST. The purpose of the second experiment was to test the effect of attention on BOLD coherence response functions in hMT and hMST.

Participants

Twenty three participants took part in this experiment. Seven participants had to be excluded due to excess head movement during the localizer scan, which prevented defining the regions of interest for the subsequent attention study. Therefore, the following analysis is based on a sample of seventeen participants (8 females and 9 males, mean age 30.0). All of them had normal or corrected-to-normal vision. None of the participants had any prior psychiatric or neurological history, and all were medically screened. An informed consent was obtained after the explanation of the experiment. Participants were paid for the time spent doing the experiment. The study protocol was approved by the ethics committee of the University of Trento.

Visual stimulation

Visual stimuli were generated using inhouse software (ASF, available from JS) which builds upon the psychophysics toolbox (Brainard, 1997; Pelli, 1997) for MATLAB 7.7 (Mathworks Inc, Natick, MA, USA). Images were presented with a liquid crystal display projector EPSON EMP 9000 to a screen at the top of the scanner bore and they were viewed via a mirror mounted on the head coil. Stimulus presentation was synchronized with data acquisition by triggering the stimulus program with the first MR pulse. Stimulus timing was controlled by synchronization to

the vertical refresh signal of the projector which ran at 60Hz. Stimuli were composed by one patch of white moving dots presented on gray background. Each dot subtended 0.25° and moved at a speed of 8°/s, with a density of 6 dots/degree2 and a luminance of 72 cd/m2. A defined percentage of dots were moving coherently (i.e., moving in the same direction for two or more frames) while the remaining dots were moving randomly (i.e., changing direction on each frame). All dots had a lifetime of 10 frames with an initial random age between 1 and 10 frames at the onset of the stimulus. Coherently moving dots moved in one of two directions (0° or 180°) with one of five levels of motion coherence (6.25, 12.5, 25, 50, 100%). The patch of dots was shown inside a circular aperture of 15° diameter, placed at the right side of the center of the screen with its center at an eccentricity of 10°. Dots leaving the border of the aperture were replaced by dots entering in the aperture from the opposite side.

Procedure

Each trial started with the presentation of a red central fixation point, which was shown on the screen for 500 ms, followed by an attention-cue that was presented for 750 ms superimposed to the central fixation point. The cue was one of two symbols ("R" or "+"). The "R" indicated to attend the dots on the right and to respond to their predominant motion direction. The cross ("+") indicated to ignore the dots and engage in a central task, in which participants had to respond which arm of the cross disappeared. The cue was followed by the presentation of a circular aperture to the right of the central fixation point in which the moving dots were presented. Motion direction of coherently moving dots (i.e., 0° or 180°) was assigned randomly in each trial. After 1000 ms, the patch of dots disappeared and the central fixation point turned green, allowing the participants to respond. After 1000 ms, the green central fixation point disappeared.

The task was to keep the gaze on the fixation point and report via button press either the motion direction of the dots (attended condition) or which arm of the cross disappeared (ignored condition). (See Figure 11).

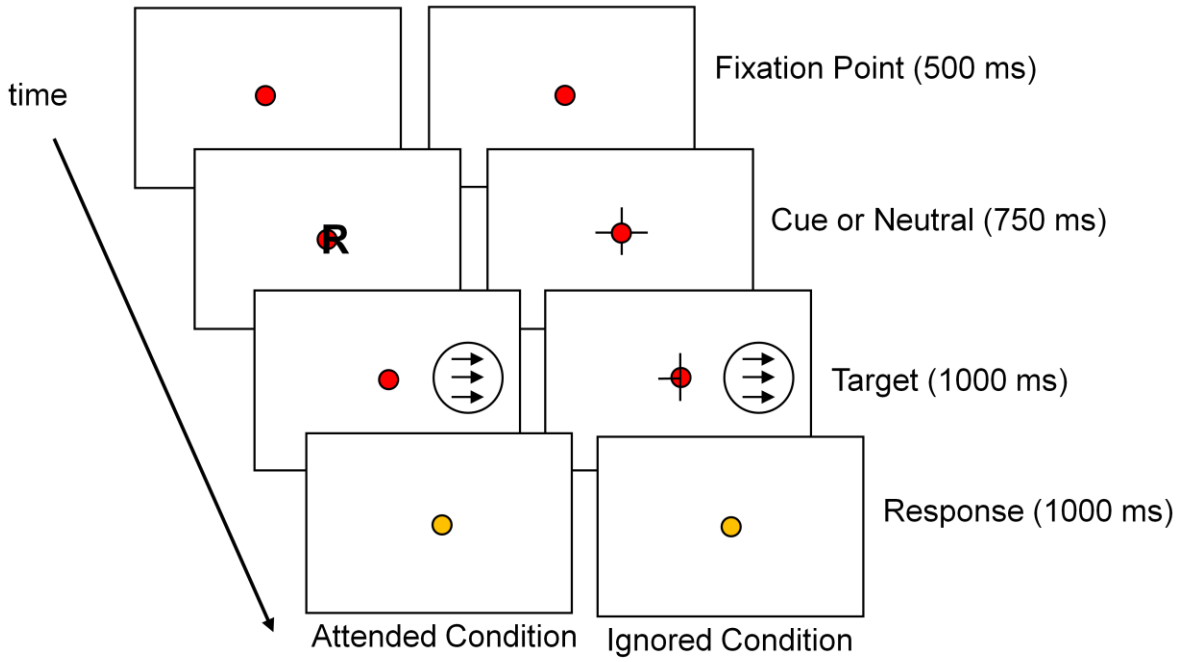

Figure 11. Each trial began with the presentation of a central fixation point (500ms), followed by the presentation of a cue (750 ms). In the attended condition (left panels), the letter R appeared at fixation, instructing participants to covertly attend the patch of moving dots, which was always on the right. After 750ms the letter disappeared and moving dots were shown for 1000ms in a circular aperture to the right of fixation, followed by a green fixation point for 1000ms which served as a marker for the period in which participants were allowed to respond whether dots were moving predominantly to the left or to the right. In the ignored condition (right panels), four arms at fixation forming a cross instructed participants to keep their attention at fixation. As in the attended condition, after 750ms, moving dots were shown for 1000ms in a circular aperture to the right. Either the left or the right arm of the cross disappeared synchronously with the onset of the moving dots. This display was followed by a 1000ms period in which participants were allowed to respond whether the left or the right arm of the fixation cross had disappeared first.

Design

hMT/ hMST localizer

We localized the human motion complex following a standard procedure for fMRI (Huk et al., 2002) that labels hMT as an area that is sensitive to contra – lateral motion only, while labeling those voxels that are sensitive to ipsi – and contra – lateral motion as hMST. The moving stimulus consisted of a circular patch (10° diameter) of dots that moved randomly in one of 8 directions (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°) with a speed of 8°/sec. Dots leaving the border of the aperture were replaced by dots entering in the aperture from the opposite side. The static stimulus had the same visual characteristics but no motion. Stimuli were presented to the left or the right of the fixation point with an eccentricity of 10°. Each dot subtended 0.25° with a density of 10 dots/degree2 and a contrast of 35%. Electrophysiological studies in monkey MT (Sclar et al., 1990; Thiele et al., 2000) and our own pilot studies in hMT+, in which we varied stimulus contrast, have shown that this contrast level leads to saturation in spike rate and BOLD in the respective motion-sensitive areas. Two types of dot motion (stationary, moving) and two sides of presentation (left, right) were used in a block design that was fully factorial leading to 4 conditions. Each condition was replicated 4 times, for a total of 16 blocks. Each block started with the presentation of a central fixation point for 16 seconds. Then the patch of dots was presented for 16 seconds at one side of the central fixation point. The side of presentation and motion of the dots were randomly changed between each block, while the direction of moving dots and the color of the central fixation point changed with a frequency of 500ms in order to avoid habituation. The direction of moving dots changed pseudorandomly to one of the eight directions. To ensure that participants kept their eyes at fixation throughout the

localizer experiment, they were instructed to pay attention to the color of the fixation dot, which changed pseudorandomly to one of four colors (red, blue, green, yellow) with the restriction that color and direction must change between trials. Participants were asked to press the response button whenever the fixation cross turned red.

Attention experiment

Moving dots were presented to the right of fixation. We used unilateral stimulation only in order to prevent crosstalk of ipsilateral hMST and contralateral hMT stimulation. Five motion coherence levels, two attentional levels (attended, ignored) and two predominant motion directions (leftwards, rightwards) were used in a fully factorial event – related design. We presented stimuli at low contrast of 1.5% in order to avoid saturation of neural activity in hMT+. In behavioral pilots at different contrast levels we ensured that participants produced a psychometric coherence response function. An example sequence of events in attended and ignored conditions is depicted in . The dependent variables were the blood-oxygen-level dependent (BOLD) signal and the percentage of correct responses. Each condition was replicated 20 times, in random order, for a total of 400 trials per participant. Each trial was followed by a variable inter-trial interval (ITI) that was jittered between 6 and 10 seconds in steps of 0.5 seconds using a random uniform distribution.

Data acquisition

Magnetic resonance images were obtained with a 4-Tesla Bruker MedSpec scanner with an eight-channel array head coil. Functional data were acquired during 8 scanning runs using an Echo Planar Imaging sequence (EPI, 34 slices, even-odd ascending interleaved acquisition order,

field of view 192mm x 192mm, slice thickness 3mm, voxel size 3x3mm, gap size = 0.45mm, TR = 2000ms, TE = 33ms, flip angle = 74°). Each run consisted of 180 volumes. Functional slices of each run were aligned to a high – resolution anatomical (T1-weighted) data set acquired in the middle of each scanning session (i.e., after 4 functional runs) using a Magnetization-Prepared Rapid Gradient Echo sequence (MP-RAGE, 176 axial slices, field of view 256mm x 224mm, 1-mm isotropic voxels, GRAPPA acquisition with acceleration factor = 2, TR = 2700ms, TE = 4.180ms, TI = 1020ms, flip angle= 7°). At the end of the scanning session we acquired one last functional scanning run (MT/MST localizer). This last scan consisted of 288 volumes using the same imaging parameters as above. An additional Point Spread Function scan (PSF) was acquired at the beginning of the session in order to (a) reduce distortion in regions of high-field inhomogeneity and (b) to correct geometric and intensity distortions whether the voxels overlap in the distorted image (Zaitsev et al., 2004; Zeng & Constable, 2002).

Definition of regions of interest (ROI)

Regions of interest were functionally defined separately for each participant. Human MT+ was defined by comparing contralateral moving dots with contralateral stationary dots. Then hMT+ was divided in two sub-regions. Human MST was defined as the sub-region activated both by contralateral and ipsilateral stimulation, while hMT was defined as the sub-region activated by contralateral stimulation only. We defined hMT as that set of voxels in hMT+ that had no overlap with hMST.

Data analysis

Data analysis was performed using Brain Voyager QX (version 1.10.4, Brain Innovation, Maastricht, The Netherlands) in combination with Matlab 7.7.

Preprocessing

Functional scans were corrected for slice scan time (using trilinear interpolation) and for 3D head motion by aligning them to the first volume of the respective run using rigid body transformation and trilinear interpolation. Linear trends and low frequency drift were removed from the data using a temporal high-pass filter of 3 cycles/scan The first three volumes of each functional run were discarded in order to remove T1-saturated images from the timeseries data. The first of the removed volumes was used as a reference to which all the functional data from the same run were coregistered. Then the data were spatially smoothed with a 4.5 mm kernel (FWHM) and spatially normalized across participants by transforming each data set to standard Talairach space (Talairach & Tournoux, 1988).

Statistical analysis

Each event type was modeled by convolving the event timing with the canonical hemodynamic impulse response function ($\delta = 2.5$, $\tau = 1.25$, Boynton et al., 1996). The resulting reference time-courses were used to fit the percent-signal-change (PSC) transformed time course of each voxel within each region of interest (i.e., hMT and hMST) by means of the general linear model. The output of the general linear model provided us with beta values representing the mean estimate in PSC across participants. Data were submitted to a three – way analysis of variance

(ANOVA) for repeated measures with region of interest (2), attention (2) and coherence (5) as within-subject factors and to *post hoc* testing with polynomial contrasts on the same factors.

Results

Behavioral Data

Behavioral performance increased as a function of motion coherence (main effect "Coherence"; $F_{4,64}=57.501$; $p<0.001$), with higher levels of coherence leading to better performance (linear trend "Coherence"; $F_{1,16}=173.027$; $p<0.001$).

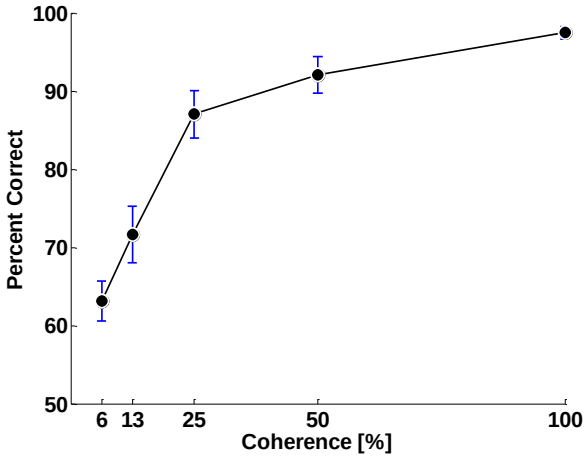

Figure 12. Average behavioral performance (n = 17 participants) for reporting the direction of moving dots (attended condition). Participants' performance clearly depended on coherence level, with higher coherence leading to higher performance. Error bars depict the standard error of the mean.

Region of Interest Analysis

We were able to define hMST and hMT in seventeen participants. Tables 5 and 6 in the appendix depict the average and individual locations. In areas hMST and hMT coherence produced a linear increase in BOLD response (main effect coherence: $F_{4,64} = 3.364$, $p=0.015$; linear trend

coherence F1,16 = 8.379, p=0.011). Coherence modulated the BOLD response equally when dots were attended or ignored (interaction Attention x Coherence: F4,64=0.618; p=0.651). Areas hMST and hMT were substantially affected by attention, with attended moving dots producing a stronger BOLD response than ignored moving dots (main effect Attention: F1,16=34.509; p<0.001). Area hMT responded stronger to moving dots than hMST (main effect "ROI"; F1,16=15.790; p=0.001), but both areas showed the same response pattern with respect to coherence and attention (interaction "ROI" x "Attention": F1,16=2.286; p=0.150; interaction "ROI" x "Coherence": F4,64=1.523; p=0.206; interaction "ROI" x "Attention" x "Coherence": F4,64=0.645; p=0.633). In the attention experiment the BOLD signal was not saturated since the maximal signal change (0.467% in hMST, and 0.639% in hMT) was well below the maximal signal change in the localizer experiment (0.933% in hMST, and 1.0734% in hMT), which was conducted at 100% coherence and 35% contrast as opposed to 1.5% of contrast in the attention experiment.

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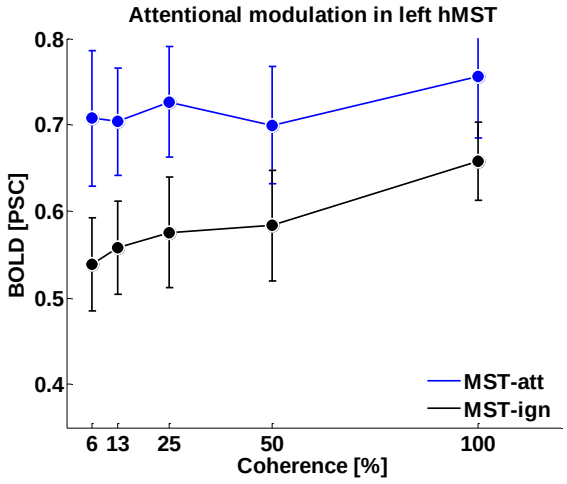

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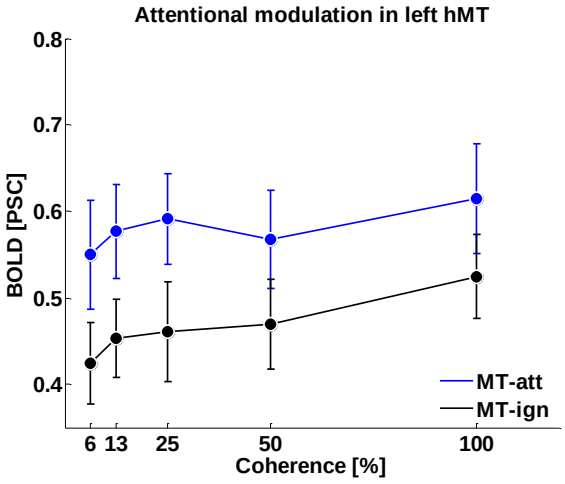


Figure 13: Coherence response functions for areas hMST (A) and hMT (B) for attended (blue) and ignored (black) moving dots. Area hMT responds stronger to moving dots than hMST, but both areas show a modulation by coherence and attention that does not differ between areas. Error bars depict the standard error of the mean.

Discussion

The effect of attention on coherence response functions

We set out to measure the hemodynamic effects of attention and motion-coherence in order to find out by which mechanism attention modulates processing of motion coherence. When participants attended to the moving dots in order to report their predominant direction, behavioral performance increased with stimulus coherence, leading to a behavioral coherence response function (Figure 12). Likewise, we observed coherence response functions in the BOLD signal in both human middle temporal (hMT) and human medial superior temporal (hMST) cortex. Moreover, attending to the moving dots increased the BOLD responses with respect to ignoring the motion stimulus. The effect of attention was additive, i.e. attention affected BOLD responses independently of the level of motion-coherence (Figure 13) These findings applied to hMT as well as to hMST, which differed only in their overall signal strength to moving stimuli. The

observed attentional effects in hMT and hMST can be characterized by a baseline-shift model taking the form

$$R(c) = \frac{R_{max} C^n}{C^n + C_{50}{}^n} + B + A \quad (4)$$

where R(c) is the predicted response as a function of coherence (c), Rmax is the maximum attainable response, c50 is the semi-saturation coherence, or the coherence at which half the maximum response is obtained, and n is an exponent that specifies the slope or steepness of the function. B represents the activity at baseline. A represents the effect of attention. We can exclude that attention directly modulates processing of coherence by increasing the input- or the response gain of coherence signals. Both mechanisms would have led to an interaction of coherence and attention, with the input gain model predicting maximal change at intermediate and the response gain model predicting maximal changes for the highest coherence-levels (see Figure 10). Additionally, we can exclude that we were insensitive to response gain due to saturation of the BOLD signal for high coherence levels since the signal-strength we observed in our main experiment in hMT and hMST was far below the signal strength we have observed in the independent MT/MST mapper that was run using the same stimuli but with 100% coherence and 100% contrast.

What does a baseline shift tell us about attentional modulation?

It has been argued that what underlies attentional modulation of performance is a change in stimulus appearance (James, 1890; von Helmholtz, 1866), in particular the change of apparent

contrast (Carrasco et al., 2004; Reynolds & Chelazzi, 2004), potentially also other stimulus features such as apparent speed (Turatto, Vescovi, & Valsecchi, 2007) or apparent coherence. Attentional modulation by baseline shift of neuronal activation could serve as an attentional bias for stimuli that compete for selection (Desimone & Duncan, 1995). Finding baseline shift-like attentional modulation of a stimulus feature such as motion coherence leaves open three not entirely independent lines of interpretation concerning the underlying mechanisms: First, attention does indeed modulate the feature in question by a baseline shift mechanism, biasing the processing of one stimulus feature at the expense of another (Saenz, Buracas, & Boynton, 2002). Second, since baseline-shift, unlike response- or input-gain, has no differential effects on parametric variations of stimulus features, one might interpret baseline-shift not as feature-based but as spatial attention where stimuli at attended locations are biased to win the competition for selection (Kastner & Ungerleider, 2000; Yantis et al., 2002) without changing the gain in feature processing. Third, attention might not modulate the feature under scrutiny at all, but it modulates instead a different stimulus feature such as speed or contrast that has been kept constant in a given experiment (see Williford & Maunsell, 2006 for a similar argument). If that were the case here, this would still mean that attention does not lead to gain-changes in processing coherence in hMT+. There is no agreement as to which of the three attention models explains best attentional modulation of stimulus features. A recent theoretical paper {Reynolds, 2009 #354) tries to reconcile the variety of effects on the responses of neurons in electrophysiological studies in monkey, by taking into account stimulus- and receptive field size, however that proposal only discusses input- and response gain. The situation is further complicated when trying to explain lack of agreement between above mentioned studies and human fMRI data, which so far has exclusively shown evidence for input gain and baseline shift. The authors of a previous fMRI

study that found that attention primarily induced a baseline shift in contrast processing (Buracas & Boynton, 2007) argued that the BOLD response is pooled over all neurons in a voxel, responsive and non-responsive ones. Therefore fMRI results in attention studies might in general be dominated by changes in baseline firing rates, which have been found to increase with attention (Luck, Chelazzi, Hillyard, & Desimone, 1997). However, there have been successful demonstrations of input gain with fMRI as well (Li et al., 2008; Schwarzbach & De Weerd, 2006). Yet, there may be a bias in fMRI against finding response gain, which could lie in the nature of the signal that reflects rather synaptic than spiking activity (Logothetis et al., 2001). Our data do not allow to finally decide whether input gain, response gain or baseline shift ultimately accounts for attentional modulation of processing motion coherence. However, our results provide constraints for the development of physiologically plausible models by making input- or response gain less likely to be the underlying mechanisms in attentional modulation of coherence processing.

Chapter 4

General discussion

I have reported two experiments in which we have tried to address the centuries-old debate on whether attention alters appearance and how this might actually be implemented in the brain. I started by pointing out the obvious similarities between psychometric functions and neural response functions. The former relate stimulus strength to subjective experience or rather its overt behavioral response, such as pressing a button to indicate that a stimulus of certain strength has been seen (Figure 14), while the latter relate stimulus strength to an objective measure of neural response strength..

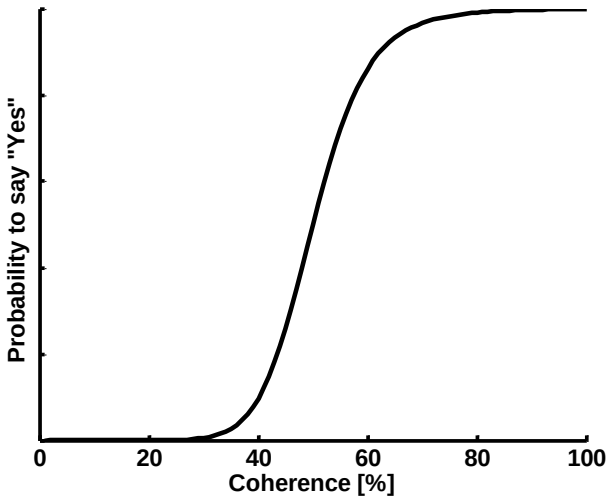


Figure 14. Hypothetical Coherence Response Function. The probability of reporting "yes, dots are moving in the same direction" is shown as a function of motion coherence. Typically, the probability that observers will respond "yes" increases with stimulus intensity.

This similarity between psychometric and neural response functions has led researchers in fact to using the same equations for describing subjective experience, i. e. psychometric functions, and measures of brain activity, such as spike rate or BOLD amplitude. For example neural as well as

psychometric contrast response functions in vision can be mathematically captured by the Naka-Rushton function

$$R(c) = \frac{R_{max} C^n}{C^n + {C_{50}}^n} + B \tag{1}$$

In this equation *R(c)* represents the predicted response as a function of contrast. R_{max} is the maximum attainable response. *C* is the contrast level. C_{50} is the semi-saturation contrast, namely the stimulus intensity at which half of the maximum response is obtained. *n* is the exponent that specifies the slope or steepness of the function. *B* represents the baseline neural activity.

It has been argued that attention alters appearance, however the mechanisms are debated. Three different types of mechanisms are currently discussed. A) Input (or contrast) gain, B) Response Gain and C) Baseline Shift (Figure 15). The mathematical expansion of the three mechanisms in the context of the Naka-Rushton function is given by the three equations below:

For the input/contrast gain model:

$$R(c) = \frac{R_{max} A C^n}{A C^n + {C_{50}}^n} + B \tag{2}$$

For the response gain model:

$$R(c) = A\frac{R_{max}C^n}{C^n + C_{50}{}^n} + B \tag{3}$$

For the baseline-shift model:

$$R(c) = \frac{R_{max}C^n}{C^n + C_{50}{}^n} + B + A \tag{4}$$

Attention operates as a multiplicative factor of contrast in the input gain model, as a multiplicative factor of overall activity in the response gain model, and as an additive factor in the baseline shift model. The resulting predictions for attention effects pertaining to the respective models are visualized in Figure 15.

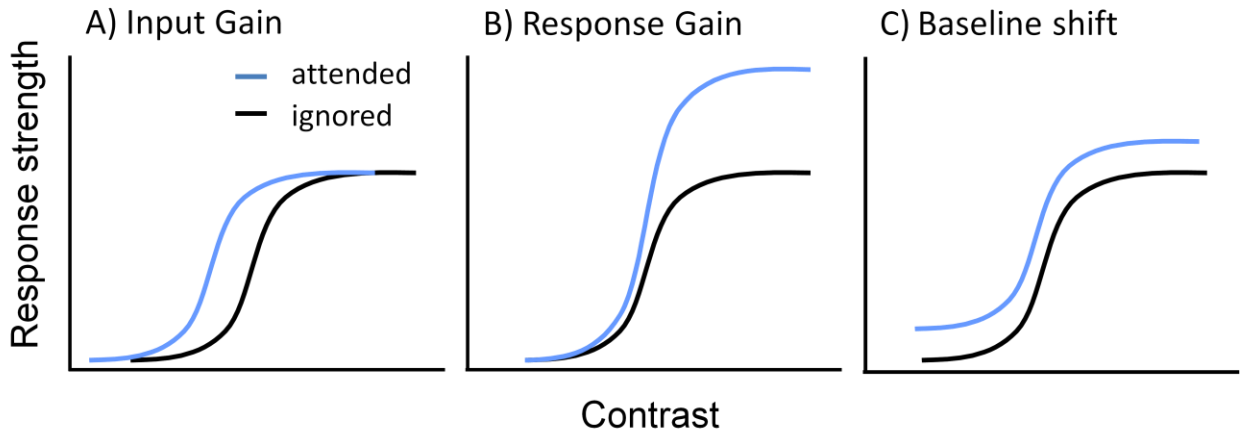


Figure 15. Three putative mechanisms of attention. Response strength (can be subjective report or some measure of brain activity) is shown as a function of contrast when stimuli are ignored (black lines) or attended (blue lines). In passive viewing, performance increases in a sigmoidal fashion as a function of contrast. When stimuli are attended, performance may be modulated differently according to the proposed mechanisms of input gain (A), response gain (B) or baseline shift (C).

Neurophysiological (Britten, Shadlen, Newsome, & Movshon, 1993) and human imaging studies (Rees et al., 2000) have shown that monkey MT and its human homologue hMT+ react parametrically to an increase of motion coherence, and that these effects are paralleled by psychometric coherence response functions in humans (Britten et al., 1992).

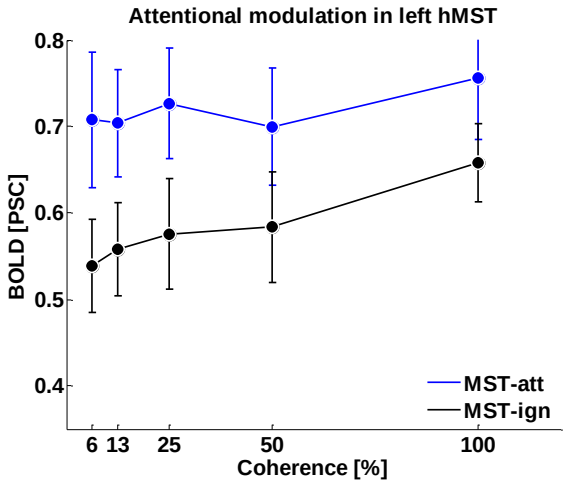
In my thesis I conducted two experiments. The first experiment aimed at assessing coherence response functions for RDMs of different contrast levels when participants ignored the RDMs. This experiment shows what kind of response pattern should be expected with fMRI if attention alters appearance by means of a contrast gain mechanism. In the second experiment I assessed coherence response functions when physical contrast was kept constant, with participants either attending or ignoring the stimulus.

In this General Discussion I attempt a synthesis of the two experiments. Experiment 1 provided the first fMRI evidence for the assumption that processing of motion coherence is susceptible to contrast gain: Moving from intermediate to high contrast we found a leftward shift of the coherence response function. However, we concluded that a study that aims at investigating attentional gain modulation needs to use suboptimal stimuli in order to avoid response saturation. Therefore we used low contrast stimuli in our second experiment, in which we assessed coherence response functions with and without attention.

In Experiment 2 we replicated our finding of coherence response functions with fMRI. Additionally, participants either attended or ignored the stimuli. We observed a clear modulation

of the BOLD amplitude with attended stimuli producing a substantially larger BOLD response than ignored ones. The main finding of this experiment however was the shape of the attentional modulation: With attention, the BOLD response increased by the same amount for all coherence levels. This result is compatible with the predictions of the baseline shift model, but neither with the input gain-, nor with the response gain account. It is important to note, that the choice of stimulus parameters in experiment 2 was based on the results of experiment 1 such that it would be possible to observe input gain or response gain, should one of these mechanisms underlie attentional modulation of coherence. Remember that low contrast levels in experiment 1 allowed the BOLD response to still increase, thus avoiding saturation, and that increases in contrast led to a leftward shift. Therefore we have strong reason to assume that our finding of baseline shift is sound (Figure 16).

A



B

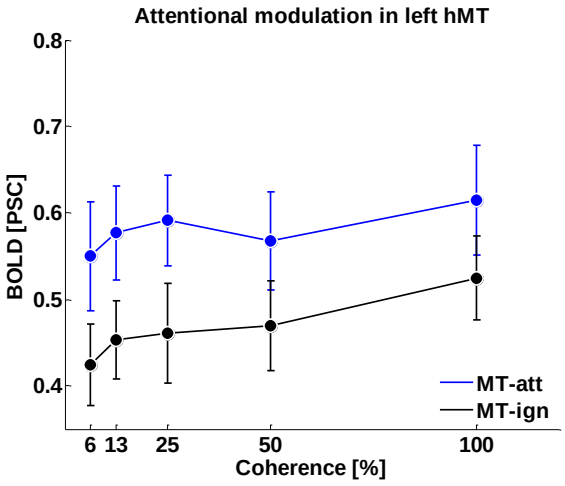


Figure 16: Coherence response functions for areas hMST (A) and hMT (B) for attended (blue) and ignored (black) moving dots. Area hMT responds more strongly to moving dots than hMST, but both areas show similar modulations for coherence and attention. Error bars depict the standard error of the mean.

Here we argue, that since attention only produced a coherence-unspecific effect (same for all coherence levels) that attention does not alter the gain of coherence-processing. At first sight our results seem add odds with the behavioral study of Carrasco and colleagues (Liu et al., 2006) who reported a leftward shift of the coherence response function with attention similar to what would be expected for input gain. However, in our view this is only an inconsistency if one assumes that neural response functions and psychometric functions represent the same.

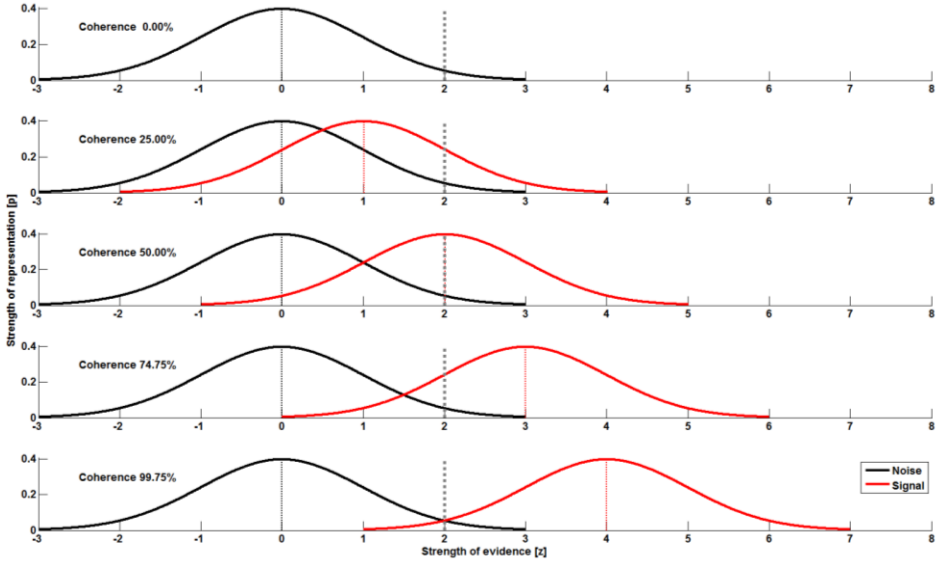
A Signal Detection Account for the effect of baseline shift on perceptual decisions

Below, I want to argue that neural response functions represent the stimuli and that psychometric functions represent the outcome of a decision based on the neural representation. This is the same as looking at our data from a point of view of Signal Detection Theory (Green & Swets, 1966) similarly to the seminal paper of (Newsome, Britten, & Movshon, 1989). The basic idea is that noise-dots evoke a Gaussian representation of noise (no-coherence) while signal dots contribute to a Gaussian representation of coherence. As the level of coherence increases, the two distributions become more separated on the representational axis for stimulus intensity (increase of d') (see Figure 17).

Assuming that the observer applies some criterion such that she decides to say "yes" for any representational strength that is greater than c, we can derive the probability of "yes" responses from the area of probability density function of the signal that to the right of c. If we do this for different coherence levels we can derive a psychometric function from the strength of neural representations (Figure 18).

If we now, based on our findings in experiment 2, assume that attention simply increases activity irrespective of stimulus parameters such as coherence, we can operationalize this as a rightward shift of both the noise distribution and the signal distribution. Since the psychometric function is derived from the area under the signal distribution to the right of the criterion, this leads to more yes responses for each coherence level with respect to the model without baseline shift. The effect of baseline shift of the neural representation of response strength is thus a leftward shift of the psychometric function although sensitivity (d') remained unchanged.

A SDT simulation for ignored condition



B SDT simulation for attended condition

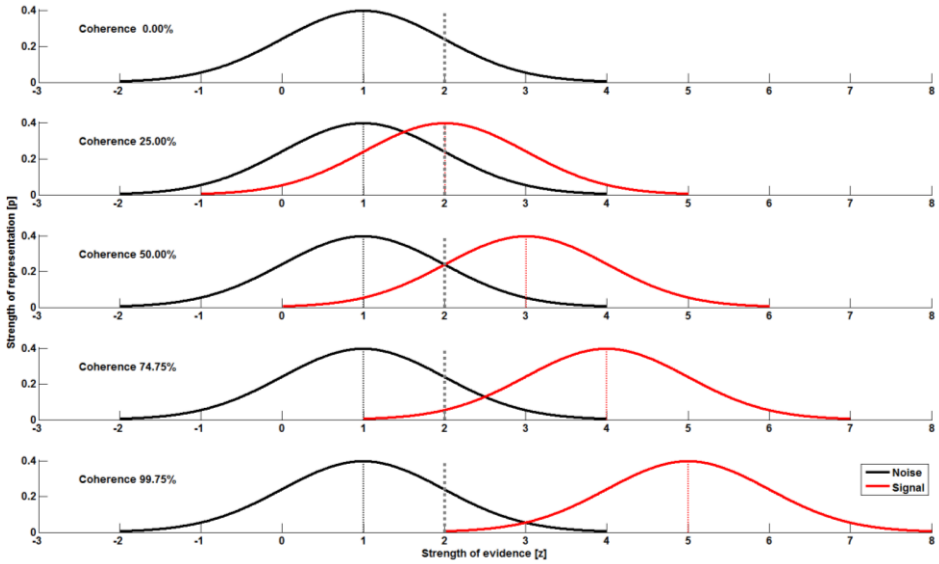


Figure 17. SDT model for the representation of signal and noise without (panel A) and with (panel B) baseline shift. Panel A (ignored): The first row depicts the Gaussian representation of noise (black line) corresponding to 0% coherence. Rows 2-5 depict the Gaussian representations of noise (black) and signal (red) for increasing levels of coherence. Thin dotted lines represent μ_{noise} (black) and μ_{signal} (red). Thick grey dotted line represents the decision criterion. The area to the right of the criterion under the signal distribution corresponds to the probability of "yes"-responses, yielding the psychometric function for the ignored condition, i.e. the black line in Figure 18.
Panel B (attended): As above, different rows depict the noise and signal distributions for different levels of motion coherence. Note however, that all stimulus representations (noise and signal) are shifted to the right by one sd-unit as a consequence of baseline shift. This leads the signal distributions to have a larger area to the right of the criterion, which in turn produces more yes responses for each level of coherence than in panel A, and a leftward shifted psychometric function for the attended condition (blue line) in Figure 18 below.

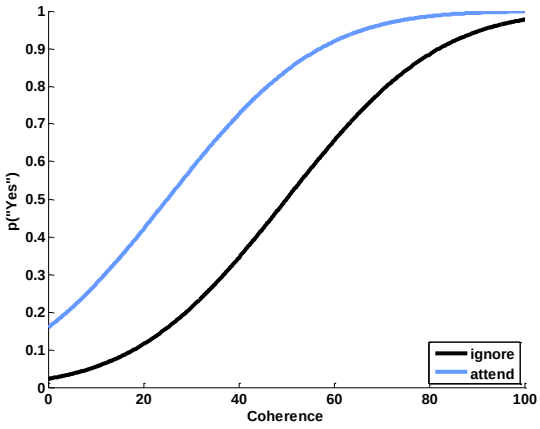


Figure 18. Psychometric functions derived from an SDT model of perceptual decision making for ignored stimuli (black line) and for attended stimuli assuming an attention-induced baseline shift (red line).

The reported behavioral effect of a leftward shift of the coherence response function can thus be reconciled with our finding of a baseline shift in activity of the human motion complex by stating that attention to motion produces an overall increase in hMT+ that leads to more "yes" responses for any given level of coherence. Note that the same behavioral effect could have been achieved by a criterion shift that makes observers to more liberal responders with attention. Our results, however suggest, that attention does change the overall activity and leaves the criterion the same.

Conclusions

In a series of experiments we have explored by which mechanism attention can modulate our perception of coherence. We think, that we convincingly have ruled out that attention changes gain, i.e. the effectiveness by which coherence is processed. Our alternative account states that attention, at least in our task, changed the overall activity in the human motion complex, which leads to an alteration in decision making. These data give a new interpretation to reported behavioral effects that may have been taken as evidence that attention alters appearance by changing the effectiveness of coherence-processing.

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Appendix

	Mean x	Mean y	Mean z	Std x	Std y	Std z	nvoxels
SUB04_RH_hMT+	42	-64	-3.2	3.9	2.5	4.6	1753
SUB05_RH_hMT+	34	-67	-5	3.8	3.1	4.2	2135
SUB06_RH_hMT+	34	-59	-0.23	2.4	4.3	4.1	1500
SUB07_RH-hMT+	38	-67	3.2	3.4	3.7	3.5	1808

Table 3. Talairach coordinates and number of voxels for the region of interest (hMT+) in the right hemisphere for individual participants for experiment 1.

	Mean x	Mean y	Mean z	Std x	Std y	Std z	nvoxels
RH_hMT+	42	-64	-3.2	3.9	2.5	4.6	1753

Table 44. Talairach coordinates and number of voxels for the region of interest (hMT+) in the right hemisphere collapsed across participants for experiment 1.

	Mean x	Mean y	Mean z	Std x	Std y	Std z	nvoxels
SUB01_RH-hMST	41	-63	-1.5	2.02	2.03	1.03	175
SUB01_LH-hMST	-52	-57	3.04	1.07	2.01	1.06	218
SUB01_RH-hMT	44	-67	3.07	4.01	5.03	3.02	1656
SUB01_LH-hMT	-44	-65	-1.1	3.09	5	4.01	2163
SUB04_RH-hMT+	48	-61	7.01	3.08	4.03	4.03	1889
SUB04_LH-hMT+	-39	-68	-1.4	3.03	6.04	3.02	1791
SUB04_RH-hMST	47	-61	5.09	1.07	1.09	2.04	300
SUB04_LH-hMST	-40	-58	-0.2	2.08	1.07	1.04	259
SUB04_RH-hMT	48	-61	7.03	4.01	4.06	4.05	1589
SUB04_LH-hMT	-39	-69	-1.5	3.04	5.06	3.04	1571
SUB05_RH-hMT+	41	-57	8	5.02	4.08	2.09	1951
SUB05_LH-hMT+	-40	-66	10	4.02	5.04	4	2114
SUB05_RH-hMST	38	-53	8	3	2.05	1.08	330
SUB05_LH-hMST	-41	-64	5.07	2.04	1.09	1.09	234
SUB05_RH-hMT	42	-58	8	5.03	4.07	3.01	1621
SUB05_LH-hMT	-39	-66	11	4.03	5.06	3.08	1907
SUB06_RH-hMT+	39	-61	2.05	4	3.01	4.01	912
SUB06_LH-hMT+	-40	-64	1.05	3.07	4.08	3.07	1513
SUB06_RH-hMST	38	-61	0,052	1.08	2.09	2.02	236
SUB06_LH-hMST	-39	-66	1.08	2.04	1.08	1.06	189
SUB06_RH-hMT	39	-61	3	4.04	3.02	4.04	684
SUB06_LH-hMT	-40	-64	1.04	3.09	5	3.09	1348
SUB07_RH-hMT+	46	-65	-0.25	4.04	5.07	3.04	2069
SUB07_LH-hMT+	-43	-70	-0.71	3.07	4.09	4.03	1982
SUB07_RH-hMST	46	-57	1.09	5.03	1.05	2	218
SUB07_LH-hMST	-38	-73	-2.9	1.09	2.09	1.05	274
SUB07_RH-hMT	46	-65	-0.49	4.03	5.03	3.05	1869
SUB07_LH-hMT	-44	-69	-0.4	3.04	5.01	4.05	1732
SUB08_RH-hMT+	44	-63	12	4.01	4.03	3.09	2140
SUB08_LH-hMT+	-43	-68	6.01	3.03	4	4.07	2188
SUB08_RH-hMST	46	-60	11	1.06	2	2.04	298
SUB08_LH-hMST	-44	-68	4.02	1.05	3.01	3	246
SUB08_RH-hMT	44	-63	12	4.03	4.04	4	1842
SUB08_LH-hMT	-43	-68	6.03	3.05	4.01	4.08	1947
SUB10_RH-hMT+	37	-64	-2.8	3.08	3.05	4	2180
SUB10_LH-hMT+	-38	-69	-4.3	5.02	5.04	3.06	2049
SUB10_LH-hMST	-40	-65	-2.9	2.08	1.09	1.03	262
SUB10_RH-hMST	37	-63	-1.2	3.01	1.06	2.04	229
SUB10_LH-hMT	-38	-70	-4.4	5.04	5.05	3.07	1792
SUB10_RH-hMT	37	-65	-3	3.08	3.06	4.02	1953
SUB11_RH-hMT+	39	-58	5.06	4.03	4	4.07	1895
SUB11_LH-hMT+	-39	-67	7.03	4.03	3.09	3.05	1859
SUB11_RH-hMST	-37	-64	6.09	1.08	1.09	2.03	212
SUB11_LH-hMST	37	-58	7	2.03	2.02	2.05	284

SUB11_RH-hMT	39	-58	5.06	4.03	4	4.07	1895
SUB11_LH-hMT	-39	-67	7.03	4.03	3.09	3.05	1859
SUB12_RH-hMT+	45	-67	-3.1	4.04	5.05	3.07	2049
SUB12_LH-hMT+	-37	-64	-2.9	4.05	4.04	4	1982
SUB12_RH-hMST	40	-57	-3.1	1.09	1.06	2.07	276
SUB12_LH-hMST	-35	-65	-3.8	3.01	2.01	2.02	278
SUB12_RH-hMT	45	-68	-3.2	4.02	4.07	3.08	1831
SUB12_LH-hMT	-38	-64	-2.8	4.06	4.07	4.02	1720
SUB17_RH-hMT+	46	-63	11	4.05	4.07	3.08	1986
SUB17_LH-hMT+	-38	-63	14	5.01	4.01	4.06	1885
SUB17_RH-hMST	47	-61	17	2.06	1.08	2.02	261
SUB17_LH-hMST	-40	-65	19	2.02	1.09	1.08	255
SUB17_LH-hMT	-38	-63	13	5.03	4.03	4.05	1642
SUB17_RH-hMT	46	-64	11	4.07	4.09	3.04	1775
SUB18_RH-hMT+	36	-58	-0.86	3	4.06	5.02	1962
SUB18_LH-hMT+	-38	-64	1.03	4.06	4.03	3.07	1901
SUB18_RH-hMST	34	-56	2.01	1.03	2.01	3	328
SUB18_LH-hMST	-36	-62	-1.7	2.05	2.02	1.07	198
SUB18_RH-hMT	36	-58	-1.5	3.02	4.08	5.03	1637
SUB18_LH-hMT	-38	-64	1.06	4.08	4.04	3.07	1707
SUB19_RH-hMT+	41	-62	-9.5	3.03	3.04	4.09	1712
SUB19_LH-hMT+	-42	-65	-9.9	3.07	4.02	2.08	1779
SUB19_LH-hMST	-44	-60	-8.3	3.01	1.03	2.03	216
SUB19_RH-hMST	39	-54	-1.5	1.04	1.07	2.03	177
SUB19_RH-hMT	42	-62	-10	3.03	3.01	4.06	1621
SUB19_LH-hMT	-42	-65	-10	3.07	4	2.08	1568
SUB20_RH-hMT+	42	-58	5.05	4	3	5	1935
SUB20_LH-hMT+	-37	-67	2.04	2.09	4	5.04	2050
SUB20_RH-hMST	46	-59	3.09	3.02	1.07	2.07	322
SUB20_LH-hMST	-37	-66	4.05	2	2.02	2.01	288
SUB20_RH-hMT	42	-58	5.07	3.09	3.01	5.03	1647
SUB20_LH-hMT	-37	-68	2	3.01	4.02	5.07	1764
SUB21_RH-hMT+	42	-61	6.07	4.01	4.02	4	2083
SUB21_LH-hMT+	-43	-74	3.09	3.07	4.01	3.03	2020
SUB21_RH-hMST	41	-62	3.02	4	2.01	1.05	307
SUB21_LH-hMST	-44	-72	4.01	2.01	2.06	1.09	318
SUB21_RH-hMT	42	-61	7.03	4.01	4.05	4	1777
SUB21_LH-hMT	-43	-74	3.08	3.09	4.02	3.05	1702
SUB22_RH-hMT+	39	-68	7.02	3.06	3.05	5	1865
SUB22_LH-hMT+	-39	-79	6.08	3.07	4.05	6	2032
SUB22_LH-hMST	-38	-76	6.06	3.02	1.01	2.05	191
SUB22_RH-hMST	39	-69	5.04	2.05	2.02	2.06	261
SUB22_RH-hMT	39	-67	7.05	3.08	3.06	5.02	1618
SUB22_LH-hMT	-39	-79	6.07	3.07	4.06	6.02	1870
SUB23_RH-hMT+	40	-67	5.04	3.04	3.06	4.02	2137

SUB23_LH-hMT+	-40	-69	1.07	3.06	4.02	4.06	2347
SUB23_RH-hMST	39	-67	6.04	1.09	2	2.02	282
SUB23_LH-hMST	-37	-67	2.03	2.03	2.03	1.07	335
SUB23_LH-hMT	-40	-69	1.06	3.06	4.04	4.09	2016
SUB23_RH-hMT	40	-67	5.03	3.05	3.08	4.04	1855

Table 5. Talairach coordinates and number of voxels for the region of interest (hMT+) in the right hemisphere for individual participants for experiment 2.

	Mean x	Mean y	Mean z	Std x	Std y	Std z	nvoxels
RH-hMT+	42	-62	3.06	3.03	3.04	5.05	1910
LH-hMT+	-40	-68	2.02	2.03	3.09	5.07	1990
RH-hMST	36	-60	4.01	19	4.02	5.01	263
LH-hMST	-36	-65	2.04	19	5.03	5.09	253
RH-hMT	42	-63	3.06	3.03	3.04	5.06	1679
LH-hMT	-40	-68	2.01	2.02	4	5.07	1769

Table 6. Talairach coordinates and number of voxels for the region of interest (hMT+) in the right hemisphere collapsed across participants for experiment 2.