

Neural Mechanisms of Attentional Selection in Vision: Locations, Features, and Objects

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Zusammenfassung

Eine typische natürliche Alltagsszenarie umfasst eine schier überwältigende Fülle sensorischer Informationen. Unser Gehirn ist jedoch nur in der Lage einen begrenzten Teil dieses sensorischen Inputs simultan mit hinreichend großer Präzision zu verarbeiten. Aus diesem Grund müssen relevante Informationen priorisiert und von irrelevantem Input separiert werden um einen Überschuss an Information zu vermeiden. In diesem Zusammenhang spielt Aufmerksamkeit eine Grundlegende Rolle, da sie einen der grundlegenden Mechanismen darstellt, welcher uns hilft unsere Ressourcen auf die relevanten Aspekte eines Ereignisses zu fokussieren und irrelevanten Input dabei zu ignorieren. Wichtig ist hierbei, dass dieser Selektionsprozess auf Grundlage von räumlichen Gegebenheiten, nicht-räumlichen Stimulusattributen wie z.B. Farbe oder Bewegung, oder sogar aufgrund eines ganzen Objektes als holistischer Entität (d.h. als integriertes Ganzes aus seinen Einzelmerkmalen) erfolgen kann. Die Zielsetzung der vorliegenden Arbeit war es vor diesem Hintergrund zu untersuchen wie räumliche und merkmalsbasierte Selektionsmechanismen die perzeptuelle Verarbeitung im visuellen System beeinflussen. Darüber hinaus sollte in einem weiteren Experiment auch erforscht werden wie die Steuerung dieser Selektionsprozesse neuronal implementiert ist.

In den ersten beiden Experimenten der vorliegenden Arbeit wurde mittels funktioneller Magnetresonanztomographie (fMRT; Experiment 1) bzw. mittels simultaner Elektro-/ Magnetoenzephalographie (EEG/MEG; Experiment 2) untersucht, wie die neuronale Verarbeitung sich bewegender transparenter Oberflächen durch merkmalsbasierte Aufmerksamkeitsallokation beeinflusst wird. Dabei sollte unter anderem überprüft werden ob die vom „Feature-Similarity Gain Model“ prädizierten multiplikativen Modulationen infolge merkmalsbasierter Aufmerksamkeitsallokation auf der Ebene neuronaler Populationsantworten nachweisbar sind. Zu diesem Zweck wurde in Experiment 1 ein Paradigma verwandt, in welchem die Aufmerksamkeit der Probanden auf eine von zwei möglichen Bewegungsrichtungen gelenkt wurde und die nachfolgend präsentierten „random-dot“ Stimuli dabei in ihrer Bewegungsrichtung und in ihrer Kohärenz variierten. Dies ermöglichte es den Einfluss von richtungsspezifischer Aufmerksamkeit auf die Verarbeitung von Stimuli unterschiedlicher Kohärenz zu untersuchen, welche sich entweder in oder entgegengesetzt zur attendierten Richtung bewegten. Die Ergebnisse zeigen, dass die Höhe der hämodynamischen Aktivierungen in hMT positiv mit der Bewegungskohärenz der Stimuli korreliert wenn die Bewegungsrichtung der Stimuli

attendiert wurde und spiegelte damit die Verhaltensperformanz der Studienteilnehmer wider. Bewegten sich die Stimuli jedoch entgegengesetzt zur attendierten Richtung waren auch die hämodynamischen Aktivierungen entgegengesetzt: Die Modulationen in hMT zeigten einen inversen Zusammenhang mit der Stimuluskohärenz. Dieses spezifische Aktivierungsmuster fand sich ausschließlich in hMT. Im Fundus des intraparietalen Sulkus (fIPS) und im Thalamus fand sich demgegenüber eine positive lineare Korrelation zwischen Aktivierungshöhe und Stimuluskohärenz welche unabhängig von merkmalsbasierter Aufmerksamkeit zu beobachten war. Attentionalen Kontrollstrukturen zeigten schließlich ein dem in hMT entgegengesetztes Aktivierungsmuster: Die höchsten Aktivierungen wurden infolge Stimuli niedriger Kohärenz beobachtet, d.h. sie korrelierten mit der jeweiligen Aufgabenschwierigkeit. Zusammengenommen unterstützen somit die Ergebnisse aus Experiment 1 die innerhalb des „Feature-Similarity Gain Models“ formulierte Annahme, dass merkmalsbasierte Aufmerksamkeit neuronale Aktivierungen auch auf Populationsebene in multiplikativer Weise moduliert.

In Anlehnung an das erste Experiment wurde in Experiment 2 der räumlich-zeitliche Verlauf merkmalsbasierter Aufmerksamkeitseffekte mittel EEG und MEG untersucht. Dabei war es die Aufgabe der Probanden auf die Bewegungsrichtung einer transparenten Oberfläche im linken visuellen Feld zu achten und eine kurzzeitig erhöhte Bewegungsgeschwindigkeit zu detektieren. Im rechten visuellen Feld wurde eine zweite transparente Oberfläche präsentiert welche sich periodisch in verschiedene Richtungen bewegte. Alle diese Stimulusbewegungen im rechten visuellen Feld waren dabei völlig Aufgabenirrelevant. Die durch diese Bewegungen ausgelösten ereigniskorrelierter Potentiale (EKPs) und Magnetfelder (EKMFs) wurden nun hinsichtlich ihrer Amplitude und Latenz miteinander verglichen. Dabei zeigte sich eine parametrische Negativierung der EKP- und EKMF-Amplituden im Zeitbereich zwischen 200 und 400 ms in Abhängigkeit der Ähnlichkeit der Bewegungsrichtung des evozierenden Stimulus zu jener des attendierten Stimulus. Somit zeigen diese Daten eine parametrische, richtungsselektive Modulation evozierter Potentiale infolge merkmalsbasierter, attentionaler Selektion. Damit liefern sie, wie schon Experiment 1, einen weiteren Beweis für die Gültigkeit des „Feature-Similarity Gain Models“ auf neuronaler Populationsebene und unterstreichen darüber hinaus die globale Wirksamkeit merkmalsbasierter Aufmerksamkeit. Allerdings zeigten die hier beschriebenen Modulationen eine relativ späten Beginn (~ 200 ms) im Vergleich zu

vorherigen Studien was möglicherweise auf die Aufgabenanforderungen bzw. die Stimuluseigenschaften zurückzuführen ist.

Im dritten Experiment wurde der Untersuchungsgegenstand um den Bereich der räumlichen Aufmerksamkeit erweitert. Um die funktionelle Beziehung zwischen orts- / und merkmalsbasierter Aufmerksamkeit zu untersuchen wurden hämodynamische Modulationen zwischen Situationen verglichen, in welchen Aufmerksamkeit auf die räumliche Position eines Stimulus, eines seiner Merkmale, oder auf beides gerichtet war. Hierbei fanden sich die höchsten Aktivierungen wenn die Selektion auf der Stimulusposition beruhte, unabhängig von seiner Merkmalszusammensetzung. Geringere Modulationen zeigten sich für die merkmalsbasierte Selektion von Objekten die innerhalb des Aufmerksamkeitsfokus präsentiert wurden. Merkmalsselektive Aktivierungen für Stimuli die räumlich nicht attendiert waren konnten jedoch nur in bewegungs- jedoch nicht in farbsensitiven Arealen nachgewiesen werden. Zusammengefasst zeigen diese Daten, dass innerhalb der visuellen Domäne räumliche Aufmerksamkeit den effizientesten Selektionsmechanismus darstellt. Sie legen darüber hinaus nahe, dass das Objektmerkmal „Bewegung“ ein besseres Ziel für die merkmalsbasierte Selektion eines Stimulus darstellt als seine Farbe.

Das letzte Experiment der vorliegenden Arbeit (Experiment 4) widmete sich schließlich der Untersuchung der neuronalen Mechanismen, welche die volitionale bzw. stimulusinduzierte Aufmerksamkeitsverschiebung zwischen Objekten bzw. räumlichen Koordinaten kontrollieren. Die Resultate dieses Experimentes zeigen, dass die verschiedenen Arten von Aufmerksamkeitsverschiebungen (willkürlich/ stimulusinduziert und räumlich/ objekt-basiert) alle ein gemeinsames Netzwerk fronto-parietaler Areale rekrutieren. Dabei unterschieden sich die verschiedenen Bedingungen lediglich in der Höhe ihrer Modulationen innerhalb verschiedener Teile dieses fronto-parietalen Netzwerkes: In dorsalen Arealen fanden sich die höchsten Modulationen wenn Aufmerksamkeit willkürlich kontrolliert wird, während ventrale Regionen ein entgegengesetztes Bild zeigten. Ähnlich wie im ventralen fronto-parietalen Kortex fanden sich auch in Regionen des „Default-Mode-Network“ die höchsten hämodynamischen Antworten, wenn Aufmerksamkeit exogen getriggert räumlich umorientiert wurde, wohingegen sie mit einer Deaktivierung reagierten, wenn Aufmerksamkeit volitionaler Kontrolle unterlag. Zusammengefasst zeigen diese Ergebnisse, dass verschiedene Aufmerksamkeitsprozesse durch ein komplexes Zusammenwirken innerhalb eines einheitlichen Netzwerkes von ventralen und

dorsalen fronto-parietalen sowie „Default-Mode-Network“ Regionen gesteuert wird, wobei Verarbeitungsressourcen je nach Aufgabenanforderungen dynamisch innerhalb dieses Netzwerkes distribuiert werden können.

Summary

The aim of the present thesis was to investigate how location-, feature-, and object-based attentional selection affects perceptual processing in the visual system and how these selection processes are controlled. Experiments 1 and 2 employed fMRI (Exp. 1) and EEG/MEG (Exp. 2) to investigate how activity elicited by motion-stimuli is modulated by feature-based attention, thus testing the validity of the feature-similarity gain model at the population level. The results from Experiment 1 show, that feature-based attention modulates hemodynamic activity in area hMT in a direction-selective manner, while attentional control regions displayed the opposite pattern. In continuation of the first experiment, Experiment 2 revealed a parametric direction-selective modulation of ERP/ERMF amplitudes by feature-based attention starting as early as 200 ms after stimulus-onset. In Experiment 3 the subject of investigation was extended into the spatial domain: Hemodynamic modulations were compared when attentional selection was based on a stimulus' location, its constituent features, or both. The highest activations were observed when attentional selection was based on a stimulus' spatial location. Relatively smaller modulations were observed when stimuli presented at the attended location were selected based on their constituent features, while for stimuli presented at unattended locations increased feature-selective activity was only visible in motion- but not in color-sensitive regions. These data suggest that spatial attention appears to be the most efficient selection-mechanism in vision, and indicate that a stimulus' motion is more efficiently targeted by feature-based attention than its color. Experiment 4, finally, was conducted to elucidate the mechanisms of attentional control during voluntary and stimulus-driven attention-shifts between objects and locations. The results show that different types of shifts recruit a common fronto-parietal network, in which modulations only differ in magnitude. In dorsal fronto-parietal regions increased activity was observed during goal-directed orienting, while ventral fronto-parietal areas showed a partially opposing pattern. Similar to ventral fronto-parietal cortex, default-mode network regions showed the highest responses during stimulus-driven spatial reorienting, while they were consistently deactivated when attention was under voluntary control. Taken together, these results imply that attention is controlled by a complex interplay within one unitary network of fronto-parietal and default-mode network regions, in which processing-resources are dynamically distributed in dependence of the particular attentional demands.

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Abbreviations

ACC	Anterior cingulate cortex
ANOVA	Analysis of variance
BOLD	Blood-oxygenation level dependent effect
EEG	Electroencephalography
EOG	Electrooculogram
ERMF	Event-related magnetic field
ERP	Event-related potential
EPI	Echo-planar imaging
FDR	False-discovery rate
FEF	Frontal eye-field
FG	Fusiform gyrus
fIPS	Fundus of the intraparietal sulcus
fMRI	Functional magnetic resonance imaging
hMT	Human analogue of the middle temporal area
IFG	Inferior frontal gyrus
IPS	Intraparietal sulcus
IT	Inferior temporal area
LG	Lingual gyrus
LIP	Lateral intraparietal area
LPC	Lateral parietal cortex
MEG	Magnetoencephalography
MNI	Montreal neurological institute
MPFC	Medial prefrontal cortex
MT	Middle temporal area
PCC	Posterior cingulate cortex
PET	Positron emission tomography
PFC	Prefrontal cortex
PHG	Parahippocampal gyrus
RANOVA	Repeated measures analysis of variance
RDK	Random-dot kinematogram
RFE	Relevant feature effect
ROI	Region of interest
RT	Reaction time

SEM	Standard-error of the mean
SFG	Superior frontal gyrus
SMA	Supplementary motor area
SMG	Supramarginal gyrus
SN	Selection negativity
SPL	Superior parietal lobe
SPM	Statistical parametric mapping
SSVEP	Steady-state visual evoked potential
TPJ	Temporoparietal junction

1. General Introduction

Our interaction with the environment generally appears to us as a coherent and continuous process: We experience what has been detected by our senses and respond to it by acting in accordance with our particular aims, needs, and goals. The perception of our physical surroundings, however, is not a simple bottom-up process, but itself already shaped according to our experiences and expectations (von Helmholtz, 1867). For example, stimuli can be ambiguous in that they can be perceived in more than one way (impressive examples are optical illusions as, e.g. the Necker cube or the Kanizsa triangle; Necker, 1832; Kanizsa, 1955), or they can even remain unnoticed despite being of high saliency (e.g. during change blindness or in the attentional blink; Kim and Blake, 2005). Although many of these phenomena have already been described before the end of the 19th century, their characterization, at that time, only occurred on the basis of introspection. However, with the development of psychophysiology and the later invention of modern neuroscientific methods, their analysis became a subject of empirical research. Therein, among the mechanisms affecting our perception one of the most extensively studied in modern psychology and cognitive neurosciences is attention. The following chapters will give an overview on the general scientific concepts of attention and on the underlying neurophysiological mechanisms that have been described.

1.1. Principles of attention

William James, in his monumental book *Principles of psychology*, remarked: “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). While this statement might be ultimately true in a phenomenological sense, it also illustrates the problems scientists are faced with, when trying to operationalize attention to make it accessible to empirical research. During the past century, multiple concepts describing and subdividing attention have been formulated. A very coarse taxonomy that is widely accepted today divides attention into alertness, orienting, and executive attention (Posner and Petersen, 1990; Raz and Buhle, 2006; Posner, 2008). Within this framework, alerting describes a state of increased readiness to execute an upcoming task. Several terms that are commonly used in the literature (e.g. vigilance,

alertness and arousal) can therein be subsumed under this definition, since they all refer to an amplified task-performance due to occurrence of a warning-signal (a temporal cue) that precedes a target-event. Neurophysiologically this alerting signal is accompanied by release of the neuromodulator norepinephrine from the locus coeruleus and the adjacent ascending reticular formation (Kinomura et al., 1996; Aston-Jones and Cohen, 2005), and concomitant alterations in the scalp-recorded EEG (e.g. a broad negative shift termed contingent negative variation; CNV) and in fMRI activations within the so-called 'alerting network' (Walter, 1964; Oken and Salinsky, 1992; Raz, 2004; Fan et al., 2005).

During attentional orienting, as opposed to arousal/alerting, a cue-signal preceding the task not only provides information about when (alerting), but also where or what kind of target will subsequently appear. Due to this directed nature of the cue, it enables an observer to focus onto the relevant aspects of the sensory input, thereby separating it from irrelevant information. In everyday life, such visual orienting responses result into the foveation of the stimulus (overt orienting/attention), while, conversely, it is also possible to prioritize the processing of the stimulus by attending to its location covertly without changing the gaze or head position (Moore et al., 2003). The majority of experiments on attentional orienting during the last decades employed paradigms that manipulated attention in such a covert manner. Therein, the classical paradigmatic approach uses a spatial cue that improves the processing of stimuli appearing at the cued location (Posner, 1980). The neural network controlling attentional orienting has been shown to encompass dorsal posterior parietal and frontal cortical areas (Corbetta and Shulman, 2002; Corbetta et al., 2008), as initially indicated by severe orienting deficits (hemi-neglect) in stroke-patients with structural damage in these regions (Damasio et al., 1980; Mesulam, 1981).

The third aspect within this taxonomy, executive attention, is believed to mediate more cognitive aspects of attentional control and coordination, including various distinct processes like response inhibition, task-switching, conflict resolution and task planning (Fernandez-Duque et al., 2000; Raz and Buhle, 2006). Thus, executive attention is typically involved in the realization of complex cognitive operations, such as changing task-requirements between trials (as e.g. during task-switching; Kiesel et al., 2010; Vandierendonck et al., 2010), or conflicts between task instruction and stimulus material like in the Stroop-task (Stroop, 1935). Neurophysiologically, these processes have been suggested to rely on signals

originating from anterior cingulate, medial prefrontal, and dorsolateral prefrontal regions, which are commonly referred to as “executive network” (Posner and Raichle, 1994; Botvinick et al., 2004; Egnor and Hirsch, 2005).

While this taxonomy provides a general reference frame for the different aspects that are encompassed by the term attention as outlined above, it does not provide a sufficiently detailed conceptualization concerning the modulatory effects of attention on perceptual processing in (early) sensory cortex. Therefore, more detailed classifications regarding attentional orienting have evolved over the past decades. On one hand, these classifications subdivide orienting based on the particular units that are selected for preferential processing and include orienting towards a stimulus’ spatial location, towards one (ore more) of its constituent features, or towards entire objects as integrated feature-ensembles (Duncan, 1984; Duncan et al., 1997; Kanwisher and Wojciulik, 2000). Following this scheme, the subsequent chapters will cover the effects attention exerts on behavioral performance and perceptual processing due to space-based (Chapter 1.1.1.1), feature-based (Chapter 1.1.1.2), and object-based (Chapter 1.1.1.3) attentional selection. On the other hand, attentional orienting also needs to be mediated by control signals that bias these selection processes. Conceptually, two separate but interconnected mechanisms of attentional control are broadly distinguished: attentional selection that is driven voluntarily based on the current goals and expectations of an observer (top-down/goal-directed/endogenous), or involuntarily by the appearance of a highly salient or unexpected event (bottom-up/stimulus-driven/exogenous; Corbetta and Shulman, 2002; Corbetta et al., 2008). In line with this classification, the last chapters of the general introduction will discuss the neural mechanisms that mediate attentional control during goal-directed (Chapter 1.1.2.1) and stimulus-driven (Chapter 1.1.2.2) orienting.

Before these specific models outlined above will be discussed in detail, Chapter 1.1.1 will give a general overview of the theoretical developments concerning attentional selection during recent decades.

1.1.1. Attentional modulations of behavioral performance and perceptual processing

The necessity for attentional selection has originally been proposed by behavioral psychologists, which observed that we possess a merely limited capacity to

process perceptual information (Broadbent, 1958; Shiffrin and Schneider, 1984; Tsotsos, 1990). These limitations have been first outlined by several experiments conducted in the early 1950's. Welford discovered that when subjects are faced with two subsequent tasks, their response times to the second one increase dramatically if it has to be executed in close temporal succession to the prior task (an effect he termed psychological refractory period; Welford, 1952). The following year, Colin Cherry published his findings from several dichotic listening experiments, in which subjects were presented with independent streams of speech, one into each ear. After attending to one of the streams (whose content they were required to repeat aloud) subjects were asked to recall the content of both auditory streams. Unsurprisingly, from today's perspective, participants showed a very poor recognition performance for information presented to the unattended ear (Cherry, 1953). Based on these results in conjunction with his own findings (split-span-paradigm; Broadbent, 1954), Broadbent formulated his influential filter model (Broadbent, 1958) which proposes that perceptual analysis proceeds in two sequential stages. In the first stage, all physical characteristics of the sensory input (the stimuli's locations and their constituent features) are extracted in parallel, while in the second stage more abstract aspects (like the semantic content of the input) become available. Due to the presumed limitation in the processing capacity of the brain, as indicated by the aforementioned findings, he assumed that only a subset of the information can enter the second stage at any given point in time. According to Broadbent, this information has to be selected at an early pre-categorical level based on the simple physical characteristics of the sensory input that are already available at the first processing stage.

While some evidence initially supported Broadbent's filter theory, numerous findings contradicted the idea of an early selection mechanism. For example, as we all know from our every-day experience, our attention might be captured by the sudden onset of a highly salient event (e.g. the sound of an explosion) despite being deeply focused onto an ongoing task. Moreover, important or well-trained information (e.g., the auditory presentation of one's own name; Moray, 1959) might be consciously perceived regardless of the concurrent attentional demands. These simple observations, alongside with other phenomena, were apparently at odds with the notion of an all-or-none filter acting at early stages of perceptual processing. Therefore, in opposition to Broadbent, an alternative framework arguing for late selection has been proposed, which depends on the response-requirements of the

task at hand (see for example Deutsch and Deutsch, 1963). Within these models, all input is suggested to undergo a high level of processing, while it rapidly decays and thus will not be consciously perceived, unless attention prolongs the representation of relevant information for more detailed analysis. Therein, relevance is defined by the semantic meaning or task-relevance of the input, in contrast to the basic stimulus-characteristics as supposed by early selection theories.

However, numerous findings could neither be adequately explained by early nor by late selection mechanisms. Inspired by this clash of conflicting views, several further attempts have been made to incorporate the partially opposing notions into a unified framework. For example, in her attenuation theory, Anne Treisman also suggested the existence of a filter-instance, which, however, does not work in an all-or-none fashion, but rather flexibly adjusts the threshold between the attended and ignored channels (Treisman, 1960). Accordingly, the filter does not completely block unwanted information, but rather amplifies important (attended) and attenuates unwanted (unattended) perceptual information in dependence of the stimulus characteristics and concomitant task-demands. With this account it became possible to explain why stimuli can sometimes still be processed (e.g., if they are of particular importance) even when they are unattended. This framework was later extended and refined by Nilli Lavie in her load theory of selective attention. In a series of experiments she could demonstrate that the extent to which irrelevant input is processed critically depends on the resources that remain available after perceptual analysis of the relevant information (Lavie and Tsal, 1994; Lavie et al., 2004; Lavie, 2005). Thus, the particular task-demands (attentional load) determine to which degree the available processing-capacity will be distributed between the relevant and irrelevant aspects of the task.

Most of these initial theoretical accounts as outlined above were primarily based on findings from behavioral experiments. However, the development of intracerebral recording techniques and functional neuroimaging methods provided novel experimental data that had to be incorporated into these established concepts. One central aspect in this respect was the characterization of the functional organization of the visual system. In most visual cortical regions, the incoming information is represented within a spatial (retinotopic) reference frame, but also within different feature-specific modules, in which different feature-dimensions (e.g. color and orientation) are processed in parallel. According to these principles, Treisman

developed her feature integration theory of visual attention (Treisman and Gelade, 1980; Treisman, 1998). In much the same fashion as Broadbent's early selection model, this theory proposes a pre-attentive stage in which features are processed in parallel within their particular specialized modules (termed feature-maps). The corresponding locations of the features are also extracted in parallel, but they are separately stored in a 'master-map of locations'. Attention now serves to conjoin the separate features (each stored in its specific feature-map) into holistic objects. This process, however, is suggested to proceed in a serial manner, whereby only one location (stored in the master-map of locations) can be selected at a time. The sequence of particular locations that are selected can either be determined exogenously (e.g., when certain stimuli are highly salient) or in a top-down manner, i.e., when attention is voluntarily shifted across locations stored in the master-map, or towards locations that have been prioritized by instruction.

While the feature integration theory provides a useful description on how particular features and locations are processed with regard to the structural composition prevailing in visual cortex, it lacks a sufficient explanation on how the coding ambiguities that result from the massive convergence along the visual hierarchy may be resolved (for a brief review of the organization of the visual cortex and its implications for theories on attention see Kastner and Ungerleider, 2000). This is of special importance considering the fact that natural visual scenes normally comprise multiple objects, which - due to the limited processing capacity of the visual system - have to compete for neuronal representation. This can be exemplified by a simple conjunction search experiment: If an observer is presented with two objects and required to identify one feature of each stimulus at the same time (e.g. the color of one and the motion-direction of the other), task-performance will dramatically decrease in comparison to situations in which the same task (identification of two features) has to be performed on only one object at a time (Treisman, 1969; Duncan, 1980, 1984). This competition can be affected in a bottom-up fashion (e.g., by a stimulus' salience), or by top-down factors as, e.g., by selective attention. Based on the results from numerous electrophysiological investigations in primates and functional neuroimaging studies in humans, two models were recently introduced to explain how selective attention modulates activity in early visual cortex to resolve this competition. The first concept (biased competition model) proposes that attention biases neural activity towards attended items by narrowing the receptive fields

covering the attended location, whereby the afferent input of irrelevant (unattended) stimuli is concurrently suppressed. This hypothesis was originally formulated by Duncan and Humphreys (1989) and transferred to the neurophysiological domain by Desimone and colleagues (Duncan and Humphreys, 1989; Desimone and Duncan, 1995; Desimone, 1998). A more recent model, the feature-similarity gain hypothesis, in turn suggests that the responses of neurons in extrastriate cortex whose feature-preference matches the attended stimulus are scaled in a multiplicative manner (Treue, 2001; Maunsell and Treue, 2006).

The following chapters will review the behavioral, neurophysiological, and neuroimaging evidence that has been put forward to elucidate how behavioral performance and perceptual processing is affected by location-, feature-, and object-based attentional selection.

1.1.1.1. Effects of space-based attentional selection

1.1.1.1.1. Psychophysical evidence

In everyday life a visual scene is typically analyzed by foveation of one spatial location after another. Therefore, it comes as no surprise that space-based mechanisms were the first that have been systematically addressed by empirical research. In analogy to the overt eye-movements during analysis of a visual scene during free vision, Posner and colleagues suggested that covert visual attention also could be focused in a location-based manner in terms of a spotlight that is directed to a unitary contiguous region of visual space. This spotlight will enhance the processing of all stimuli that fall within its focus, but it has to be shifted whenever stimuli located at a different part of the visual field need to be analyzed in more detail (Posner, 1980). Experimentally the spotlight metaphor was based on findings from a letter identification task in which attention was spatially cued to one location (a bright flash in the left or the right visual field; exogenous cueing), while the target letters subsequently were presented either at the attended or unattended location. This experiment demonstrated that target identification proceeds faster and more accurate at the cued location. This result was later generalized to situations in which attention was controlled endogenously (a central cue directed the location to attend), in that subjects were faster and more accurate in response to validly cued targets, whereas performance was worse upon invalidly in comparison to neutrally cued targets (Posner et al., 1984). These findings have been extended by multiple other psychophysical

experiments, which reported an increased discrimination- and contrast-sensitivity (Hawkins et al., 1990; Luck et al., 1996; Lu and Doshier, 1998; Cameron et al., 2002), a reduced distractor interference (Shiu and Pashler, 1995), and enhanced spatial resolution (Yeshurun and Carrasco, 1998) within the focus of attention.

While the original spotlight model proposed the existence of one spatial focus in which processing is enhanced, other evidence also indicated that the focus of attention can be split into disjunctive areas in terms of multiple spotlights (Shaw and Shaw, 1977; Juola et al., 1991). Supporting this view, several studies found that attention can enhance processing (in terms of faster and more accurate responses or lower detection thresholds) across non-contiguous locations (Castiello and Umilta, 1992; Kramer and Hahn, 1995; Hahn and Kramer, 1998; Schmidt et al., 1998; Bichot et al., 1999; Awh and Pashler, 2000), whereby performance is markedly impaired at intervening parts of space (Awh and Pashler, 2000).

Both the single and the multiple spotlight hypotheses regarded the focus (foci) of attention as uniform and invariant spots that might be deployed at distinct locations throughout the visual field. In extension to these accounts, Eriksen and colleagues introduced the 'zoom-lens model', which posits that the spotlight of attention does not possess a uniform distribution, but that it can vary in size and shape (Eriksen and Yeh, 1985; Eriksen and St James, 1986). This notion was based on size estimations that ranged from about 1° to over 10° of visual angle in dependence on the particular task-demands (Eriksen and Hoffman, 1973; LaBerge, 1983; Hughes and Zimba, 1985). The size of the attentional focus, however, is inversely related to processing efficacy, suggestive of a limited amount of resources that can be distributed over a given spatial region (Eriksen and St James, 1986; Castiello and Umilta, 1990).

Although the zoom lens model takes into account that the distribution of processing resources is flexible with regard to the size of the attentional focus, it assumes that resources are evenly distributed across the attended region, or that they at least display a gradual decrease with eccentricity to the attended location. This notion was fostered by findings that distractor interference gradually decreases with distance to the target (Eriksen and Hoffman, 1973) and that reaction times to targets increase with growing distance between an exogenous cue (or probe) and a subsequently presented target (Shulman et al., 1985; Henderson and Macquistan, 1993; Handy et al., 1996), or between two targets presented in rapid succession (LaBerge, 1983). However, recent computational models predict that the spatial profile

of the attentional focus might be more complex than such a simple gradient, but instead comprises a suppressive zone that surrounds the actual focus of attention (Tsotsos, 1990; Cutzu and Tsotsos, 2003). While originally motivated by the structural and functional properties of the primate visual system (Tsotsos, 1990), this center-surround (or Mexican hat) shaped profile was supported by a number of psychophysiological findings. In agreement with other theoretical accounts on spatial attention, psychophysiological performance was highest within the immediate focus of attention. However, probe-detection at locations close to a search target is slowed relative to more distant locations (Cave and Zimmerman, 1997) and the discrimination of a probe presented in close proximity to an exogenous cue is diminished in comparison to probe locations farther away (Mounts, 2000a, b).

1.1.1.1.2. Neurophysiological and functional neuroimaging evidence

In single-cell recording studies, effects of space-based attentional selection have been assessed by comparing conditions in which an animal's attention was directed towards a stimulus presented within the receptive field of a neuron, or directed towards a location outside the particular receptive field. With this approach numerous studies have shown that attending to a stimulus inside the receptive field typically enhances the response strength of the respective neuron. Given the spatiotopic organization of most visual areas it comes as no surprise that such spatial attention effects have been observed across multiple regions along the visual hierarchy starting from primary visual cortex (Motter, 1993; Luck et al., 1997), across ventral areas like V2 (Motter, 1993; Luck et al., 1997) and V4 (Moran and Desimone, 1985; Spitzer et al., 1988; Motter, 1993; Luck et al., 1997; McAdams and Maunsell, 1999), but also in dorsal extrastriate cortex as in MT (Treue and Maunsell, 1996, 1999) and LIP (Bushnell et al., 1981; Colby et al., 1996). This attentional gain enhancement increases with task difficulty (Spitzer et al., 1988; Spitzer and Richmond, 1991), but also when multiple stimuli compete for representation, i.e., if they are simultaneously presented within the receptive field (Moran and Desimone, 1985; Motter, 1993; Luck et al., 1997; Treue and Maunsell, 1999). Importantly, spatial attentional modulations have not only been observed when a neuron's activity was driven by a stimulus within its receptive field, but also in absence of direct visual stimulation (Colby et al., 1996; Luck et al., 1997; Reynolds et al., 1999). Finally, one very recent study also provided support for center-surround models of spatial attention

by demonstrating gain amplification of V1 neurons whose receptive fields covered the focus of attention and a suppressed firing rate when their receptive field surrounded it (Chen et al., 2008).

Similar results to those of single-cell electrophysiological studies have also been observed on a larger scale with fMRI in human observers. These studies demonstrated spatial attention effects correspondent to the sensory retinotopy of many striate and extrastriate cortical regions (O'Craven et al., 1997; Hadjikhani et al., 1998; Tootell et al., 1998; Brefczynski and DeYoe, 1999; Gandhi et al., 1999; Martinez et al., 1999; Martinez et al., 2001), which even could be observed in absence of direct visual stimulation (Chawla et al., 1999; Kastner et al., 1999; Muller et al., 2003b; Serences and Boynton, 2007). Moreover, fMRI studies provided evidence for spotlight adaptivity according to the zoom-lens model (Muller et al., 2003b; McMains and Somers, 2005), but also for the existence of multiple spotlights of attention (McMains and Somers, 2004, 2005; Brefczynski-Lewis et al., 2009). Finally, functional neuroimaging research could show that all items that fall into an attended part of visual space become enhanced regardless of their relevance to the task, and that this gain enhancement occurs in those brain regions that process the physical attributes of the attended stimuli (Heinze et al., 1994; Schoenfeld et al., 2007).

In addition to the findings from neurophysiological investigations in primates and functional neuroimaging studies in humans, non-invasive electrophysiological techniques (EEG/MEG) contributed important insights related to the timing of the space-based modulations and also concerning the spatial profile of the focus of attention. Most ERP studies indicated that space-based selection enhances sensory processing in early sensory cortex as reflected by increased P1- and N1-amplitudes (the first major positive and negative deflections in the canonical ERP), which are believed to index early visual cortical activity (Harter et al., 1982; Hillyard and Munte, 1984; Hillyard and Mangun, 1987; Heinze et al., 1990; Luck and Hillyard, 1994; Hillyard et al., 1998). Since these amplitude modulations occurred in absence of significant alterations in the onset-latency or scalp topography of the P1- and N1-components, space-based selection was considered to rely primarily on sensory gain amplification (Hillyard and Mangun, 1987; Hillyard et al., 1998). This gain amplification has been shown to decline with increasing distance between the focus of attention and the location at which stimuli were actually presented (Hillyard and Mangun, 1987), congruent with the gradient hypothesis concerning the profile of the focus of attention.

Recent studies, however, could nicely demonstrate that the profile of the attentional spotlight does not follow this simple gradient but instead shows a center-surround shaped profile as indicated by computational theories (Hopf et al., 2006a; Boehler et al., 2009). Finally, some recent electrophysiological studies also provided evidence for the zoom lens (Eimer, 2000; Hopf et al., 2006b; Song et al., 2006) and split spotlight hypotheses (Muller et al., 2003a; Malinowski et al., 2007) as outlined above.

1.1.1.2. Effects of feature-based attentional selection

Most attentional models suggest that space plays a unique role in attentional processing: Spatial selection is believed to be an inevitable prerequisite for processing of featural information, or to accomplish the binding of independent features into holistic objects when stimuli compete for processing resources (Treisman and Gelade, 1980; Treisman and Sato, 1990; Cave and Bichot, 1999). Stimulus features, however, are not only passive recipients of attentional resources that are deployed based on prior spatial selection, but can - according to theories of visual search - themselves guide the allocation of spatial attention to potential target objects (Wolfe et al., 1989; Treisman and Sato, 1990; Wolfe, 1994; Cave, 1999). Given that feature information thus might also be the target of attentional selection, numerous studies have addressed the behavioral and neural effects of feature-selection, which will be outlined in the following sections.

1.1.1.2.1. Psychophysical evidence

Similar to pre-knowledge about a stimulus' location improves its detection, feature-based attention also enhances behavioral performance. For example, the detection of a moving object is remarkably improved by prior knowledge of its motion-direction or speed (Sekuler and Ball, 1977; Britten et al., 1992; Liu et al., 2007a) and similar facilitatory effects have also been observed for other features like a stimulus' color (Saenz et al., 2003), size (Vickery et al. 2005), spatial frequency (Davis et al., 1983; Rossi and Paradiso, 1995), or orientation (Spitzer et al., 1988; Rossi and Paradiso, 1995; Baldassi and Verghese, 2005; Vickery et al., 2005). Moreover, such improvements are not confined to objects that are presented at spatially attended locations, but can spread to stimuli at unattended regions of visual space if they share a common feature with the target in comparison to stimuli comprising different/opposing features (Saenz et al., 2003). Conversely, task performance (in a

variety of tasks) is reduced if attention is captured by the occurrence of stimuli (at unattended locations) that match the (featural) attentional set of the observer (contingent capture; Folk et al., 1992; Gibson and Kelsey, 1998; Theeuwes et al., 2010).

Moreover, while early theories on attentional selection suggested that multiple stimulus-features could be extracted in parallel (e.g. Treisman and Gelade, 1980), recent evidence indicates that only one individual feature-value can be selectively attended at a time (Morales and Pashler, 1999). This notion has recently been supported by an elegant study showing that the perception of the colors of two objects was significantly improved by successive compared with simultaneous presentation, whereas perception of their locations was not (boolean-map theory; Huang et al., 2007).

1.1.1.2.2. Neurophysiological and functional neuroimaging evidence

One of the first demonstrations of feature-selective attentional effects at the single-neuron level has been provided by Moran and Desimone (Moran and Desimone, 1985). In their study, two stimuli were presented within the receptive fields of neurons located in macaque regions V4 and IT. One of the stimuli matched the feature-selectivity of the recorded neuron, while the other stimulus was ineffective in driving its response. If attention now was directed towards the neurons' preferred stimulus it reacted with an increase in its firing rate, while the response strength was reduced if the non-effective stimulus was attended (Moran and Desimone, 1985). While in the study by Moran and Desimone attention was directed towards a target's location and not explicitly towards one of its particular stimulus features, the results nevertheless clearly show that a neuron's response critically depends on the degree of overlap between the features of an attended stimulus and the feature-selectivity of the respective neuron (for comparable studies see e.g. Haenny and Schiller, 1988; Spitzer et al., 1988). Similar modulations have been observed for multiple different features within many visual areas including color-selective modulations in V2, V4, and IT (Motter, 1994; Luck et al., 1997; Reynolds et al., 1999), orientation-specific effects in V1, V2, and V4 (Motter, 1993; McAdams and Maunsell, 1999), motion-selective effects in MT (Treue and Maunsell, 1996, 1999), and modulations based on complex objects in V4 and IT (Chelazzi et al., 1993; Chelazzi et al., 1998; Chelazzi et al., 2001).

Based on these findings researchers proposed the biased competition model (Desimone and Duncan, 1995; Reynolds et al., 1999), which asserts that simultaneously presented objects activate competing neural populations, and that this competition may be biased in favor of neurons that are selective for an attended stimulus' features, at advantage over neurons that represent the unattended stimulus. This bias signal is believed to induce a narrowing of the receptive fields of neurons that are selective for the attended features, whereby inhibitory interactions would concomitantly eliminate the influence of the unattended stimuli. More recent data, however, indicate that a neurons' response can also be directly modulated if attention is deployed to a particular stimulus' feature. By recording activity from single neurons located in the macaque MT region, Treue and co-workers could demonstrate that the response profile of direction-selective neurons scales in a multiplicative manner when attention is directed towards a stimulus' motion-direction (Treue and Martinez Trujillo, 1999; Martinez-Trujillo and Treue, 2004). More generally speaking, neurons whose feature-preference closely match the attended feature-value (e.g. a specific motion-direction) increase their firing rate, while responses of neurons tuned to opposite feature-values (e.g. opposed to the attended direction) are suppressed. These findings gave rise to the 'feature-similarity gain model', which postulates that an individual neuron's response depends on the feature-similarity between a behaviorally relevant target and the feature-preference of that neuron. Importantly, these feature-specific modulations were observed even when attention was directed towards a stimulus located outside the neurons' receptive field, demonstrating that feature-based attention operates in a spatially global manner (Martinez-Trujillo and Treue, 2004). Similar results have recently also been obtained for orientation stimuli in primate area V4 (McAdams and Maunsell, 2000) and for spectral tuning of V4 neurons during natural vision (David et al., 2008).

In agreement with neurophysiological investigations in primates, previous fMRI and PET studies in humans showed similar feature-selective activations based on a stimulus' color, shape, orientation, or motion-direction. These modulations have been described across multiple regions of the human visual cortex as, e.g., in V1 (Huk and Heeger, 2000; Kamitani and Tong, 2005; Liu et al., 2007b), V2 (Kamitani and Tong, 2006; Liu et al., 2007b), V3 (Büchel et al., 1998; Chawla et al., 1999; Saenz et al., 2002), V4/V8 (Corbetta et al., 1990; Saenz et al., 2002; Liu et al., 2007b), IT (Corbetta et al., 1990), and MT (Corbetta et al., 1990; O'Craven et al., 1997; Büchel et al., 1998;

Chawla et al., 1999; Huk and Heeger, 2000; Saenz et al., 2002). In analogy to the data from primate neurophysiology, these feature-selective activations occurred even in absence of direct visual stimulation, evident as baseline-increases in anticipation of the features to be presented (Chawla et al., 1999; Kastner et al., 1999; McMains et al., 2007; Serences and Boynton, 2007; Shibata et al., 2008). Moreover, these modulations appeared in a spatially global manner, in that all stimuli whose feature-content matches the attended feature are amplified throughout the visual field (Saenz et al., 2002; Serences and Boynton, 2007). While conventional neuroimaging studies have repeatedly demonstrated changes of activity related to feature-based selection, none of the studies specifically investigated attentional modulations within a single feature dimension. To date, with the exception of three recent studies that employed classifiers for fMRI analysis (Kamitani and Tong, 2006; Serences and Boynton, 2007; Serences et al., 2009), functional neuroimaging research thus far has failed to demonstrate direction-selectivity in human visual cortex. With this said, it is important to note that the feature-selective activations observed in these pattern-classification studies were not confined to those cortical regions that are known to process the physical attributes of the presented stimuli, as evident from primate neurophysiology. Within these studies feature-selective activity, in fact, could be decoded across multiple stages along the visual hierarchy (Kamitani and Tong, 2006; Serences and Boynton, 2007). Thus, their results do not necessarily imply the existence of direction-selective neuronal populations within all of these visual areas (Serences and Boynton, 2007), since the response profile across a neural population within a given voxel could also reflect feedforward/feedback activity from lower/higher order visual regions (Sillito et al., 2006) instead of a true direction-selective population-response.

Although PET and fMRI investigations have been particularly successful in defining the anatomical structures that are activated during feature-based deployment of attention, their temporal resolution is too limited to reveal a precise pattern of the timing of the underlying attentional modulations. Fine-grained information about the time course of feature-based selection has therefore been determined primarily based on data from noninvasive EEG/MEG recordings in humans. By this means it has been demonstrated that the selection of task-relevant features (such as the spatial frequency, orientation, color, motion-direction or shape of a stimulus) is initiated in the time range between 120 and 180 ms after stimulus onset (Harter and Aine, 1984; Kenemans et al., 1993; Motter, 1994; Anllo-Vento and Hillyard, 1996; Smid et al.,

1999; Torriente et al., 1999; Kenemans et al., 2000; Martinez et al., 2001; Beer and Roder, 2004, 2005), which (in most cases) is reflected by a broad negativity over centro-posterior electrodes in the ERP (the so-called selection-negativity, SN; for review see Harter and Aine, 1984; Hillyard and Anllo-Vento, 1998). The SN can be observed in difference potentials, in which the ERP elicited by a stimulus whose features are unattended is subtracted from the ERP due to the same stimulus when its constituent features are attended. Dipole modeling and source analyses on the SN suggest that these modulations can be attributed to the same neural generators as observed in corresponding fMRI investigations (Hillyard and Anllo-Vento, 1998). While the configuration of the SN is highly similar across studies, its onset latencies differed substantially between them. This has been suggested to result from paradigmatic differences between studies. For example, if a spatially attended feature dimension (e.g., a stimulus' motion) has to be selected from another one (e.g., a stimulus' color), the attentional enhancement begins as early as 100 ms after stimulus onset (Schoenfeld et al., 2007). If, on the other hand, the selection occurs within a single feature dimension (e.g., selecting one motion direction from another) the enhancement starts about 50 ms later (Hillyard and Munte, 1984; Anllo-Vento and Hillyard, 1996; Karayanidis and Michie, 1996; Lange et al., 1998). Thus, the signs of feature-based attentional selection due to features presented within the spotlight of attention can be observed quite early (100-180 ms after stimulus onset). These modulations only seem to vary according to the difficulty of the discrimination process: selection between feature-dimensions proceeds faster than within a single dimension. If, in contrast, a feature is task-irrelevant and is selected only by virtue of being part of an attended object, feature-selective activity starts around 230-240 ms if the irrelevant feature belongs to an object presented at an attended location (Schoenfeld et al., 2003b), and not until 270 ms after stimulus onset if the irrelevant feature is confined to an object located in the unattended visual field (Boehler et al., 2010). While the latter findings together with other ERP data and results from studies using steady-state visual ERPs (e.g. Hopf et al., 2004; Muller et al., 2006; Andersen et al., 2009; Andersen et al., 2011) again emphasize the global nature of feature-based attention, they also imply that the timing of these modulations depends on the particular selection process that is engaged.

Temporal flexibility of attentional selection has also been observed for the comparison of space- and feature-based attentional modulations. Under most

circumstances location-based selection might play a special role in attentional orienting, given that all studies except one (which demonstrated feature-selective modulation of the P1 amplitude under conditions of increased stimulus competition; Zhang and Luck, 2009) revealed a modulation of the initial feed-forward flow of information along the visual hierarchy (as indexed by the P1 wave) only during location-based attentional selection (for review on the timing attentional selection see Hopf et al., 2005). However, a recent study using combined EEG/MEG recordings also demonstrated that even this general temporal priority of location-based over feature-based selection might depend on the particular stimulus characteristics and task demands. This study could demonstrate that feature-selective effects precede the indices of correspondent spatial modulations in visual search (Hopf et al., 2004), which is well in accordance with visual search models proposing that feature information may be used to guide the allocation of resources to spatial locations that are likely to contain a target (Treisman and Sato, 1990; Wolfe, 1994; Cave and Bichot, 1999).

1.1.1.3. Effects of object-based attentional selection

1.1.1.3.1. Psychophysical evidence

Inspired by the concepts of Gestalt psychology, assuming that objects are perceived as holistic entities instead of just as a collection of simple features, cognitive psychologists provided evidence for object-based selection mechanisms in visual attention. Object-based accounts suggest that pre-attentive processing not only operates on the individual attributes of a stimulus, but also involves grouping mechanisms such as closure, proximity, common fate and similarity (Wertheimer, 1923; Neisser, 1967). Features that are bound into objects in this way can be targeted by attention, whereby the selection of one particular object-attribute will also enhance processing of all other of its constituent features (for detailed review see Kanwisher and Driver, 1992; Driver and Baylis, 1998; Scholl, 2001).

Some of the first demonstrations of object-based selection came from Neisser and colleagues (Neisser, 1967; Neisser and Becklen, 1975). In their experiments subjects were required to attend to one out of two spatially superimposed movies and to count particular actions that took place within the attended scenery. When engaged in this task the subjects were completely unaware of changes occurring within the unattended movie, even if these changes were of high visual salience. While by

today's methodological standards these early studies were confounded to some degree, they nevertheless intriguingly demonstrate that attentional selection can also operate in an object-based rather than location-based manner, since the two scenes were globally superimposed.

Following the experimental basis established by Neisser and co-workers, Duncan also used a paradigm in which subjects were presented with two superimposed objects (a box and a single line drawn through it). Both objects could vary on two dimensions: the box was either tall or small and contained a small gap on either its left or the right side, while the line was either tilted to the left or right from the vertical meridian and was either dashed or dotted. The subject task was to judge either two dimensions of a single object (e.g. the box' size and the location of its gap) or one of each object (e.g. the size of the box and the orientation of the line). With this approach Duncan could demonstrate that the subjects' performance was much better when the two target dimensions were part of the same than when they were distributed across two separate objects (an effect termed "same-object advantage"; Duncan, 1984). In fact, the subjects' performance on the single-object condition was equivalent to a control condition, in which only a single object-attribute (e.g., the line's orientation) had to be discriminated. While the same-object advantage was subject to considerable debate due to putative methodological confounds, numerous studies have replicated the effect with alterations to the task-instructions and the stimulus material that has been employed (Duncan, 1993a, b; Egly et al., 1994; Vecera and Farah, 1994; He and Nakayama, 1995; Duncan and Nimmo-Smith, 1996; Kramer et al., 1997; Vecera and Farah, 1997; Lamy and Tsal, 2000).

Many of the object-based findings still have been controversial, in particular with respect to possible explanations based on space-based accounts (Gibson, 1994; Lavie and Driver, 1996). However, the use of superimposed moving transparent surfaces for the investigation of object-based attention has rebutted these concerns to some degree. In analogy to the same-object advantage obtained by the use of concrete objects, Valdes-Sosa and colleagues showed that simultaneous judgments on the speed and direction of two superimposed moving transparent surfaces were more accurate when they had to be performed on only one of the surfaces than when they involved both objects (Valdes-Sosa et al., 1998a). Similarly, two brief directional changes were discriminated accurately when both occurred within the same surface, but poorly if they affected different surfaces (Valdes-Sosa et al., 2000).

Similar results (refusing space-based explanations) have been obtained in a very elegant study by Blaser, Pylyshyn, and Holcombe, in which subjects were presented with one circular patch that dynamically changed its orientation, spatial frequency and color (Blaser et al., 2000). Importantly, due to these gradual feature-changes the patch was perceived as being composed of two individual 'Gabor' stimuli that were transparently superimposed onto each other. The subjects' were asked to track one of these patches solely based on its changing appearance (in terms of its changing color, orientation, and spatial frequency), while small discontinuities could occur in the otherwise smoothly changing feature-trajectories within each of the two objects. The subjects' task was to judge the direction of these discontinuities (e.g., the direction of a color change). In this way discrimination-performance could be compared between conditions in which such judgments were made within a single patch (e.g., reporting the direction of the color and orientation change for a particular Gabor), and conditions where both judgments had to be performed on separate objects (e.g., reporting the direction of the color change for one Gabor, and the orientation change for the other). Similar to the aforementioned results, subjects showed an increased discrimination performance when both judgments had to be performed on feature-changes within only one compared to within both objects. Moreover, these results extended the hitherto existing object-definition (which so far only included items with well-defined spatio-temporal trajectories) to include items/stimuli that are assembled based on coherent featur-temporal trajectories.

1.1.1.3.2. Neurophysiological and functional neuroimaging evidence

While numerous psychophysiological studies indicated that objects might be represented as integrated feature-ensembles within the visual system, evidence from primate neurophysiology is rather sparse. Some early experiments were based on certain visual illusions to show object-based processing in early visual cortex. In modal and amodal completion, for example, the presentation of object-fragments induces a vivid perception of the object as a whole, even if particular contours of the object have no physical representation within the image that is shown (modal completion), or if an object is partially occluded by another (amodal completion). Neurons in monkey area V1 increase their firing to such modally or amodally completed contours when they are presented within their receptive field, indicating that an endogenous representation of a holistic object has been build within the brain (Sugita, 1999; Lee and Nguyen, 2001).

Similar results have been obtained with experiments using the so-called 'barber-diamond' display, in which the perceived motion of a grating (induced by the depth of the grating relative to bounding regions in the display) is signaled by single neurons in area MT that are selective for the perceived direction, even when the particular parts of the stimulus that induce the illusion are presented outside the neurons' receptive fields (Duncan et al., 2000).

In 1998, Roelfsema and colleagues were the first providing direct neurophysiological evidence for object-based attentional selection. They recorded activity from neurons in area V1 while the monkeys performed in a curve-tracing task, in which one curve had to be attended and an overlapping curve needed to be ignored. With this approach they demonstrated that the firing of neurons whose receptive fields covered parts of the attended curve was enhanced, which was not the case for neurons with receptive fields covering parts of the distractor curve (Roelfsema et al., 1998). More recently, the elegant paradigm developed by Valdes-Sosa and colleagues described in section 1.1.1.3.1 (Valdes-Sosa et al., 1998b; Valdes-Sosa et al., 1998a, 2000), was employed to investigate the neurophysiological signs object-selection completely unconfounded by spatial attention. In one study, monkeys were biased to attend to one of two superimposed transparent surfaces (composed of rotating dots) due to a delayed motion onset of one of the surfaces. By this means it could be demonstrated that V4 neurons increased their firing if the attended surface's color matched the neurons' color-preference, while it was suppressed when it was of the neurons' non-preferred color (Fallah et al., 2007). These results clearly demonstrate that the processing of task-irrelevant features can be facilitated solely by being part of the attended object. A similar cross-featural spread of attentional enhancement has recently also been described for cells located in primate area V5/MT (Katzner et al., 2009).

A cross-featural enhancement by object-based attention with fMRI has first been demonstrated by O'Craven and colleagues (O'Craven et al., 1999), who presented subjects with superimposed transparent pictures of houses and faces, one of which was moving while the other image remained stationary. While subjects were cued to attend either to the houses, faces, or the stimulus' motion, increased hemodynamic activations were observed in those cortical regions that processed the attended stimulus attribute (e.g., in the fusiform area for faces or in area hMT for motion), but more importantly also in the respective regions selective for the task-

irrelevant feature of the attended object. Similar results have been obtained in an attention-shifting study by Serences and colleagues (Serences et al., 2004). While the stimuli used in the study by O'Craven et al. were globally superimposed, some researchers nevertheless questioned the interpretation of an object-based mechanism by arguing that subjects might still have used a space-based selection strategy (e.g., due to differences in local-contrast between the face- and house-images). This explanation, however, has been refuted by several fMRI studies conducted during the last decade. First, it has been shown that activity in early visual cortex not only was enhanced at retinotopic coordinates covering the spatial focus of attention, but also at retinotopic representations of other locations covered by an object of which only one specific part has been attended (Muller and Kleinschmidt, 2003; Shomstein and Behrmann, 2006). Moreover, hemodynamic modulations by object-based selection have also been observed using transparent moving surfaces as previously employed in psychophysical studies (Schoenfeld et al., 2003b; Safford et al., 2010; Ciaramitaro et al., 2011). Finally, purely object-based modulations of hemodynamic activity have also been demonstrated to spread across features that belong to different modalities (e.g. enhanced processing of a sound that is perceived as belonging to an attended visual stimulus; Busse et al., 2005) and across spatially non-contiguous location (i.e. the object-based enhancement occurs in a spatially global manner, similar as during simple feature-based attentional selection; Busse et al., 2005; Sohn et al., 2005).

Similar (if not the same) paradigms that were used to investigate object-based accounts of attentional selection psychophysically or with fMRI have been employed to assess the timing of object-based attention with non-invasive electrophysiological methods. Valdes-Sosa and colleagues used the same paradigm by means of which they provided psychophysical evidence for object-based selection (Valdes-Sosa et al., 1998a) to investigate the underlying temporal correlates (Valdes-Sosa et al., 1998b; Pinilla et al., 2001). When attention was endogenously directed to one of two superimposed counter-rotating transparent surfaces, brief translational movements of this surface elicited higher P1 and N1 amplitudes than the same movements if they occurred within the unattended object. In a follow-up study Rodriguez and Valdes-Sosa used current source localization to demonstrate that this object-based enhancement (i.e., the associated N200 component) is likely to originate from hMT (Rodriguez and Valdes-Sosa, 2006). Similar results have been obtained in two more recent studies from the same group. For one they could demonstrate that the N1

amplitude to brief translations of an attended versus unattended surface also was enhanced when it had been cued exogenously (Khoe et al., 2005). On the other hand it has been shown that the ocular dominance during binocular rivalry could be sustained by cueing one of two superimposed counter-rotating surfaces by a brief translational movement before a subsequent switch to dichoptic presentation of the surfaces (Mitchell et al., 2004). This behavioral effect was accompanied by an increase in P1 and N1 amplitudes to a second translational movement subsequent to the cue if it occurred within the attended (cued) in comparison to the unattended surface (Khoe et al., 2008). Importantly, this object-based effect was only evident during dichoptic but not during monocular viewing conditions and was interpreted to reflect object-based selection mechanisms that occur at early processing stages during dichoptic viewing. Accordingly, Mishra and Hillyard could demonstrate highly similar object-based modulations using the same experimental paradigm, but with endogenous instead of exogenous cueing (Mishra and Hillyard, 2009). While all these studies demonstrated that attended objects are preferentially processed in comparison to ignored ones, they were paradigmatically restricted in that they could not reveal signs of the same-object advantage as indicated by psychophysiological studies.

This question was recently addressed by a study that combined electrophysiological and hemodynamic recordings, while participants were presented with two transparent surfaces that moved into opposite directions. The subjects were cued to attend one of the motion directions, while a task-irrelevant color change could either occur within the attended or the unattended surface (Schoenfeld et al., 2003b). When the color-changes occurred in the attended surface, increased hemodynamic activity was observed in color selective visual region V4, relative to trials in which the color of the unattended surface changed. More importantly, electrophysiological signs in terms of this same-object advantage also were observed in the EEG and MEG data. These were evident as amplitude increases starting around 220-240 ms after a color change appeared in the attended in comparison to its occurrence in the unattended surface. In agreement with the pattern of hemodynamic activations, the neural generators of this object-based feature-enhancement were localized on identical sites within visual area V4. This amplification of task-irrelevant feature information was concluded to participate in the feature-binding process underlying the formation of an integrated perceptual object according to the integrated competition model (Duncan et al., 1997; Desimone, 1998; Driver and Baylis, 1998).

1.1.1.4. Summary

As outlined in prior chapters, attention is an important mechanism by which the overwhelming amount of sensory input can be selected with regard to its relevance within given circumstances. This selection process can be based on spatial locations (Posner, 1980), particular features such as color, motion, or shape (Corbetta et al., 1990; Maunsell and Treue, 2006), or entire objects as integrated feature-ensembles (Duncan, 1984; Egly et al., 1994; Schoenfeld et al., 2003b). Space-based models propose different modes of operation, suggesting the focus of attention to be sequentially deployed like a spotlight (Posner, 1980), to possess an adaptive shape like a zoom lens (Eriksen and St James, 1986), and to involve a profile that enhances perceptual processing in a graded or center-surround shaped manner (Tsotsos, 1990; Hopf et al., 2006a). Feature-based theories, in contrast, suggest that visual attention enhances processing of distinctive stimulus attributes (Corbetta et al., 1990; Desimone, 1998; Maunsell and Treue, 2006), and that this improvement occurs in a location-independent manner (Motter, 1994; Saenz et al., 2002; Martinez-Trujillo and Treue, 2004). Object-based accounts, finally, assume that attention might select entire objects as integrated feature-ensembles leading to an enhanced processing of all their constituent features (Duncan, 1984; Egly et al., 1994; O'Craven et al., 1999; Schoenfeld et al., 2003b). While empirical evidence has supported all of these accounts, many aspects are still unresolved. Therein, the open questions that have been addressed in the present work will be outlined in Chapter 1.2.

1.1.2. Neural mechanisms of attentional control

The first part of the General Introduction (Chapter 1.1.1 and the respective subchapters) dealt with the behavioral and neural consequences of attentional orienting. In contrast to the effects that attention exerts on behavioral performance and perceptual processing in early visual cortex, the following sections will summarize recent knowledge on the neural mechanisms which control how and whereon attentional resources are deployed. Following a scheme commonly used in the literature, two general mechanisms of attentional control will be distinguished: orienting based on internal goals or expectations (top-down/goal-directed/endogenous) and reorienting towards unexpected salient or behavioral relevant events (bottom-up/stimulus-driven/exogenous). Over the past decades it has become clear that these two mechanisms are controlled by two largely separate but

functionally interconnected cortical networks located in ventral and dorsal fronto-parietal cortex (Corbetta and Shulman, 2002; Corbetta et al., 2008). The dorsal part of this network (dorsal fronto-parietal system) is believed to control the allocation of attentional resources in a goal-directed fashion, while the ventral fronto-parietal system is involved in the detection of salient or relevant events, towards which attention then is reflexively reoriented (Corbetta and Shulman, 2002; Corbetta et al., 2008). Evidence from neuroimaging, neuropsychology, and neurophysiology on the role of the dorsal network during goal-directed orienting will be discussed.

1.1.2.1. Goal-directed allocation of attention

Before the mechanisms of attentional control have been investigated with neurophysiological and neuroimaging methods, patient studies showed that lesions to certain areas within posterior parietal (Heilman and Watson, 1977; Bisiach and Vallar, 1988; Marshall and Halligan, 1988; Petersen et al., 1989; Marshall and Halligan, 1995; Heilman et al., 2000), superior frontal (Heilman and Valenstein, 1972; Damasio et al., 1980), and cingulate cortex (Watson et al., 1973), as well as in the pulvinar and (Watson and Heilman, 1979; Heaton et al., 1982; Petersen et al., 1987; Rafal and Posner, 1987) in the superior colliculi (Mesulam, 1981), led to pronounced attention deficits referred to as neglect or hemi-neglect. Based on these findings and additional evidence from animal studies, it has been proposed that these regions are differentially involved during orienting (Mesulam, 1981; Posner and Petersen, 1990). The posterior parietal cortex (i.e., regions in the superior parietal lobe (SPL) and intraparietal sulcus (IPS)) has been suggested to entail a representation of extra-personal space and to mediate the disengagement of attention from the current focus. Moreover, parietal areas convey signals about the particular spatial representations to the superior colliculi (mediating spatial shifts of attention) and to the pulvinar (controlling the final re-engagement at a new location). Superior frontal regions (commonly referred to as frontal eye field (FEF) and supplementary motor area (SMA)) and the anterior cingulate cortex (ACC), in contrast, were proposed to mediate more cognitive aspects of attentional control, i.e. they are involved in the detection of relevant events and to control the planning/coordination of appropriate actions (sometimes these areas are therefore also termed executive network). While this early classification prepared the ground for later neurophysiological and neuroimaging studies in the intact (non-lesioned) brain, it has recently been argued that lesions to

the ventral rather to the dorsal fronto-parietal network might be the actual cause for neglect symptoms (Corbetta et al., 2008). Evidence for this notion will be reviewed in the chapter on the neural mechanisms of stimulus-driven attentional orienting (Chapter 1.1.2.2), while the following paragraphs will discuss recent neurophysiological and neuroimaging advances concerning the control of goal-directed orienting (for detailed review see Corbetta and Shulman, 2002; Corbetta et al., 2008).

The first body of neuroimaging work that used positron emission tomography (PET) and fMRI to investigate the neural substrates of attentional control used block designs in which attentional control signals could not be separated from activity that reflects the processing of target stimuli and modulations related to motor responses. These studies, nevertheless, consistently observed increased activations within parietal (SPL and IPS) and frontal (FEF and SMA) areas across diverse detection and discrimination tasks (Corbetta et al., 1993; Corbetta et al., 1995; Vandenberghe et al., 1997; Corbetta et al., 1998; Gitelman et al., 1999; Wojciulik and Kanwisher, 1999; Corbetta et al., 2000). Later on, studies employed rapid event-related fMRI to disentangle activity upon cues to which subjects voluntarily directed their attention in anticipation of upcoming stimuli from the modulations elicited by their actual appearance. Sustained periods of focused spatial attention therein were shown to evoke sustained hemodynamic activity within the IPS, FEF and SMA (Hopfinger et al., 2000; Sereno et al., 2001; Bisley and Goldberg, 2003; Serences and Yantis, 2007), while more transient responses time-locked to the actual attention shifts between locations were observed within the SPL (Hopfinger et al., 2000; Yantis et al., 2002; Kelley et al., 2008; Shulman et al., 2009). Similar results were obtained when subjects were not required to shift their attention across locations but between particular features (Liu et al., 2003), objects (Serences et al., 2004; Shomstein and Behrmann, 2006), or sensory modalities (Macaluso et al., 2002; Shomstein and Yantis, 2004). The respective activated regions have been suggested to be the homologues of monkey areas LIP and FEF (Paus, 1996; Van Essen et al., 2001) and have been found to increase their firing rate when the monkeys anticipated an upcoming stimulus-onset (Bushnell et al., 1981; Colby et al., 1996; Nakamura and Colby, 2000; Bisley and Goldberg, 2003). Finally, the magnitude of this anticipatory activity has been shown to be predictive for the performance in the detection of subsequently presented targets, which further underscores the importance of the dorsal-

frontoparietal system in voluntary orienting of attention [(Sapir et al., 2005; Giesbrecht et al., 2006), for an opposite account see (Sadaghiani et al., 2009)].

Additional evidence for the existence of an unitary domain-general system that mediates voluntary orienting comes from some recent studies that employed within-subject designs to demonstrate that different types of attention shifts recruit similar brain regions, e.g., by comparing shifts between colors and locations (Giesbrecht et al., 2003), objects and locations (Shomstein and Behrmann, 2006), or voluntary and stimulus-driven shifts of attention (Peelen et al., 2004). However, considerable evidence also favors the existence of several domain-specific or at least of a compartmentalized cortical network for voluntary attentional control (Rushworth et al., 2001). A functional parcellation of fronto-parietal regions has been indicated by within-subjects comparisons of spatial orienting and cue–symbol interpretation (Woldorff et al., 2004), shifts between features and locations (Slagter et al., 2007), spatial shifts and remapping of attentional priorities (Molenberghs et al., 2007), and for attention-shifts and decoupling attention from fixation (Kelley et al., 2008). While these results of an at least partial separation of attentional control processes were obtained by use of conventional univariate statistical procedures, recent studies corroborated this notion with multivariate pattern classification methodology for fMRI analysis. Thereby it could be demonstrated that specific spatiotemporal activation patterns within distinct neuronal subpopulations in dorsal fronto-parietal cortex are associated with different aspects of attentional control across perceptual domains (Chiu and Yantis, 2009; Esterman et al., 2009; Greenberg et al., 2010; Liu et al., 2011).

1.1.2.2. Stimulus-driven allocation of attention

As outlined above, earlier work considered spatial neglect symptoms to be caused by structural damage to regions located in dorsal fronto-parietal cortex. With the development of methods that provided a higher spatial resolution for the analysis of structural deficits, it became evident that the classical neglect symptoms might be based on lesions to ventral rather than dorsal fronto-parietal regions (Husain and Kennard, 1996; Mort et al., 2003; Karnath et al., 2004). These ventral lesions in turn lead to a physiological imbalance of activity between left and right dorsal parietal cortex, which has been suggested to be the final cause of the classical spatial neglect symptoms (Corbetta et al., 2005; He et al., 2007). By this means the ventral attention system might indirectly influence the goal-directed allocation of resources. However,

the primary role that has been attributed to the ventral system is the detection of salient and behaviorally relevant events and the generation of signals controlling the subsequent (re-)orienting processes (Corbetta et al., 2008).

Reorienting has been suggested to occur reflexively, based on the inherent sensory salience of the unexpectedly appearing events (Jonides and Yantis, 1988), but certain objects may also attract attention more effectively based on their particular relevance to the task (Yantis and Egeth, 1999). In this respect, it is still controversial to what extent particular events may capture attention based on their relevance given the current attentional set of an observer (Jonides and Yantis, 1988; Folk et al., 1992; Gibson and Kelsey, 1998; Yantis and Egeth, 1999; Theeuwes et al., 2010) or just passively, i.e., based on their “general” salience or biological importance (Rauschenberger, 2003). Therein, enhanced responses within the right temporoparietal junction (TPJ) and right inferior frontal gyrus (IFG), which are suggested to be the core regions of the ventral network, have been described under many different circumstances as, e.g., to presentation of infrequent or invalidly cued targets (McCarthy et al., 1997; Linden et al., 1999; Corbetta et al., 2000; Marois et al., 2000; Macaluso et al., 2002; Kincade et al., 2005; Vossel et al., 2006), to stimuli comprising target-defining features (Kincade et al., 2005; Indovina and Macaluso, 2007), to abrupt changes within a given context as, e.g., auditory event-boundaries (Sridharan et al., 2007), or even to unattended/unexpected stimuli that appear within the focus of attention (Asplund et al., 2010).

However, recent evidence converges to the notion that task-relevance rather than the pure salience of a stimulus determines whether an object is capable to activate the ventral network (for recent review see Corbetta et al., 2008). For example, presentation of exogenous cues has been shown to activate the dorsal attention system and to concurrently affect behavioral performance, but to spare the ventral attention network (Corbetta et al., 2005). Similar results have been obtained by presentation of salient but task-irrelevant distracters that diminished performance and activated dorsal but not ventral fronto-parietal areas (de Fockert et al., 2004). Conversely, ventral network activations by targets or target-like stimuli of very low salience are much higher than to highly salient but task-irrelevant distracters (Serences et al., 2005; Indovina and Macaluso, 2007). Taken together these data imply that the ventral attention system is not recruited during voluntary orienting or by salient but irrelevant events, but rather during reorienting towards stimuli that comprise

target-defining features, suggestive of a particular task-relevance within the given context.

1.1.2.3. Summary

Evidence from lesion-studies as well as neurophysiological and neuroimaging investigations over the past decades converges to the common view that attentional control is mediated by two partially separate but interacting systems (Corbetta et al., 2008). The dorsal fronto-parietal system generates the endogenous signals that bias the processing of particular features, objects or spatial locations, according to expectations and current goals (Kastner et al., 1999; Corbetta et al., 2000; Hopfinger et al., 2000), while the ventral part of the system is not activated by expectations or task preparation, but is recruited when attention is involuntarily oriented towards behaviorally relevant events as targets or target-like stimuli (Kincade et al., 2005; Indovina and Macaluso, 2007; Asplund et al., 2010). Beyond this general framework it has recently been argued that the interplay between these two networks controls the allocation of attentional resources regardless of the particular perceptual domain (Corbetta et al., 2008; Chiu and Yantis, 2009). This notion is based on recent observations that different attention-shifts (e.g. between features (Liu et al., 2003), objects (Serences et al., 2004), or locations (Hopfinger et al., 2000; Yantis et al., 2002)) recruit fronto-parietal regions in a similar manner. However, other evidence favors the existence of several domain-specific or at least one compartmentalized network for attentional control (Rushworth et al., 2001; Giesbrecht et al., 2003; Peelen et al., 2004; Woldorff et al., 2004; Shomstein and Behrmann, 2006; Molenberghs et al., 2007; Slagter et al., 2007; Kelley et al., 2008). Novel multivariate analysis methods for fMRI analysis emphasize this notion by demonstrating that specific spatiotemporal activation patterns within distinctive voxels are associated with different aspects of attentional control, even within regions that have been shown to be commonly activated across perceptual domains (Chiu and Yantis, 2009; Esterman et al., 2009; Greenberg et al., 2010; Liu et al., 2011).

1.2. Aims of the thesis

As outlined in the first part of the General Introduction, numerous studies investigated by which modes of operation attention may influence neural processing of perceptual information and concurrent behavioral performance. Traditional theories viewed the attentional selection process in a spatial framework (Posner, 1980), while recent models accentuate the importance of objects (Duncan, 1984; Desimone, 1998) or individual stimulus features (Maunsell and Treue, 2006) as the units of attentional selection. One of these models, the feature-similarity gain hypothesis, is primarily based on the neurophysiological finding that the firing of single neurons scales in a multiplicative manner when attention is directed towards their preferred stimulus-attribute (Treue and Martinez Trujillo, 1999; Martinez-Trujillo and Treue, 2004). This is observed even in cases when the attended feature is presented outside the focus of attention (Martinez-Trujillo and Treue, 2004). While conventional neuroimaging studies have corroborated this view (Corbetta et al., 1990; O'Craven et al., 1997; Buchel et al., 1998; Chawla et al., 1999; Huk and Heeger, 2000; Saenz et al., 2002; Liu et al., 2007b), they did not address the influence of feature-based attention on perceptual processing within a single feature dimension (a hallmark of neurophysiological investigations in primates that modulated the feature-values in a parametric fashion). This lack of direct experimental evidence was addressed in Experiment 1, which aimed to validate the predictions from the feature-similarity gain model at the level of integrated population responses as measured by fMRI. For this purpose, the coherence of a moving transparent surface and direction-selective attention were concurrently manipulated, allowing for the investigation of hemodynamic activations as a function of feature-selective attention and motion-coherence, and thus to test the predictions drawn from the feature-similarity gain hypothesis at the population level. In continuation of Experiment 1, the timing of global feature-based attentional selection was investigated by means of simultaneous electro-encephalographic (EEG) and magneto-encephalographic (MEG) recordings in Experiment 2. To this end, the magnitude and latency of ERPs and ERMFs evoked by a spatially unattended surface was compared in dependency of the similarity between its motion-direction and the direction of an attended surface. Experiment 3 finally extends the subject of investigation into the spatial domain. While independent demonstrations of both spatial and feature-specific modulations are numerous, direct evidence regarding the functional relation between both selection mechanisms is rare. This issue was

addressed by comparing the hemodynamic modulations to physically identical stimuli when attentional selection was based on spatial locations, features, or both.

While Experiments 1-3 primarily focused on the effects attentional selection exerts on the processing of particular stimulus attributes in early sensory cortex, the last experiment (Experiment 4) was conducted to elucidate the mechanisms that control the allocation of attentional resources during voluntary and stimulus-driven shifts of attention between objects and locations using fMRI. The neural substrates, which control such goal-directed and reflexive orienting, have already been investigated over the past decade, but none of the studies directly compared multiple types of attention-shifts in a within-subjects design. Thus it comes as no surprise that it is still a controversial issue whether attentional control is mediated by separate domain-specific networks (Rushworth et al., 2001), or by one unitary domain-general system (Yantis and Serences, 2003; Corbetta et al., 2008). Experiment 4 was specifically designed to address this question.

2. Experiment 1 - Feature-based attention modulates direction-selective hemodynamic activity in human MT ¹

2.1. Introduction

As described in detail in the General Introduction, feature-based attention modifies the firing-rate of individual neurons selective for an attended feature in a multiplicative manner (Treue and Martinez Trujillo, 1999; Martinez-Trujillo and Treue, 2004). These multiplicatively scaled responses of individual neurons have been suggested also to result in an improved selectivity for the attended feature at the population level. Such feature-based attentional modulations have previously been observed with fMRI for moving stimuli presented within or outside the focus of spatial attention (O'Craven et al., 1997; Saenz et al., 2002). However, parametric direction-selective modulations thus far have only been demonstrated using pattern classification methods for fMRI data analysis (Kamitani and Tong, 2006; Serences and Boynton, 2007). In these studies, direction-selective information could be decoded from multiple stages across the visual hierarchy. These findings, however, do not necessarily imply the actual existence of direction-selective neural populations within all of these regions (Serences and Boynton, 2007), since the response profile of a given voxel also could reflect feedforward/feedback activations instead of true direction-selective population-activity (Sillito et al., 2006).

Experiment 1 was designed to test the validity of the feature-similarity gain hypothesis using conventional fMRI analysis techniques for stimulus-features that are presented within the focus of spatial attention. Therefore, direction-selective attention and the coherence of a moving transparent surface were concurrently manipulated. In this way attention could either be directed into or opposed to the motion-direction of the surface, while its coherence was parametrically varied. This approach allowed to investigate hemodynamic activations in motion responsive regions as a function of attention and motion-coherence under identical physical conditions and thus to test the predictions from the feature-similarity gain hypothesis at the population level.

¹ The chapter is partially based on an article by Stoppel CM, Boehler CN, Strumpf H, Heinze HJ, Noesselt T, Hopf JM, and Schoenfeld MA. Feature-based attention modulates direction-selective hemodynamic activity within human MT. *Hum Brain Mapp.* 2011; 32(12):2183-92.

2.2. Methods

2.2.1. Subjects

Twelve students of the University Magdeburg (9 females; mean age: 25.0 years; all right-handed) participated as paid volunteers in Experiment 1. All subjects were neurologically normal, had normal or corrected-to-normal visual acuity and gave written informed consent before participation.

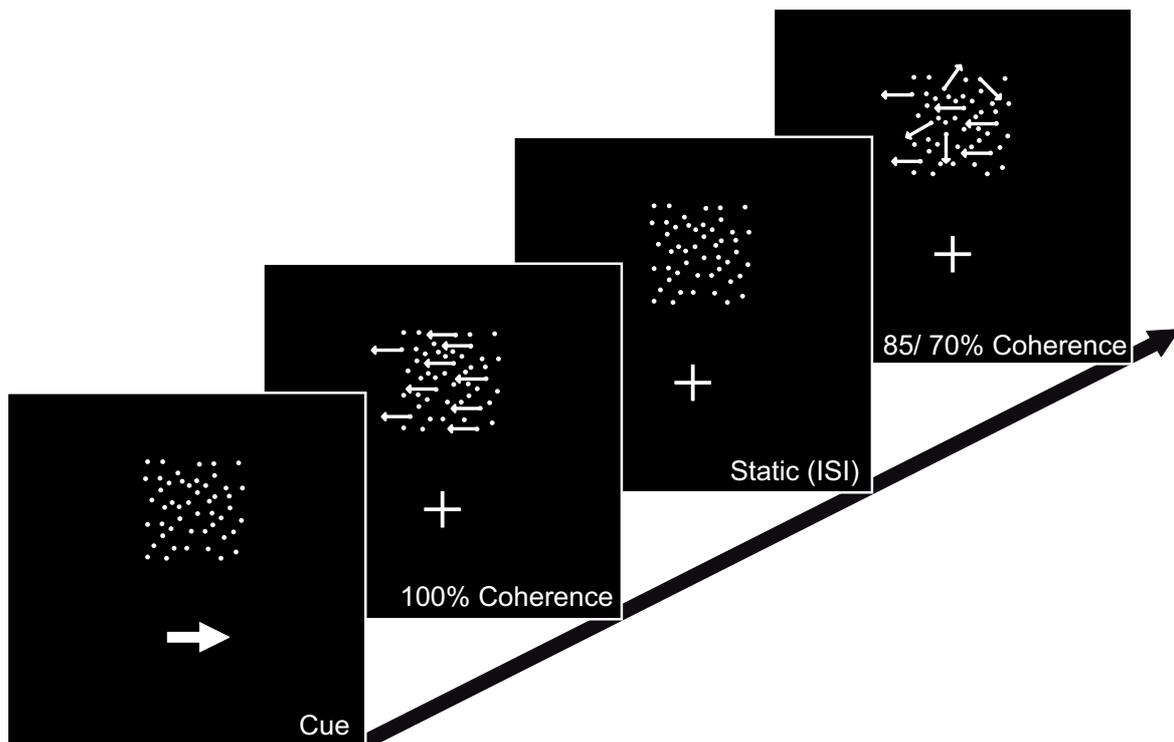


Fig. 1: Schematic illustration of the paradigm from Experiment 1. At the beginning of each block an arrow indicated the motion-direction that had to be attended by the subjects (left- or rightward motion). During the inter-stimulus interval the dots remained stationary, while during each trial they moved either left- or rightward for 300 ms. These movements could occur in three alternative coherence-levels for both motion-directions (100, 85, and 70% coherence). On some of the trials, the dots moved with a higher velocity, and subjects were required to make a button-press response if those movements occurred in the attended direction independent of the motion-coherence of the dots.

2.2.2. Stimuli and experimental design

One hundred white dots (200 cd/m^2) were presented against a dark background (45 cd/m^2) within a square region ($8^\circ \times 8^\circ$) that was located above a central fixation cross (4° to the lower edge of the square) and centered on the vertical meridian (see Fig. 1). During the inter-trial intervals all dots remained stationary. During each trial a certain fraction of the dots (100, 85, and 70%) moved coherently in the same direction (either left- or rightward) for 300 ms and thus was perceived as a transparent surface. All remaining dots were randomly displaced with the same motion speed as the transparent surface. The motion velocity of the transparent surface could either be

slow (4 °/s) or fast (6 °/s) predefined on a pseudo-random basis. The inter-trial interval varied randomly between 1 and 7 s following a gamma function to allow trial separation in an event-related analysis (Hinrichs et al., 2000). Subjects received six scanning runs of 8 min, which consisted of 10 blocks of 20 trials each, resulting in 212–233 trials per condition. Before each block, a central cue (a white arrow pointing to the left or right) replaced the fixation cross for 2 s, thereby indicating which direction of motion had to be attended by the subjects. Upon the detection of a fast movement of the transparent surface into the attended direction subjects were required to make a speeded button-press response. Such target-trials occurred in 20% of the cases while in the remaining 80% the movements were slow (standards). Thus the neuronal modulations elicited by moving transparent surfaces of variable coherence (100, 85, and 70%) could be compared, while their motion direction was either attended or opposed to the attended direction.

2.2.3. fMRI acquisition and analysis

2.2.3.1. Data acquisition

fMRI data were acquired at a 3-Tesla MR scanner (Siemens Magnetom Trio, Erlangen, Germany) using an 8-channel head coil. Stimuli were back-projected onto a screen positioned behind the head coil and viewed by the subjects via a mirror attached to the coil reflecting the images displayed on the screen. Functional data were acquired with T2*-weighted echo planar imaging (EPI) in an odd-even interleaved sequence (TR = 2000 ms, TE = 30 ms, flip angle = 80°, 30 slices, thickness = 4 mm, in plane resolution 64 x 64 mm, FoV 224 x 224 mm, no gap, resulting voxel size = 3.5 x 3.5 x 4 mm, AC-PC oriented). Each experimental session consisted of 205 volumes. Before functional data acquisition a sagittal whole-head T1-weighted high-resolution image was collected from each subject (48 slices, thickness = 4 mm, 64 x 64 matrix, FoV 224 x 224 mm, gap = 0.8 mm, spatial resolution = 0.9 x 0.9 x 4 mm, TE = 4.9 ms, TR = 15000 ms).

2.2.3.2. Image processing and statistical analysis

The functional data were analyzed using SPM5 software (Wellcome Department of Cognitive Neurology, University College London, UK) and MATLAB 7.4 (The Mathwork Inc.). The EPI volumes were corrected for differences in slice acquisition time, realigned to the first volume and spatially normalized to the standard EPI template provided by SPM5. Finally, the images were resliced to a final voxel size

of $2 \times 2 \times 2$ mm and spatially smoothed using an 8-mm full-width at half-maximum isotropic Gaussian kernel. For statistical analysis blood-oxygen level-dependent (BOLD) responses were separately modeled for each condition of interest by delta functions time-locked to the onsets of the respective stimuli. The resultant event-regressors were entered into a general linear model and convolved with the standard hemodynamic-response function implemented in SPM5, including the movement parameters derived from the realignment procedure as covariates (Friston et al., 1998). Contrasts of parameter estimates comparing trials of different motion coherence levels vs. baseline were calculated for both attention conditions and the corresponding contrast images were subsequently entered into a random-effects group-analysis treating inter-subject variability as a random effect to account for inter-individual variance. Stereotactic coordinates for voxels with maximal F-values within activation clusters are reported in MNI standard space (the significance threshold was set at a whole-brain corrected false discovery rate (FDR) of $p < 0.01$ with a minimum cluster extent of $k = 20$ contiguous voxels). For data visualization, the resultant activation maps for each contrast were superimposed onto a semitransparent surface-based representation of the MNI canonical brain using the SPM surfrend toolbox (<http://spmsurfrend.sourceforge.net>) and NeuroLens (<http://www.neurolens.org/NeuroLens/Home.html>).

To directly compare the magnitude of hemodynamic modulations induced by the different conditions, a region of interest (ROI) analysis was performed using the MarsBar toolbox in SPM5 (Brett et al., 2002). The ROIs were functionally defined based on the local activation maxima given by the overall effects of interest F-contrast of a second-level 2×3 factorial analysis of variance (ANOVA) including all 6 condition of interest (2 attention conditions \times 3 motion coherence levels; see Tab. 1 for activation-maxima of the effect of interest F-contrast and Tab. 2 for ROI-coordinates). For all ROIs (anterior cingulate cortex (ACC), fundus of the intraparietal sulcus (fIPS), human analogue of the middle temporal area (hMT), lateral parietal cortex (LPC), superior frontal gyrus (SFG), superior parietal lobe (SPL), thalamus and V3a) mean beta values were extracted from the individual subjects' data. These data were subjected to a repeated-measures ANOVA (RANOVA) with the factors region, hemisphere (left vs. right), attention condition (direction attended vs. anti-direction attended), and motion coherence (100, 85, and 70%). The significance threshold was set to $p < 0.05$ following Greenhouse-Geisser correction for non-sphericity if

necessary. No significant main effect or interactions were observed for the factor hemisphere, thus data were collapsed over both hemispheres before further analysis. Finally, these collapsed data from each ROI were separately analyzed by RANOVAs with the factors attention condition and motion coherence.

Tab. 1: Peak activation foci to motion-stimuli in the group random-effects analysis

Anatomical structure	Cluster-size (voxels)	FDR-corrected p -value	Hemi-sphere	Maximum F-value	MNI- coordinates (x, y, z)		
ACC	143	<0.01	L	15.13	-10	40	32
	274	<0.01	R	18.10	4	38	38
Cuneus	213	<0.001	L	32.20	-10	-78	2
	231	<0.001	R	36.66	16	-76	4
Dorsolateral PFC	96	<0.005	L	22.86	-42	10	30
	185	<0.005	R	22.89	42	4	30
FEF	148	<0.001	L	38.60	-48	-4	58
	173	<0.001	R	27.12	36	-4	54
FG	476	<0.001	L	92.21	-44	-70	-4
	498	<0.001	R	95.33	34	-76	-2
fIPS	36	<0.005	L	24.64	-24	-70	42
	215	<0.001	R	32.14	26	-72	42
hMT	512	<0.001	L	261.33	-42	-74	22
	514	<0.001	R	437.43	42	-68	18
IFG	229	<0.001	L	38.24	-48	40	10
LPC	283	<0.001	L	28.55	-38	-66	54
	178	<0.001	R	29.78	52	-70	40
SFG	102	<0.01	L	17.45	-14	36	52
	265	<0.001	R	34.60	16	22	60
SMA	156	<0.005	L	24.43	-10	12	44
	71	<0.001	R	26.56	8	14	52
SMG	229	<0.001	L	35.61	-54	-30	26
	311	<0.001	R	56.35	50	-26	28
SPL	143	<0.001	L	38.75	-22	-38	70
	397	<0.001	R	84.34	22	-40	72
Thalamus	240	<0.001	L	32.93	-10	-14	2
	158	<0.001	R	39.86	16	-14	6
V3a	439	<0.001	L	73.46	-10	-90	30
	417	<0.001	R	62.74	10	-90	26

FDR-corrected cluster p -value < 0.01; extent threshold k = 20 voxels. Abbreviations: ACC, anterior cingulate cortex; FEF, frontal eye field; FG, fusiform gyrus; fIPS, fundus of the intraparietal sulcus; hMT, human analogue of the middle temporal area; IFG, inferior frontal gyrus; LPC, lateral parietal cortex; PFC, prefrontal cortex; SFG, superior frontal gyrus; SMA, supplementary motor area; SMG, supramarginal gyrus; SPL, superior parietal lobe.

2.3. Results

2.3.1. Behavioral results

On target trials subjects responded correctly in 73.1% of the trials (standard error of the mean; SEM: 6.3%) with a mean reaction time (RT) of 701 ms (SEM: 46 ms). To investigate the influence of motion coherence on the subjects' behavioral responses, RTs and the percentage of correct responses were separately submitted to RANOVAs with the factor motion coherence (100, 85, and 70% coherence). These analyses revealed a significant main effect of motion coherence on the hit rate ($F(2,22) = 8.7, p < 0.005$), but not on the RTs of the subjects ($F(2,22) = 1.6, p > 0.2$), consistent with a speed-accuracy trade-off under increased perceptual demands (low coherence-levels). The main effect of motion coherence on the subjects' hit rates resulted from significantly more correct responses on full coherent stimuli in comparison to 70% coherent motion ($p < 0.01$) and an almost significantly higher hit rate on 85% coherent stimuli in comparison to 70% coherent motion ($p = 0.07$).

Tab. 2: MNI-coordinates of the ROIs

Anatomical structure	MNI coordinates (left hemisphere)			MNI coordinates (right hemisphere)		
	x	y	z	x	y	z
ACC	-10 ± 4	40 ± 4	32 ± 4	4 ± 4	38 ± 4	38 ± 4
fIPS	-24 ± 4	-70 ± 6	39 ± 5	27 ± 5	-72 ± 6	38 ± 6
hMT	-43 ± 5	-73 ± 5	21 ± 5	45 ± 5	-71 ± 7	15 ± 5
LPC	-46 ± 4	-66 ± 4	52 ± 4	46 ± 4	-62 ± 4	42 ± 4
SFG	-14 ± 4	36 ± 4	52 ± 4	16 ± 4	22 ± 4	60 ± 4
SPL	-22 ± 4	-38 ± 4	70 ± 4	22 ± 4	-40 ± 4	72 ± 4
Thalamus	-10 ± 4	-15 ± 7	3 ± 5	15 ± 3	-15 ± 3	2 ± 4
V3a	-20 ± 4	-82 ± 4	32 ± 4	12 ± 4	-92 ± 4	24 ± 4

Abbreviations: ACC, anterior cingulate cortex; fIPS, fundus of the intraparietal sulcus; hMT, human analogue of the middle temporal area; LPC, lateral parietal cortex; SFG, superior frontal gyrus; SPL, superior parietal lobe.

2.3.2. fMRI results

2.3.2.1. Group random-effects analysis

In the effects of interest contrast from the 2 x 3 factorial ANOVA group analysis clusters of significant attention and/ or coherency-dependent activations were identified within fronto-parietal (ACC, frontal eye-field (FEF), LPC, SFG, supplementary motor area (SMA) and SPL), extrastriate visual (fusiform gyrus (FG), hMT, fIPS and V3a) and thalamic regions (see Tab. 1 for MNI coordinates and F-values). ROIs were centered on the local maxima within several of these fronto-

parietal, extrastriate and thalamic regions (see Tab. 2 for the corresponding MNI coordinates) to directly assess the influence of feature-based attention on the magnitude of neural modulations induced by stimuli of different coherence-levels.

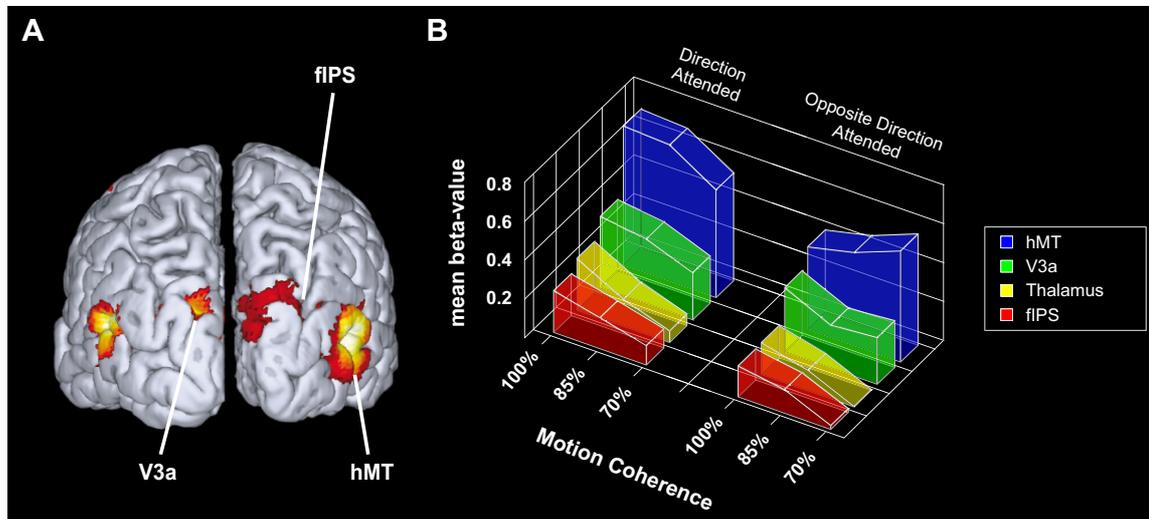


Fig. 2: A) Activation map from the group random-effects analysis of Experiment 1. The activation map shows regions that are more active during (non-target) motion-trials than during presentation of stationary dots. The significance threshold for visualization was set at a (corrected) family-wise error level of $p < 0.05$. **B) Attentional modulation of neural activations to visual motion coherence within extrastriate and thalamic regions.** The mean beta values for all coherence-level are separately depicted for both attention conditions. Beta parameter estimates are averaged over subjects ($n=12$) and hemispheres for each ROI. Note that hMT displays an inverse linear relationship between motion-coherence and the magnitude of the signal estimates for attended and unattended conditions, which is in contrast to all other regions. Abbreviations: fIPS, fundus of the intraparietal sulcus; hMT, human analogue of the middle temporal area.

2.3.2.2. Region of interest analyses

Analysis of the ROI-data by a RANOVA with the factors region (ACC, fIPS, LPC, SFG, SPL, thalamus, V3a, hMT), hemisphere (left vs. right), coherence (100, 85, and 70% coherence) and attention condition (direction attended vs. anti-direction attended) showed significant main effects for the factors region ($F(7,77) = 66.9$, $p < 0.001$) and attention ($F(1,11) = 6.1$, $p < 0.05$), as well as a significant 3-way interaction between the factors region, coherence, and attention condition ($F(6,66) = 4.9$, $p < 0.005$). No significant main effect, or interactions were observed for the factor hemisphere. Thus data were collapsed over hemispheres before data for each ROI were separately subjected to RANOVAs with the factors attention condition and motion coherence.

The analyses from the individual ROIs revealed remarkable differences in the activation pattern between lower-tier regions of the visual cortex (fIPS, thalamus, V3a, and hMT; see Fig. 2) and higher-tier attentional control structures (ACC, LPC, SPL, and SFG; see Fig. 3). For the fIPS and the thalamic ROIs a nearly linear relationship

between the magnitude of the hemodynamic response and the coherence of the moving transparent surface was observed (see Fig. 2B), which was independent of attention. This was reflected by a significant main effect for the factor motion coherence (fIPS: $F(2,22) = 7.2, p < 0.005$; thalamus: $F(2,22) = 10.1, p < 0.001$) in absence of a main effect of attention, or an interaction between both factors, while for V3a no significant main effects or interactions were observed. In contrast, hMT showed a significant main effect for the factor attention ($F(1,11) = 28.9, p < 0.001$) and a significant attention x motion coherence interaction ($F(2,22) = 5.5, p < 0.05$), which was due to an opposite near-linear coherence-dependency for the attended and unattended motion direction: hemodynamic activity in hMT showed a positive linear relationship with motion coherence when the direction of the moving transparent surface was attended, while it was inversely correlated with the stimulus' coherence when its motion-direction had to be ignored (see Fig. 2B).

Analyses of the ROI-data from fronto-parietal attentional control regions revealed an entirely different pattern: the SPL showed main effects of attention ($F(1,11) = 16.3, p < 0.005$) and motion coherence ($F(2,22) = 16.5, p < 0.001$), but no attention x motion coherence interaction. The attentional main effect was due to higher modulations to unattended than attended stimulus motion, whereas the main effect of motion coherence was reflected by an inverse linear dependency of the modulation magnitude on the coherence of the stimuli, irrespective of attention. The other fronto-parietal regions (ACC, SFG, and LPC), in contrast, showed no main effects for the factors attention or motion coherence but a significant interaction between both factors (ACC: $F(2,22) = 24.1, p < 0.001$; SFG: $F(2,22) = 9.3, p < 0.001$; LPC: $F(2,22) = 4.5, p < 0.05$). The hemodynamic modulations within these regions were opposed to the pattern observed for area hMT: When the direction was attended, the highest modulations occurred for the least coherent stimuli, while for stimuli moving opposed to the attended direction the modulation magnitude showed a positive linear relationship with stimulus-coherence (see Fig. 3B).

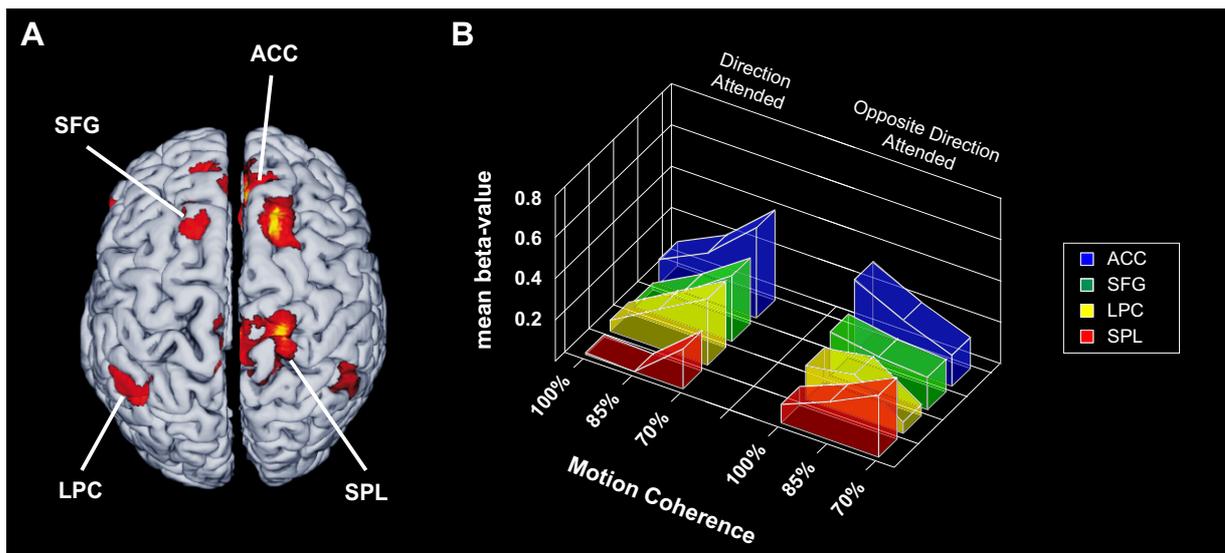


Fig. 3: A) Activation map showing activated regions that are more active during presentation of attended incoherent (70% coherence) than attended coherent (100% coherence) motion-trials. The significance threshold for visualization was set at $p < 0.001$ (uncorrected). **B) Attentional modulation of neural activations to visual motion coherence within fronto-parietal attentional control structures.** The mean beta values to all coherence-levels are separately depicted for both attention conditions. Beta parameter estimates are averaged over subjects ($n=12$) and hemispheres for each ROI. Abbreviations: ACC, anterior cingulate cortex; LPC, lateral parietal cortex; SFG, superior frontal gyrus; SPL, superior parietal lobe.

2.4. Summary

The results of Experiment 1 demonstrate that activity in hMT is positively correlated with a stimulus's coherence when its motion-direction is attended, mirroring the subjects' behavioral performance. In contrast, hMT activation magnitude is inversely related to the motion-coherence of the stimuli if their predominant motion-direction is opposed to the attended one. It is important to note that hMT was the only region that exhibited this specific pattern, while in the fIPS and the thalamus the positive linear correlation with motion-coherence occurred irrespective of feature-based attention. Attentional control regions, on the other hand, displayed an activation pattern opposed to the one observed in hMT: In accordance with a signal-detection theory perspective, their activation magnitude varied in dependence of the particular task-demands, i.e., higher hemodynamic activity was observed when the stimuli were of lower coherence. Taken together, these results provide strong support for the validity of the feature-similarity gain hypothesis at the level of entire neural populations (Martinez-Trujillo and Treue, 2004) and suggest that feature-based attention improves behavioral performance by modulation of direction-selective population-activity within area hMT.

3. Experiment 2 - Global feature-based attention parametrically modulates direction-selective electromagnetic responses in humans ²

3.1. Introduction

Using fMRI, Experiment 1 provided evidence that the multiplicative gain enhancement observed in single-cell recordings indeed results in an improved selectivity for the attended feature at the level of an integrated population response, within the cortical module that is specialized in processing the respective feature attributes. Besides these feature-based modulations for spatially attended stimuli, feature-based selection also has been shown to modulate the firing-rate of neurons in an entirely location-independent manner: a neuron's response is modified even if it is not directly driven by a stimulus within its spatial receptive field (Treue and Martinez Trujillo, 1999; Martinez-Trujillo and Treue, 2004; Bichot et al., 2005). Recently, such spatially global feature-selective modulations have also been described at the population-level using fMRI (Saenz et al., 2002; Kamitani and Tong, 2006; Serences and Boynton, 2007) and recordings of steady-state visual evoked potentials (SSVEPs) in humans (Andersen et al., 2009; Andersen et al., 2011). However, these studies did not address the timing of the attentional modulations for features presented at spatially unattended locations.

In Experiment 2, electroencephalographic (EEG) and magneto-encephalographic (MEG) activity was simultaneously recorded time-locked to the motion-onset of a spatially unattended random-dot kinematogram (RDK) to investigate the time-course and the neural substrates of global feature-based attentional selection at the population level. Participants were required to attend a moving transparent surface to perform in a motion-discrimination task in one visual field, while a second surface presented to the opposite visual field moved into 8 varying directions. This design permitted the quantification of the magnitude and latency of event-related potentials (ERPs) and event-related magnetic fields (ERMFs) evoked by the unattended surface, in dependence of the similarity between its motion-direction and the direction of the attended surface in the opposite visual field.

² The chapter is partially based on a manuscript by Stoppel CM, Boehler CN, Strumpf H, Krebs RM, Heinze HJ, Hopf JM, and Schoenfeld MA. Spatio-temporal dynamics of feature-based attention spread: Evidence from combined EEG and MEG recordings. *J Neurosci*. In Revision.

3.2. Methods

3.2.1. Subjects

Sixteen right-handed neurologically normal subjects (mean age: 27.0 years, 4 males), all with normal or corrected-to-normal visual acuity, participated as paid volunteers in the study. The local ethics committee of the Otto-von-Guericke University Magdeburg approved the experiment and all subjects gave written informed consent before participation.

3.2.2. Stimuli and experimental design

Stimuli were presented against a dark background (0.5 cd/m^2) within two square apertures ($4.2^\circ \times 4.2^\circ$) centered 5.7° to the left and right of a central fixation cross ($0.8^\circ \times 0.8^\circ$, see Fig. 4). Each aperture contained 100 randomly distributed isoluminant white dots (brightness 200 cd/m^2 ; dot size 0.08°). All dots within the left aperture moved either coherently up- (during even runs) or downward (during odd runs; velocity: $10^\circ/\text{s}$) and thus were perceived as a transparent surface. The subjects' task was to attend this surface and to make a speeded button-press response after detecting an accelerated movement of the attended surface (velocity: $22^\circ/\text{s}$ for 300 ms). Within the right aperture all dots remained stationary throughout the experiment except during probe trials in which all of them coherently performed a short displacement into one of the eight cardinal or ordinal directions (velocity: $10^\circ/\text{s}$ for 200 ms). These probe movements thus deviated from the motion-direction of the attended surface by 0° , 45° , 90° , 135° , or 180° (see Fig. 4) and were completely irrelevant to the task. All trials (target and probe trials) were presented equally often throughout the experiment in a predefined pseudo-random sequence. The inter-trial interval randomly varied between 1250 and 1750 ms (mean 1500 ms). Subjects received seven scanning runs of 385 seconds, which consisted of 252 trials each, resulting in 294 trials per condition. Throughout the experiment subjects were instructed to keep accurate fixation, which was monitored by electro-oculogram (EOG, see below).

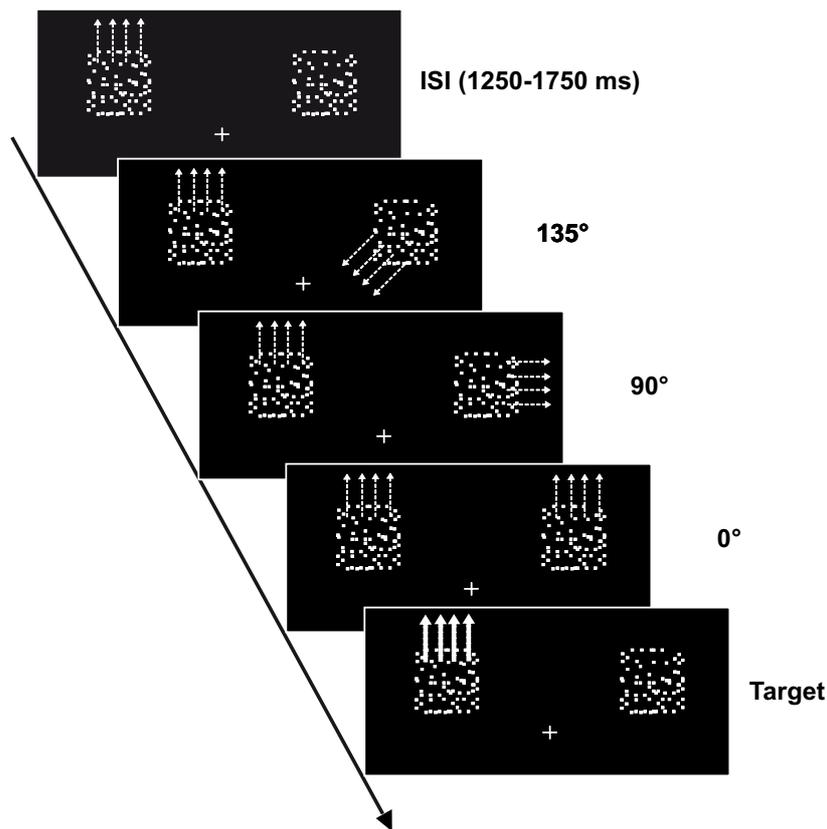


Fig. 4: Schematic illustration of the paradigm from Experiment 2. Subjects viewed two squared apertures presented to the left and right visual field. In the left aperture all dots moved either coherently up- (during even runs) or downward (during odd runs) and thus were perceived as a transparent surface. On some trials, this surface moved with a higher velocity, and subjects responded to those as targets. Within the right aperture all dots remained stationary during the inter-stimulus interval. On probe trials, all dots within the right aperture performed a short coherent displacement into one of the eight cardinal or ordinal directions, thus deviating from the motion-direction of the attended surface by 0°, 45°, 90°, 135° or 180°. These movements in the unattended aperture were completely irrelevant to the task and had to be ignored by the subjects.

3.2.3. EEG/MEG data acquisition and analysis

3.2.3.1. Data acquisition

Event-related potentials (ERP) and event-related magnetic fields (ERMF) were simultaneously recorded using a Magnes 3600 whole-head MEG-system (4-D Neuroimaging/Biomagnetic Technologies Inc., San Diego, CA) with 248 magnetometers and 32 EEG-channels (NeuroScan, Inc., Herndon, VA). The signals were digitized at a rate of 508 Hz with an online bandpass of DC to 200 Hz. The horizontal EOG was recorded using a bipolar montage with 2 electrodes behind the lateral orbital angles, whereas the vertical EOG was recorded from an electrode below the right orbital limb. Impedances were kept below 5 k Ω and an electrode placed at FPZ served as ground. MEG signals were submitted to online and offline noise reduction (Robinson, 1989), and an artifact rejection was applied with peak-to-peak limits of 2-4 pT for the MEG and 80-200 μ V for the EOG signal (thresholds individually adjusted for each subject, but constant over all experimental conditions). Individual head shapes were co-registered with the sensor coordinate system by digitizing (Polhemus 3Space Fastrak system, Polhemus Inc., Colchester, VT) skull landmarks (nasion, left, and right pre-auricular points) and determining their locations relative to

sensor and electrode positions using signals from 5 spatially distributed coils attached to the subjects' heads.

3.2.3.2. ERP/ERMF analyses

Separate ERP and ERMF average waveforms were computed time-locked to the motion onset for each of the 5 probe conditions. Attention effects were quantified in these average waveforms as mean amplitude measures within latency intervals of 110-210 and 210-310 ms after stimulus onset (with respect to a 200 ms pre-stimulus baseline) at the sensor/electrode sites showing the largest amplitudes. Statistical analysis of the data was performed using within-subjects RANOVAs (Greenhouse-Geisser correction was applied when necessary). To determine the time of onset of the attention effects, amplitude measures were taken over successive 10-ms intervals and tested for significant differences between conditions with a criterion of $p < 0.05$. The earliest significant interval followed by 5 (or more) successive significant intervals was taken as the onset latency (Guthrie and Buchwald, 1991; Schoenfeld et al., 2003b; Schoenfeld et al., 2007)

3.2.3.3. Source Localization

For source localization, current source density estimates were computed by means of standardized low-resolution electromagnetic tomography (sLORETA, Pascual-Marqui, 2002) as implemented in the neuroimaging software Curry 6.01 (Compumedics Neuroscan, El Paso, TX). The sLORETA represents an extension of the minimum norm least square (MNLS) method (Hamalainen and Ilmoniemi, 1994; Fuchs et al., 1999), where current estimates at each source location are weighted by their measurement error, yielding a pseudo-F-value distribution of currents over the cortical surface, called source density estimates (SDEs). Source localization results provided in Figs. 5 and 6 represent such estimates. All inverse computations were constrained by realistic anatomical models of the volume conductor and source compartment derived by 3-dimensional surface reconstructions of the head, cerebrospinal fluid space, and cortical surface, respectively (boundary element method, Hamalainen and Sarvas, 1989). The anatomical basis for the source analysis was the MNI brain (average of 152 T1-weighted stereotactic volumes).

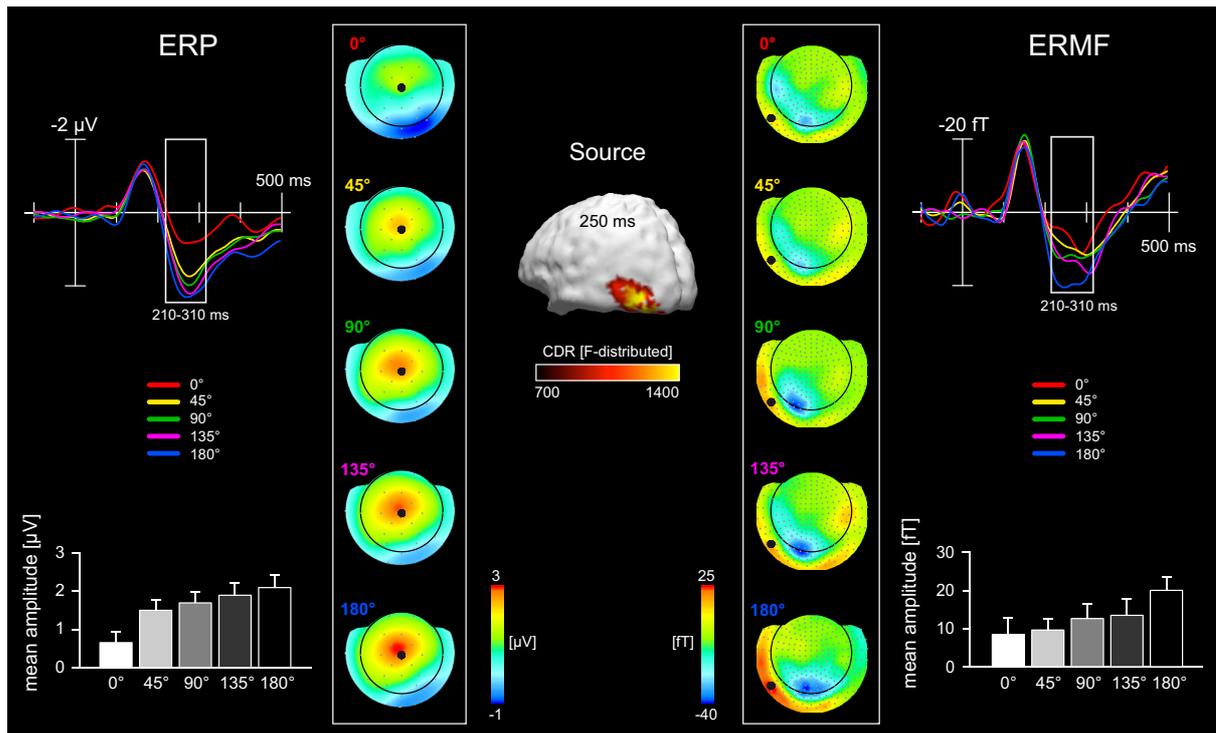


Fig. 5: Global feature-based attentional modulations between 210 and 310 ms after stimulus onset. Time courses and mean amplitudes (210-310 ms after stimulus onset) of the probe-related ERP (left column) and ERMF (right column) responses. Recording sites are indicated as black dots within the field distribution maps. Note that the magnitude of the ERP and ERMF amplitudes parametrically depends on the deviation of the probes' motion direction from the direction of the attended surface. The topographical field distributions show a maximal positivity over midline central electrode sites for the ERPs (left topography maps) and one maximum/minimum pair located over left occipito-temporal sensors for the ERMFs (right topography maps). The estimated current source density distribution 250 ms after stimulus onset (displayed in the middle of the figure) shows one maximum located in the left middle occipito-temporal cortex.

3.3. Results

3.3.1. Behavioral results

Subjects were accurate at detecting the faster moving targets, with a mean hit rate of 95.5% (SEM: 1.0%) and a false alarm rate of 2.9% (SEM: $\pm 0.7\%$). Mean reaction times (RTs) ranged from 414 to 501 ms (mean \pm SEM: 458 ± 31 ms).

3.3.2. ERP/ERMF results

The effects of feature-based attention on direction-selective neural activity were assessed, by comparing the ERP/ERMF waveforms elicited by the different probe stimuli. This comparison revealed that the magnitude of the ERP/ERMF amplitudes in the time-range between 210-310 ms depended on the similarity between the motion direction of the probes and the direction of the attended surface, with more negative ERP ($F(4,60) = 10.8$; $p < 0.0001$; see Fig. 5, left column) and ERMF amplitudes ($F(4,60) = 3.6$; $p < 0.05$; see Fig. 5, right column) for probe stimuli more closely matching the attended direction. In contrast, the magnitude of ERP/ERMF amplitudes

within the time-range of the N1-component (110-210 ms) was not significantly modulated by the similarity between the motion directions of the attended surface and that of the moving probe stimuli (ERPs; $F(4,60) = 2.0$; $p > 0.4$; see Fig. 6, left column; ERMFs; $F(4,60) = 2.0$; $p > 0.4$; see Fig. 6, right column).

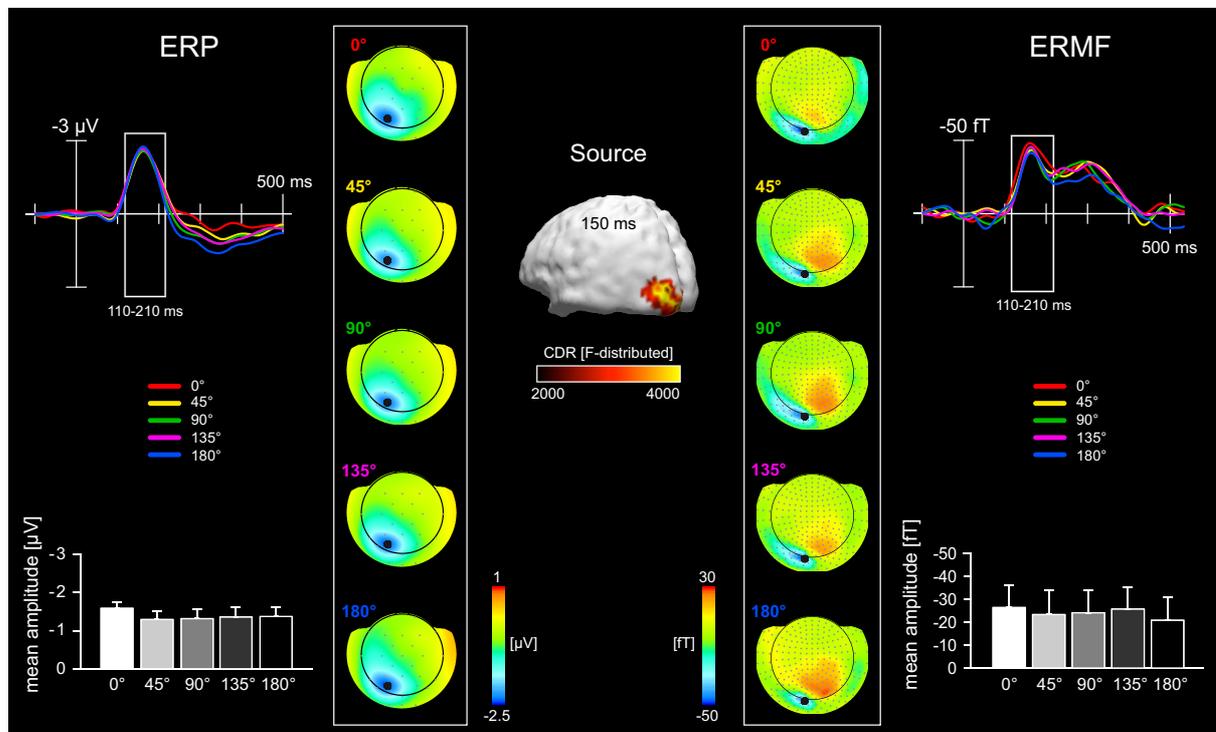


Fig. 6: No global feature-based attention effects in the time-range of the N1-component (110-210 ms after stimulus onset). Time courses and mean amplitudes of the probe-related ERP (left column) and ERMF (right column) responses in the time-range between 110 and 210 ms after onset of the probe stimuli. Recording sites are indicated as black dots within the field distribution maps. The magnitude of ERP and ERMF amplitudes shows no dependency on the motion-direction of the attended surface. A minimum in the ERP field distribution can be seen over left parieto-occipital electrode sites (left topography maps), accompanied by one maximum/minimum pair for the field distribution of the ERMFs, which is located over left occipital sensors (right topography maps). The estimated current source density distribution 150 ms after stimulus onset shows one maximum located in left ventro-lateral extrastriate cortex.

To illustrate these effects, mean ERP and ERMF amplitudes within the 110-210 and 210-310 ms intervals are separately depicted for each probe condition as bar graphs at the bottom of the left and right columns in Figs. 5 and 6. Note that the magnitude of the ERP and ERMF amplitudes between 210 and 310 ms parametrically depends on the deviation of the probes' motion direction from that of the attended surface. Statistical comparison in successive 10 ms epochs indicated that these differences between probe conditions became significant around 200 ms post-probe. In the N1 time-range, the corresponding topographical field distributions for all probe conditions showed a maximal negativity over left parieto-occipital electrodes in the ERPs (Fig. 6, left topography maps) and one maximum/minimum pair located over left

occipital sensors for the ERMFs (Fig. 6, right topography maps). In the subsequent interval between 210 and 310 ms, the ERP field distribution map showed a maximal positivity over midline central electrode sites (Fig. 5, left topography maps), accompanied by one maximum/minimum pair located over left occipito-temporal sensors for the ERMFs (Fig. 5, right topography maps). The corresponding current source distribution (sLORETA estimates, see Materials and Methods) within the N1 time-range (at 150 ms after stimulus onset) showed a single clear source-activity maximum located in the left lateral ventral extrastriate cortex, while the later time range (at 250 ms after stimulus onset) was dominated by a single maximum in left middle occipito-temporal cortex, most likely corresponding to region hMT.

3.4. Summary

The data from Experiment 2 demonstrate a global feature-based attentional modulation of ERP and ERMF amplitudes, which depends on the similarity between the motion-directions of an attended and an unattended surface. Attempts to localize the cortical generators of these modulations using current-source reconstruction and inspection of the underlying field distributions suggest them to originate from occipito-temporal cortex, probably correspondent to area hMT. The analysis of the time-courses of ERP and ERMF waveforms indicates that these modulations, in terms of a graded negativity (selection negativity, SN), occur comparatively late, starting at around ≈ 200 ms after the motion-onset. A comparison of N1-component magnitudes, in contrast, reveals no significant differences between ERPs and ERMFs elicited by the motion-probes of varying directionality. Source localization estimates suggest these modulations to originate from regions located in lower-tier regions along the visual hierarchy, as the source maxima can be observed over lateral occipital cortex. Taken together, these results demonstrate a parametric direction-selective attentional modulation of ERP and ERMF amplitudes, in support for the validity of the feature similarity gain hypothesis on the population-level (Treue and Martinez Trujillo, 1999) and further emphasize the global nature of feature-selective attention. The onset latency of these attentional modulations, however, was comparatively late (see General Discussion), with earliest effects starting around 200 ms after stimulus-onset.

4. Experiment 3 - Neural mechanisms of spatial- and feature-based attention: A quantitative analysis³

4.1. Introduction

The results from Experiments 1 and 2 convincingly demonstrate a parametric direction-selective modulation of fMRI and MEG/EEG activity, which is well in line with findings from previous fMRI and ERP studies in humans (Anllo-Vento and Hillyard, 1996; Saenz et al., 2002; Kamitani and Tong, 2006; Schoenfeld et al., 2007), and neurophysiological investigations in primates (Treue and Martinez Trujillo, 1999; Stoppel et al., 2011). The data from Experiment 2 moreover emphasize the global nature of feature-based selection (Treue and Martinez Trujillo, 1999; Saenz et al., 2002; Hopf et al., 2004), since these modulations even were observed in response to stimuli presented at unattended locations. However, in addition to its non-spatial properties, a stimulus can also be selected based on its spatial location. Common analogies of location-based selection include the spotlight or zoom lens models (Posner, 1980; Eriksen and St James, 1986), which propose that the spatial focus of attention is shifted across the visual field. Thereby enhanced processing resources are assigned to all items that fall into that spatial region regardless of their relevance to the task (Heinze et al., 1994). While convincing evidence indicates that attentional selection can be based on both the spatial and non-spatial properties of a stimulus, the direct functional relation between both (location- and feature-based) selection mechanisms has only rarely been investigated.

To test for such a direct functional relationship, Experiment 3 sought to directly compare the neuronal modulations to physically identical stimuli, while the attentional selection was directed to a stimulus' spatial location, its constituent features, or both. For this aim subjects were presented with two squared apertures located in the left and right visual field, each consisting of two different-colored dot-populations (see Fig. 7). During the task subjects were concurrently cued to attend one particular feature-value (red vs. green dot color) within one of the two apertures (left vs. right), while during each trial one dot-population (red or green) within one of both apertures executed a brief coherent movement. This design permitted to directly compare the magnitude of attentional modulations during space- and/or feature-based attentional selection to physically identical stimuli (standards).

³ The chapter is partially based on an article by Stoppel CM, Boehler CN, Sabelhaus C, Heinze HJ, Hopf JM, and Schoenfeld MA. Neural mechanisms of spatial- and feature-based attention: a quantitative analysis. *Brain Res.* 2007; 21;1181:51-60.

4.2. Methods

4.2.1. Subjects

Fifteen right-handed neurologically normal subjects (11 females; mean age: 24.1), all with normal or corrected-to-normal vision, participated as paid volunteers in the study. All gave informed consent and the local ethics committee of the Otto-von-Guericke University Magdeburg approved the study.

4.2.2. Stimuli and experimental design

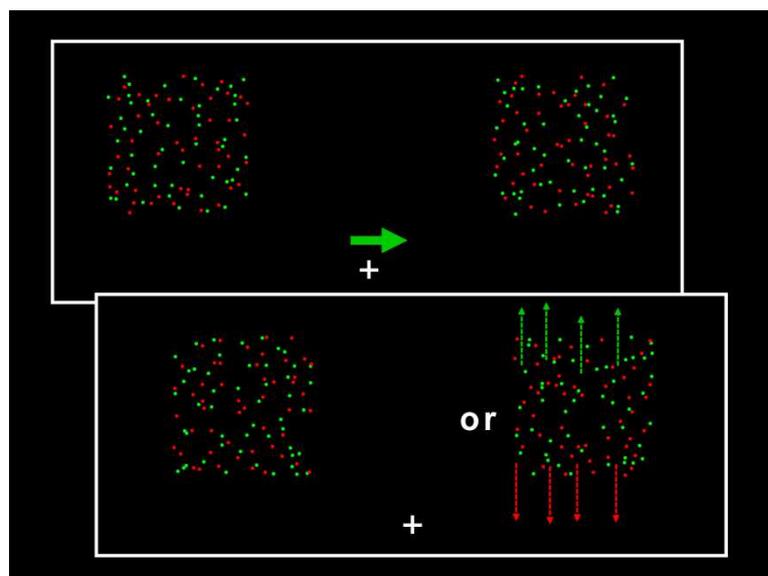


Fig. 7: Schematic illustration of the paradigm from Experiment 3. A central cue (red or green arrow) indicated the color (red vs. green) and the location (left vs. right) that had to be attended by the subjects. In the upper left and right visual field two superimposed transparent surfaces (each formed by 50 red and 50 green dots) were continuously present during the experiment. Within these transparent surfaces, fast as well as slow movements could occur at the attended as well as the unattended location in the attended or unattended surface (defined by its color). Subjects were required to press a button upon the detection of a fast movement of the attended surface at the attended location.

Subjects were presented with two square apertures ($2^\circ \times 2^\circ$), located in the upper left and right visual quadrant at 8° eccentricity (inner edge) of a central fixation cross (see Fig. 7). Each aperture contained 50 red and 50 green randomly distributed isoluminant dots (200 cd/m^2), which were presented against a grey background (luminance set at 45 cd/m^2). The fixation cross and the dots were continuously present on the screen during every run. Before each block, a central cue was presented for 1 s (red or green arrow pointing to the left or right), thereby directing the subject's attention to a particular subset of dots (either red or green) at a particular location (left or right aperture). During the inter-trial intervals all dots remained stationary, while during each trial either the red or green dots within one of the apertures moved coherently up- or downward for 500 ms. The velocity of these movement could be either slow ($4^\circ/\text{sec}$) or fast ($6^\circ/\text{sec}$). The sequence of the transparent surfaces' movements (the respective color, location, and speed) was predefined on a pseudo-random basis. Subjects were instructed to press a button as rapidly as possible when detecting a fast movement of the attended subset of dots (red or

green) within the attended location (either within the left or right aperture). Such fast movements (targets) occurred in 10 % of the cases while 90 % of the movements were slow (standards). The inter-trial interval varied randomly between 1 and 7 s following a gamma function to allow for trial separation in an event-related analysis (Hinrichs et al., 2000). Data acquisition consisted of six scanning runs of 7.5 - 8.2 minutes, including 11-12 blocks of 16-24 trials each, resulting in ~180 trials for each of the non-target conditions. For quantification of the modulation magnitudes during space- and/ or feature-based deployment of attention the following contrasts were formed:

- S+F+:** Attended feature at attended location vs. unattended feature at unattended location (reflecting attentional modulations during concomitant feature- and location-based selection).
- S+:** Attended feature at attended vs. unattended location (reflecting solely space-based attentional modulations).
- F+:** Attended vs. unattended feature at attended location (reflecting feature-based attentional modulations within the focus of spatial attention).
- RFE:** Attended vs. unattended feature at unattended location (reflecting feature-based attentional modulations outside the focus of spatial attention).

RFE: relevant feature effect.

The magnitudes of these location- and/ or feature-based modulations were compared using a ROI-analysis in which the activity was separately assessed for stimuli presented to the ipsilateral (e.g., iS+F+) as well as the contralateral visual field (e.g., cS+F+) concerning the ROIs' locations. For the RFE the ipsilateral and contralateral values were averaged resulting in only one RFE value per ROI.

4.2.3. fMRI acquisition and analysis

4.2.3.1. Data acquisition

During functional data acquisition, stimuli were presented via a projector-mirror system. fMRI data were collected using a 3-Tesla MR scanner (Siemens Magnetom Trio, Erlangen, Germany) equipped with an 8-channel head coil. Functional images were acquired with a T2*-weighted EPI-sequence (TR = 2000 ms, TE = 30 ms, flip angle = 80°). Thirty axial (AC-PC oriented) slices were acquired in an odd-even interleaved sequence (thickness = 3.5 mm, in-plane resolution 64 × 64 mm, no gap, resulting voxel size =

3.5 x 3.5 x 3.5 mm³) for 245 volumes during each of the 6 functional sessions. In a structural session, sagittal whole-head T1-weighted images (spatial resolution, 1 x 1 x 1 mm³; 256 x 256 matrix; 192 slices, no gap) were acquired using an MP-RAGE sequence (TR = 2500 ms, TE = 3.82 ms, TI = 1100 ms, flip angle = 7°).

4.2.3.2. Image processing and statistical analysis

Image pre-processing and statistical analysis of the data was performed using SPM99 software (Wellcome Department of Cognitive Neurology, University College London, UK) and MATLAB 7.4 (The Mathwork Inc.). Following correction for differences in slice acquisition time, EPI volumes were realigned and resliced using sinc interpolation and then spatially normalized to stereotactic space of the MNI brain (for normalization the standard EPI volume included in the SPM99 software package was employed as template). The normalized functional images were spatially smoothed with a 6-mm isotropic Gaussian kernel. For statistical analysis BOLD responses were separately modeled for each condition of interest by delta functions time-locked to the onsets of the respective stimuli. The data for each attention condition were collapsed over both colors used in the experiment. The resultant event-regressors were convolved with the standard hemodynamic-response function implemented in SPM99 in an event-related design for each subject, including the movement parameters derived from the realignment procedure as covariates (Friston et al., 1998). Group data were analyzed with a random-effects analysis. Stereotactic coordinates for voxels with maximal T-values within activation clusters are reported in MNI standard space ($p < 0.001$ (uncorrected) with a minimum cluster extent of 10 contiguous voxels).

To directly compare the magnitude of attentional modulations between the different attention conditions, a ROI analysis was performed using the MarsBar toolbox in SPM99 (Brett et al., 2002). Six ROIs (see Figs. 8 and 9) were functionally defined for each hemisphere based on the local activation maxima given by the overall effects of interest F-contrast of a second-level ANOVA including all conditions of interest (each condition vs. baseline). The ROIs were located in the anterior IPS, FEF, fIPS, FG, hMT, and lingual gyrus (LG). Mean beta values for the functionally defined ROIs were extracted from the individual subjects' data for each attention condition. These values were subjected to a RANOVA with the factors region (anterior IPS, FEF, FG, fIPS, hMT, and LG), hemisphere (left vs. right) and attention condition (cS+F+, iS+F+, cS+, iS+, cF+, iF+, and RFE). The significance threshold was set to $p < 0.05$ following Greenhouse-Geiser correction for

non-sphericity. For evaluation of differences in the magnitude of the attentional modulations, the data for each ROI were separately subjected to a RANOVA with the factor attention condition. If statistical significance ($p < 0.05$) was obtained, a paired t -test (*Bonferroni* corrected if necessary) was applied for *post hoc* comparison between the attention conditions.

Tab. 3: Local maxima from the group random-effects analysis

Anatomical structure	MNI coordinates (left hemisphere)			Maximum T-value	MNI coordinates (right hemisphere)			Maximum T-value
	x	y	z		x	y	z	
FEF	-38	20	28	5.86	34	6	20	7.27
LG	-12	-14	-14	6.14	8	-78	-14	5.22
FG	-40	-12	-12	6.57	32	-76	-12	8.71
Anterior IPS	-32	38	44	3.57	30	-70	38	5.73
fIPS	-34	14	16	5.57	26	-80	14	7.65
hMT	-44	-6	-2	5.56	48	-74	-6	10.02

Local maxima of ROIs showing significant attentional modulations. Values represent coordinates in mm in MNI-space and max. T-values. Abbreviations: IPS, intraparietal sulcus; FEF, frontal eye field; FG, fusiform gyrus; fIPS, fundus of the intraparietal sulcus; hMT, human analogue of the middle temporal area; LG, lingual gyrus.

4.3. Results

4.3.1. Behavioral results

Mean RTs (mean \pm SEM: 1.6 ± 0.02 s) and hit rates (mean \pm SEM: $90.4 \pm 1.6\%$) were separately submitted to RANOVAs with the factors cued color (green vs. red) and cued location (left vs. right). For the RTs this analysis revealed a significant main effect of the cued location ($F(1,14) = 13.8$, $p < 0.001$), but not of the cued color ($F(1,14) = 0.9$, $p > 0.3$), as well as a significant interaction between both factors ($F(1,14) = 22.8$, $p < 0.001$). Analysis of the subjects' hit rates, in contrast, showed a significant main effect for the factor color ($F(1,14) = 5.3$, $p < 0.05$), but not for the cued location ($F(1,14) = 1.7$, $p > 0.2$), and revealed a significant color \times location interaction ($F(1,14) = 9.0$, $p < 0.01$). *Post hoc* comparisons of cued color/ location pairs indicated that the main effect for the RTs was due to faster responses upon stimuli presented to the right visual field regardless of the stimulus color, whereas significantly higher hit rates were only observed upon green stimuli presented to the right visual field.

4.3.2. fMRI results

4.3.2.1. Group random-effects analysis

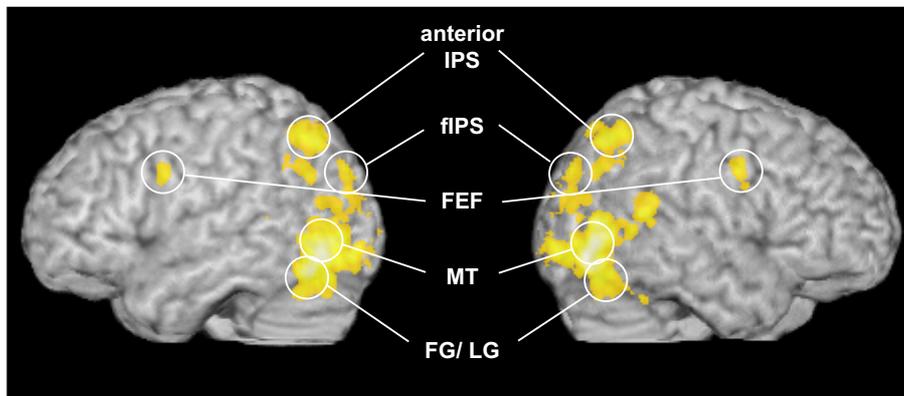


Fig. 8: Activation maps from the group random-effects analysis of Experiment 3. The figure shows foci of significant activations from the effects of interest F-contrast from the group random-effects analysis.

In the effects-of-interest F-contrast from the group analysis significant activations were identified in several brain regions located in ventral (FG and LG) and dorsal (anterior IPS, hMT and fIPS) visual stream regions, as well as in the FEF (see Fig. 8 for illustration and Tab. 3 for MNI coordinates and maximum T-values).

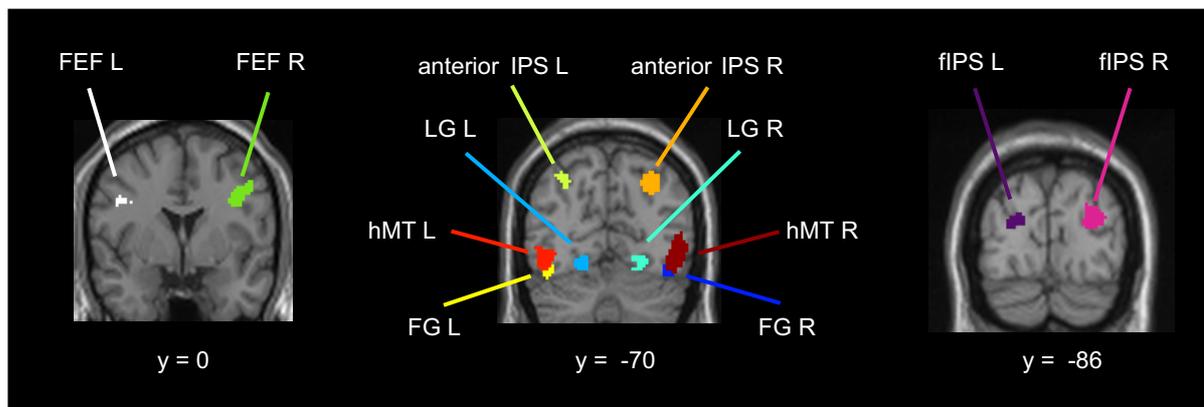


Fig. 9: Graphical illustration of the ROIs. y-coordinates in MNI-space are depicted below each slice. Abbreviations: FEF, frontal eye field; FG, fusiform gyrus; fIPS, fundus of the intraparietal sulcus; hMT, human analogue of the middle temporal area; IPS, intraparietal sulcus; LG, lingual gyrus; L/R, left/right hemisphere.

4.3.2.2. Region of interest analyses

To directly compare the magnitude of hemodynamic modulations between the different attention conditions, ROIs were centered at the local activation maxima from the effects-of-interest F-contrast from the group random-effects analysis, and beta values were extracted from the individual subjects' data (see Fig. 9 for a graphical illustration of the ROIs and Tab. 4 for the corresponding MNI coordinates). Attentional modulations for each ROI are depicted in Fig. 10 (anterior IPS and hMT), Fig. 11 (FEF and fIPS), and Fig. 12 (FG and LG).

Tab. 4: MNI-coordinates of the ROIs						
Anatomical structure	MNI coordinates (left hemisphere)			MNI coordinates (right hemisphere)		
	x	y	z	x	y	z
FEF	-41 ± 7	3 ± 5	30 ± 4	41 ± 9	-2 ± 8	30 ± 14
FG	-39 ± 7	-76 ± 12	-13 ± 7	40 ± 4	-71 ± 9	-16 ± 4
LG	-20 ± 4	-71 ± 3	-10 ± 4	22 ± 6	-68 ± 8	-10 ± 4
Anterior IPS	-34 ± 8	-61 ± 9	45 ± 9	28 ± 8	-63 ± 9	43 ± 9
fIPS	-24 ± 10	-82 ± 10	18 ± 10	27 ± 7	-81 ± 11	21 ± 7
hMT	-45 ± 7	-73 ± 9	-7 ± 9	47 ± 7	-69 ± 9	-3 ± 13

Values represent coordinates in mm in MNI-space. Abbreviations: FEF, frontal eye field; FG, fusiform gyrus; fIPS, fundus of the intraparietal sulcus; hMT, human analogue of the middle temporal area; IPS, intraparietal sulcus; LG, lingual gyrus.

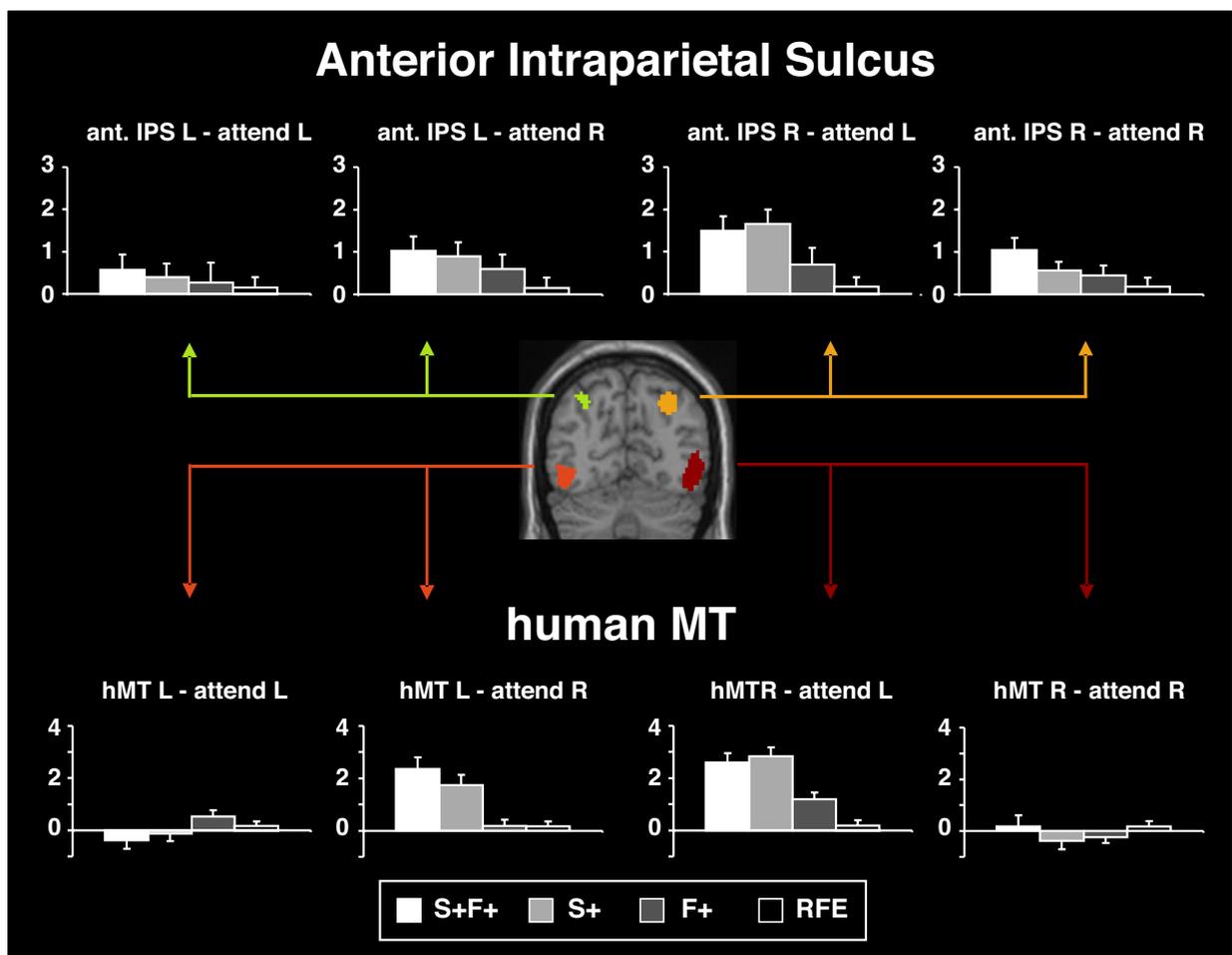


Fig. 10: Attentional modulation of neuronal activity in the anterior IPS and hMT by the different attention conditions. The bar color indicates the particular attention condition [white: attended feature at the attended location > unattended feature at the unattended location (S+F+); light grey: attended feature at the attended > at the unattended location (S+); dark grey: attended > unattended feature at the attended location (F+); black: attended > unattended feature at the unattended location (relevant feature effect, RFE)]. Abbreviations: IPS, intraparietal sulcus; hMT, human analogue of the middle temporal area; L/R, left/right hemisphere.

Statistical evaluation of the ROI analysis data by a RANOVA with the factors region (anterior IPS, FEF, FG, fIPS, hMT, and LG), hemisphere (left vs. right), and attention condition (cS+F+, iS+F+, cS+, iS+, cF+, iF+, and RFE) showed significant main effects for the factor region ($F(5,65) = 12.4, p < 0.001$), whereas a very strong trend towards significance was observed for the factors hemisphere ($F(1,13) = 4.2, p = 0.06$) and attention condition ($F(6,78) = 2.6, p = 0.076$). Moreover the analysis revealed a significant 3-way interaction between the factors region, hemisphere, and attention condition ($F(30,390) = 10.2, p < 0.001$). For direct comparison of the magnitude of attentional modulations within each ROI, RANOVAs with the factor attention condition were separately applied to the data of each ROI. If statistical significance ($p < 0.05$) was assured, paired t -tests were applied for *post hoc* comparison (*Bonferroni* corrected if necessary).

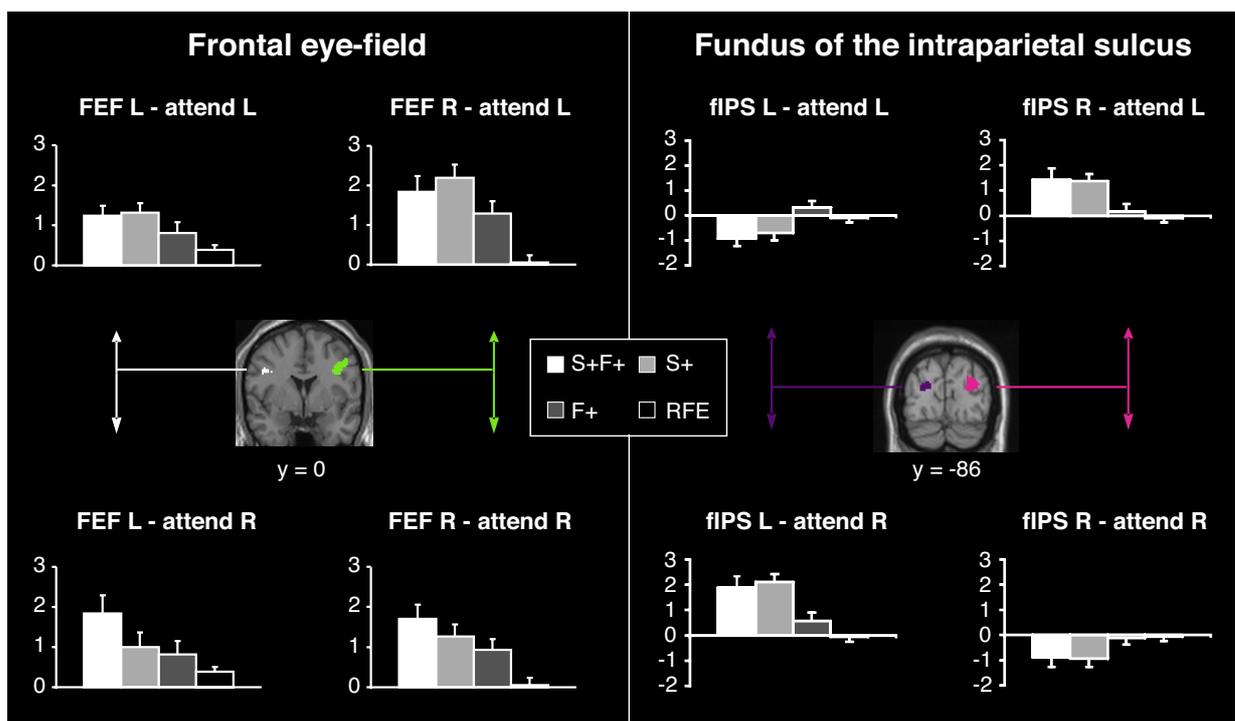


Fig. 11: Modulation of hemodynamic activity in the frontal eye field (FEF) and the fundus of the intraparietal sulcus (fIPS) by the different attention conditions. The bar color indicates the particular attention condition [white: attended feature at attended location > unattended feature at unattended location (S+F+); light grey: attended feature at attended > at unattended location (S+); dark grey: attended > unattended feature at attended location (F+); black: attended > unattended feature at unattended location (relevant feature effect, RFE)]. Abbreviations: FEF, frontal eye field; fIPS, fundus of the intraparietal sulcus; L/R, left/right hemisphere.

For the anterior IPS the RANOVA revealed a significant main effect within the right hemisphere ($F(6,78) = 3.2, p < 0.05$), but none of the *post hoc* comparisons between the conditions remained significant after *Bonferroni* correction (for illustration of the data from the anterior IPS see Fig. 10). The RANOVA applied on the ROI data

from the FEF also showed a significant main effect only for the right hemisphere ($F(6,78) = 6.5$, $p < 0.001$), which was due to significantly higher attentional modulations upon the cS+F+, cS+, and iS+F+ conditions in comparison to the RFE (see Fig. 11 for illustration).

Analysis of the beta parameter estimates from the hMT-ROIs revealed significant main effects for both hemispheres (left hMT: $F(6,78) = 12.6$; right hMT: $F(6,78) = 6.0$; $p < 0.001$ for both ROIs). Pairwise comparisons showed that within both hMT ROIs the highest attentional modulations occurred to the cS+F+ and cS+ contrasts. Within the right hMT, both conditions differed significantly from all other conditions except each other, while the left hMT was modulated in a similar manner whereas both cS+F+ and cS+ conditions were not significantly different from the iF+ contrast (see Fig. 10 for illustration of the hMT data).

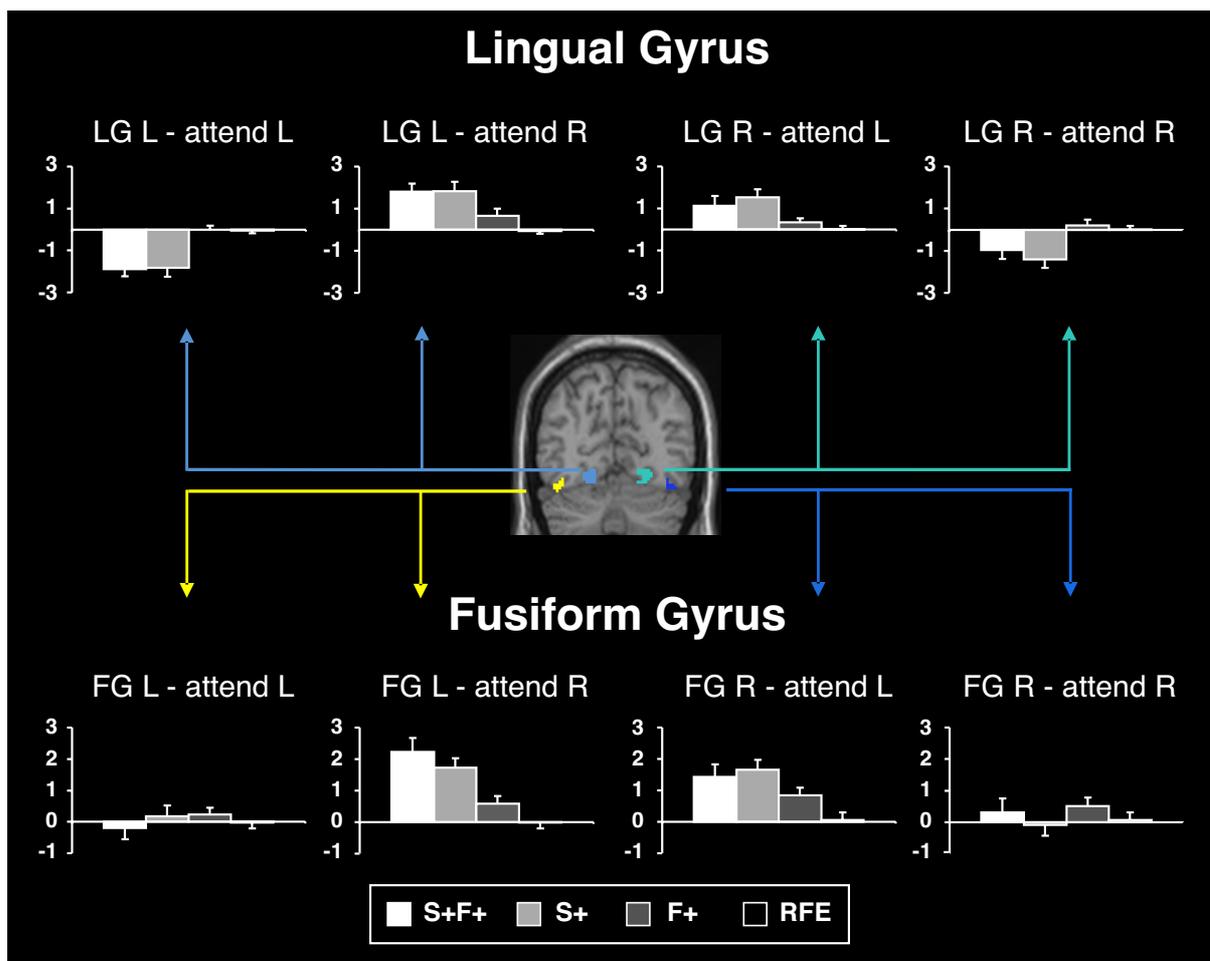


Fig. 12: Attentional modulation of neuronal activity in the fusiform gyrus (FG) and lingual gyrus (LG) by the different attention conditions. The bar color indicates the particular attention condition [white: attended feature at the attended location > unattended feature at the unattended location (S+F+); light grey: attended feature at the attended > at the unattended location (S+); dark grey: attended > unattended feature at the attended location (F+); black: attended > unattended feature at the unattended location (relevant feature effect, RFE)]. Abbreviations: FG, fusiform gyrus; LG, lingual gyrus; L/R, left/right hemisphere.

Significant main effects for both hemispheres were observed in RANOVAs applied to the fIPS as well as the LG data (left fIPS: $F(6,78) = 10.0$; right fIPS: $F(6,78) = 13.2$; left LG: $F(6,78) = 19.6$; right LG: $F(6,78) = 8.2$; $p < 0.005$ for all ROIs). *Post hoc* analysis showed that in both fIPS ROIs and in the left LG neural activity increased if spatially attended stimuli were presented to the contralateral visual field (cS+F+ and cS+, differing significantly from all other contrasts but not from each other), whereas it decreased for stimulus presentations to the ipsilateral visual field (iS+F+ and iS+, differing significantly from all other contrasts but not from each other). For illustration of the data from the fIPS see Fig. 11 and for the LG data see Fig. 12).

Statistical evaluation of the FG data showed a significant main effect for both hemispheres (left FG: $F(6,78) = 11.1$; right FG: $F(6,78) = 6.0$, $p < 0.001$ for both ROIs). Pairwise comparison revealed that the highest attentional modulations occurred upon spatially attended stimuli presented to the contralateral visual hemifield (cS+F+ and cS+; see Fig. 12 for illustration of the FG data). For the left hemisphere the cS+F+ condition differed significantly from all conditions except cS+, which in turn showed higher modulations in comparison to the cF+, iS+F+, and RFE contrasts. The right FG showed the highest attentional modulations upon the cS+ (differing significantly from all ipsilateral conditions and the RFE).

4.4. Summary

In Experiment 3, hemodynamic activations elicited by physically identical stimuli were compared, while attention was either directed towards or opposed to their spatial location and constituent features. The highest hemodynamic modulations were observed when attentional selection was based on the stimulus' spatial location, regardless of whether its color was attended or not. Positive, though relatively smaller, modulations could also be seen for purely feature-based attentional selection within the focus of attention, i.e., for spatially attended stimuli that also comprise the attended relative to the unattended color. However, feature-selective activity to stimuli presented at unattended locations was only evident in motion- but not in color-sensitive regions. In summary, these data suggest that spatial attention appears to be the more efficient selection-mechanism in vision. Moreover, they also indicate that a stimulus' motion is more efficiently targeted by feature-based attention than its color, emphasizing the high biological priority of moving stimuli.

5. Experiment 4 - Overlapping networks control the voluntary and stimulus-driven shifts of attention between objects and locations⁴

5.1. Introduction

Experiments 1-3 investigated how feature- and/or location-based attention affects neural activity within regions that process the perceptual attributes of the presented stimuli. Therefore the subjects were cued to deploy their attention to a particular feature and/or location, while neural activity in response to subsequent stimulus-presentation was assessed. However, conceptually, it is important to distinguish these modulations of neural activity within target regions located in striate and extrastriate visual cortex, from the attentional control signals that bias this selection process. Experimentally, this distinction is achieved by temporal separation of the preparatory control signals from the responses elicited by the subsequently presented stimuli. Although this prerequisite was generally fulfilled within Experiments 1-3 (the cues were temporally separated from the targets/standards), the particular experimental designs did not allow for a detailed investigation of these control signals that bias the selection of particular features, objects, or locations.

Besides the distinction based on the particular units that are selected for preferential processing (e.g., particular features, locations, or objects), attentional control can also be characterized based on the origin of this guidance process: thus, attentional selection can be driven by endogenous (voluntary/goal-directed) as well as exogenous (involuntary/stimulus-driven) factors. The neural mechanisms underlying such voluntary and stimulus-driven mechanisms of attentional control have been extensively investigated using neurophysiological recordings in primates and functional neuroimaging in humans (for recent reviews see: Maunsell and Treue, 2006; Corbetta et al., 2008; Reynolds and Heeger, 2009). However, it is still a matter of debate whether attentional control is mediated by separate domain-specific networks (Rushworth et al., 2001), or by one unitary domain-general system (Yantis and Serences, 2003; Corbetta et al., 2008).

Experiment 4 was conducted to investigate the neural correlates of these attentional control signals during voluntary and stimulus-driven shifts of attention

⁴ The chapter is partially based on a manuscript by Stoppel CM, Boehler CN, Strumpf H, Krebs RM, Heinze HJ, Hopf JM, and Schoenfeld MA. Distinct representations of attentional control during voluntary and stimulus-driven shifts across objects and locations. *Cereb Cortex*, In Revision.

between objects and locations. Therefore, subjects were explicitly cued to (i) maintain their attention at a currently attended surface, (ii) switch to another surface at the same location, or (iii) to switch to a surface located in the opposite visual field. In addition, the subjects' attention could be involuntarily captured (iv) by target-like movements of the unattended surface at the attended location or (v) of an unattended surface located in the opposite visual field (see also Fig 13). This design permitted to directly compare the neural modulations to voluntary and stimulus-driven shifts of attention between objects and locations in the absence of sensory confounds.

5.2. Methods

5.2.1. Subjects

Sixteen neurologically normal right-handed subjects (9 females), all with normal or corrected-to-normal vision, participated as paid volunteers in the study (mean age: 25.9 years). All gave written informed consent before participation and the local ethics committee approved the study. To ensure high performance, all subjects completed three practice sessions outside and one inside the scanner before participating in the main experiment.

5.2.2. Stimuli and experimental design

Two square apertures ($4.0^\circ \times 4.0^\circ$) centered 6.8° to the left and right of, and 4.0° above, a central fixation cross ($0.7^\circ \times 0.7^\circ$, see Fig. 13) were presented against a dark background (0.5 cd/m^2). Each aperture contained 100 randomly distributed isoluminant white dots (brightness 200 cd/m^2 ; dot size 0.1°), of which each half continuously moved coherently into opposite directions (horizontal in the left and vertical in the right aperture; velocity: $8.7^\circ/\text{s}$). In this way, two transparent moving surfaces located in the same region of visual space were generated within each aperture.

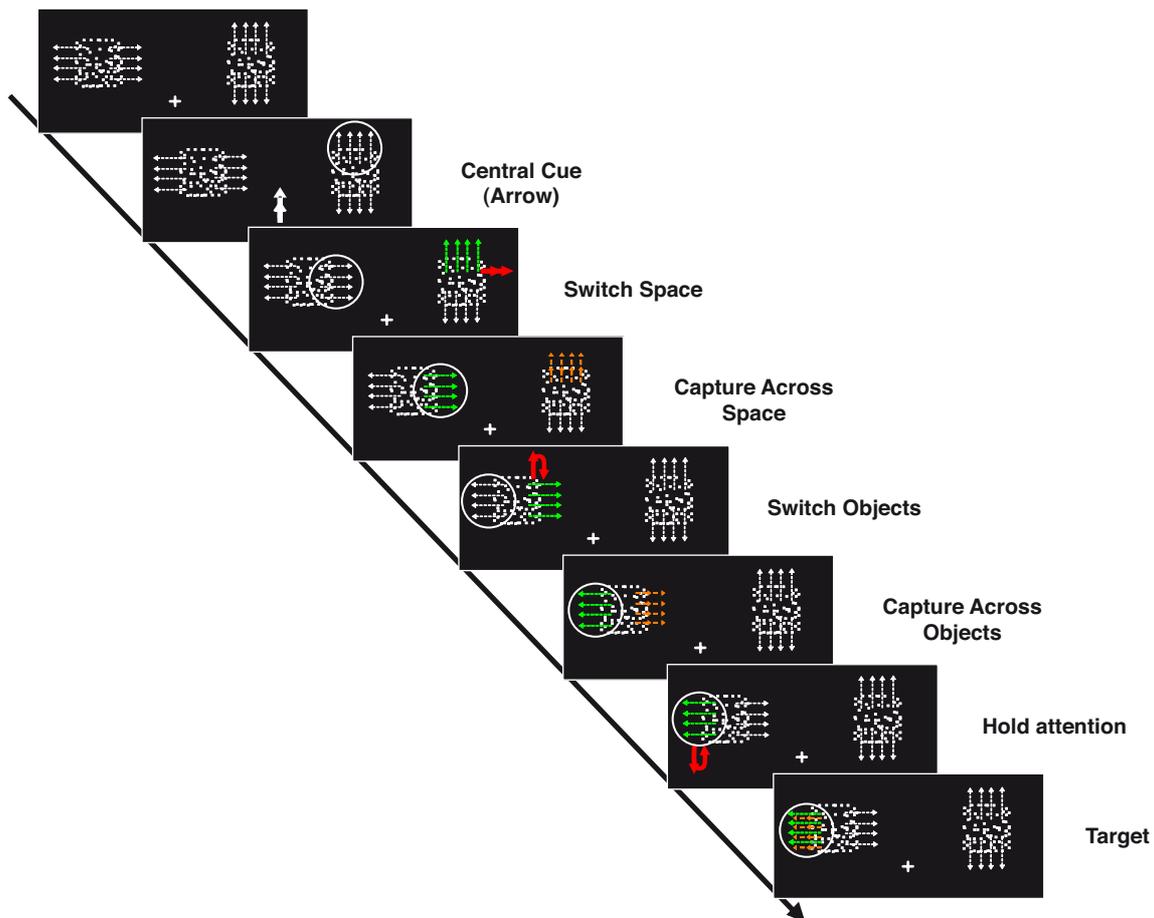


Fig. 13: Schematic illustration of the paradigm from Experiment 4. Within two apertures located in the left and right visual field two overlapping transparent surfaces continuously moved into opposite horizontal (left aperture) and vertical (right aperture) directions. At the start of each run (and every 10th trial thereafter) a central cue indicated the surface to be attended (2nd screenshot). Green arrows and white circles illustrate the surfaces to be attended before onset (green arrows) and after completion (white circles) of the trial. Red arrows indicate the cue sequences instructing the subjects to either voluntarily maintain (7th screenshot), or shift their attention between surfaces presented at the same (5th screenshot) or at different spatial locations (3rd screenshot). The cue sequences consisted of two short displacements orthogonal to the predominant motion-direction of the attended surface. Orange arrows symbolize fast movements in this predominant motion-direction, which served as targets (fast movement of an attended surface; bottom screenshot), or involuntarily captured the subjects' attention across surfaces (fast movement of unattended object at attended location; 6th screenshot) or across spatial locations (fast movement of unattended object at unattended location; 4th screenshot).

At the beginning of each run, a central cue (a white double-arrow pointing into one of the four standard movement directions of the transparent surfaces for 1.5 s) indicated which of the surfaces had to be attended initially by the subjects. During subsequent trials, beside target (fast movements in the attended surface) and non-target (fast movements in the unattended surfaces) stimuli, one out of four simple motion sequences (cue sequences) could also occur within the attended surface (for an illustration of the task see Fig. 13). Each of these cue sequences consisted of a combination of two short subsequent displacements orthogonal to the standard movement direction of the surface (each displacement lasted for 300 ms and was separated by an interval of 200 ms; velocity 21.2 °/s). Intense training prior to the

scanning session ensured that upon these motion sequences subjects either maintained their attention at the same surface, switched their attention to the other surface within the same aperture, or switched their attention to one specific surface located in the opposite visual field (a detailed description of the individual motion sequences that were used to guide the subjects' attention voluntarily is given in Figure 14A). Thus, the instructional cue sequences resulted in three attention conditions upon which the subjects voluntarily directed their attention to one of the presented surfaces (Hold Attention, Switch Object, Switch Space).

The subjects' task was to deploy attention according to the instructional cue sequences and to perform a button press response whenever they detected the occurrence of a fast coherent movement ($21.2^\circ/\text{s}$) in the predominant motion direction of the currently attended surface. In addition, fast movements also could occur within one of the non-attended surfaces, thereby capturing the subjects' attention in a stimulus-driven manner (a detailed description of the target- and the capture-trials is given in Figure 14B). These capture-trials either could occur within the unattended surface at the attended location (attentional capture within space across objects) or within one of the surfaces located in the unattended visual field (attentional capture across space). Thus, the fast movements not only served as targets, but resulted in two additional attention conditions, in which the subjects' attention was reallocated in a stimulus-driven manner (Capture Across Objects, Capture Across Space). To guarantee that the task-performance was high throughout the entire experiment, a central cue was presented every 10th trial (a white arrow pointing into the motion-direction of the currently to-be-attended surface for 1.5 s), allowing the subjects to re-engage in the task, in case that they had lost the currently to-be attended surface. All experimental manipulations (arrow cues, targets, capture trials, and instructional cue sequences) were considered as trials of independent conditions. The interval between the trials randomly varied between 3 and 8 s (mean inter-trial interval: 3.7 s) following a gamma function to allow for trial separation in an event-related analysis (Hinrichs et al., 2000). Subjects performed seven scanning runs of 6.3 min, each consisting of 12 blocks (time between arrow presentations) of nine trials, resulting in 51-65 trials per condition.

A

Condition	Attended Object at Trial-Onset	Motion-Sequence of Attended Object	Attended Object after Trial-End
Hold Attention L			
Hold Attention R			
Switch Object L			
Switch Object R			
Switch Space L			
Switch Space R			

B

Condition	Attended Object at Trial-Onset	Fast Movements	Attended Object after Trial-End
Capture across Objects L			
Capture across Objects R			
Capture across Space L			
Capture across Space R			
Target L			
Target R			

Fig. 14: Schematic illustration of the A) instructional cue sequences and B) target and capture trials. The particular surfaces that had to be attended at particular trial onsets are shown within the left column. The right column indicates the respective surfaces that had to be attended after completion of a particular trial. **A)** Red arrows (middle column) indicate the motion-directions of the cue sequence that guided the subjects' attention voluntarily. **B)** Orange arrows in the middle column indicate the particular surface that executed a fast movement. Target-trials were defined as fast movements in the predominant motion-direction of the attended surface, while fast movements of the unattended surfaces involuntarily captured the subjects' attention across objects (fast movement of the unattended object at the attended location) or across spatial locations (fast movement of an unattended object at the unattended location).

5.2.3. fMRI acquisition and analysis

5.2.3.1. Data acquisition

MR data were acquired on a 3-Tesla MR scanner (Siemens Magnetom Trio, Erlangen, Germany) using an 8-channel head coil. An LCD projector back-projected the stimuli on a screen positioned behind the head coil, which was viewed by the subjects via a mirror attached to the coil. Functional images were acquired with a T2*-weighted EPI sequence (32 AC-PC oriented slices, thickness = 3.5 mm, in plane

resolution 64 x 64 mm, FoV 224 x 224 mm, no gap, resulting voxel size = 3.5 x 3.5 x 3.5 mm, TR = 2000 ms, TE = 30 ms, flip angle = 80°) in an odd-even interleaved sequence. Each scanning session consisted of 190 volumes. In a structural session, whole-head T1-weighted images of each subject's entire brain were collected using an MP-RAGE sequence (96 sagittal slices, thickness = 2 mm, FoV 256 x 256 mm, no gap, spatial resolution = 1 x 1 x 2 mm, TR = 1650 ms, TE = 5 ms, TI = 1100 ms).

5.2.3.2. Image processing and statistical analysis

Pre-processing and statistical analysis of the fMRI data were performed using the SPM5 software package (Wellcome Department of Cognitive Neurology, University College London, UK) and MATLAB 7.4 (The Mathwork Inc.). The functional volumes were corrected for slice-acquisition time, realigned to the first volume, and spatially normalized to an EPI template in standard MNI space. After re-sampling to a final voxel size of 2 x 2 x 2 mm, the normalized images were smoothed with an isotropic 8-mm full-width at half-maximum Gaussian kernel and highpass-filtered (cut-off 128 s).

For statistical analysis, BOLD responses were modeled by delta functions at the time of stimulus onsets. For each subject, the resultant event-regressors were entered into a general linear model and convolved with the standard hemodynamic-response function implemented in SPM5, including the movement parameters derived from the realignment procedure as covariates (Friston et al., 1998). The parameter estimates for each of the 10 conditions of interest per subject (Hold Attention left/right, Switch Objects left/right, Switch Space to the left/right, Capture Across Objects left/right, Capture Across Space to the left/right) were then entered into a second-level, random-effects group-analysis treating inter-subject variability as a random effect to account for inter-individual variance. Individual maxima within contiguous activation-clusters are reported if they are separated by more than 16 mm. Stereotactic coordinates for voxels with maximal z-values within significant activation clusters are reported in the MNI standard space (corrected at a whole-brain FDR of $p < 0.01$ with a minimum cluster extent of $k = 20$ contiguous voxels).

For visualization of the data, activation maps were superimposed on a semitransparent surface-based representation of the MNI canonical brain using the SPM surfrend toolbox (<http://spmsurfrend.sourceforge.net>) and the open source application NeuroLens (<http://www.neurolens.org>), as well as MRICron software (<http://www.sph.sc.edu/comd/rorden/MRiCron/main.html>). In addition, to visualize the activation overlap between conditions, SPM activation maps for each condition (collapsed across both sides of stimulus presentation) were superimposed onto an anatomical template image using the MRICro software package (<http://www.sph.sc.edu/comd/rorden/mricro.html>). The resultant color-coded maps indicate the activation density (number of overlapping statistical parametric maps) within each region (whole-brain FDR corrected threshold of $p < 0.01$, with a minimum cluster size of $k = 20$ contiguous voxels).

Tab. 5: Peak activation foci from the main effect of the group random-effects analysis

Anatomical structure	Hemisphere	MNI coordinates (x,y,z)			Maximum z-value
FEF	L	-24	6	64	7.32
	R	28	-8	52	7.00
FG	L	-18	-70	4	> 8
	R	22	-70	0	> 8
fIPS	L	-20	-78	32	> 8
	R	24	-78	32	> 8
IFG	R	44	22	22	4.81
LPC	L	-48	-62	44	5.88
	R	50	-52	40	7.08
MPFC	-	2	42	40	> 8
hMT	L	-42	-76	24	> 8
	R	46	-72	16	> 8
PCC	L	-4	-44	46	6.95
	R	6	-50	42	> 8
SMA	L	-8	6	52	5.00
	R	8	-6	66	6.78
SPL	L	-12	-62	58	> 8
	R	16	-64	58	> 8
Temporal Pole	L	-40	20	-32	6.85
	R	34	20	-30	6.65

Coordinates represent the peak activation foci from the main effect of the group random-effects analysis including all attention conditions. Values represent coordinates in mm in MNI-space and maximum z-values. Abbreviations: FEF, frontal eye field; FG, fusiform gyrus; fIPS, fundus of the intraparietal sulcus; IFG, inferior frontal gyrus; LPC, lateral parietal cortex; MPFC, medial prefrontal cortex; hMT, human analogue of the middle temporal area; PCC, posterior cingulate cortex; SMA, supplementary motor area; SPL, superior parietal lobe;

In addition to the analysis of their spatial distribution, the magnitude of the hemodynamic modulations elicited by the individual attention conditions was directly compared in a ROI-analysis using the MarsBar toolbox in SPM5 (Brett et al., 2002). For this purpose, spherical ROIs with a radius of 4 mm were centered based on the local activation maxima given by the main effect of interest F-contrast of a second-level random-effects analysis including all 10 condition of interest (Hold Attention left/right, Switch Objects left/right, Switch Space to the left/right, Capture Across Objects left/right, Capture Across Space to the left/right; see Tab. 5 for the coordinates of activation maxima/ROIs and corresponding z-values). An additional ROI was defined in the right temporo-parietal junction (TPJ) on the basis of a local activation maximum in the conjunction-analysis of the 10 attention conditions (see Tab. 6 for the local activation maximum within the right TPJ) indicating that this area was activated by more than one condition. For all ROIs [FEF, FG, fIPS, right inferior frontal gyrus (IFG R), LPC, medial prefrontal cortex (MPFC), hMT, posterior cingulate cortex (PCC), SMA, SPL, temporal pole, and right TPJ] mean beta values were extracted from the individual subjects' data for all conditions. The values for the bilateral ROIs were subjected to a RANOVA with the factors region (FEF, FG, fIPS, LPC, hMT, PCC, SMA, SPL, and temporal pole), hemisphere (left vs. right), side of attentional allocation (ipsi-/contralateral to the respective ROI), and attention condition (Hold Attention, Switch Objects, Switch Space, Capture Across Objects, Capture Across Space). Since no significant main effect was observed for the factor hemisphere ($F(1,15) = 0.5, p > 0.4$), the data were collapsed over hemispheres before further analysis. For direct comparison of the attentional modulations, the data were separately analyzed for each ROI by two-way RANOVAs with the factors side of attention (ipsi-/contralateral to the respective ROI) and attention condition (Hold Attention, Switch Objects, Switch Space, Capture Across Objects, Capture Across Space). Given that only one ROI had been defined within the right IFG, MPFC, and right TPJ, the factor "side of attention" constitutes the absolute (left vs. right visual field) instead of the relative attended visual field (ipsi-/contralateral to the respective ROI). The significance threshold for all RANOVAs was set to $p < 0.05$ and significance levels were corrected using the Greenhouse–Geisser correction when appropriate; however, original degrees of freedom are reported.

5.2.3.3. Analysis of eye-tracking data

Eye-movements were monitored during data acquisition using a custom-built MR-compatible eye-tracking device (for a detailed description of the eye-tracking system see Kanowski et al., 2007). Recordings were performed using a modified version of the “Pupiltracker” software package (HumanScan AG, Erlangen). Before each run, an elliptic part of the monitored eyes’ image was defined as the template for tracking. During data-acquisition, the software stored the pupils’ position as X- and Y-coordinates by computing the best match of each actual image (each lasting for 20 ms) with the template image within an adjustable search area. Data of four subjects had to be excluded from the analysis due to overly frequent mismatches between the template-location and the actual pupil-position during task-performance. For statistical evaluation, the data were subjected to a 6 x 2 (condition vs. side of stimulus-presentation) within-subject RANOVA. The significance threshold for the RANOVA was set to $p < 0.05$ following Greenhouse-Geisser correction for non-sphericity.

5.3. Results

5.3.1. Behavioral results

Average target-detection performance across all subjects was high during the functional runs (mean \pm SEM: 96.2 \pm 0.7%), while false alarms were rare (mean \pm SEM: 2.4 \pm 0.6%). On average, the subjects’ RT was 825 ms (SEM: \pm 30 ms) ranging from 646-1024 ms. One-way RANOVAs with the factor side of target presentation (left vs. right visual field) were separately performed on the RT data and on the subjects’ hit rate. These analyses revealed neither a significant main effect of the side of target presentation for the hit rate ($F(1,15) = 2.6$, $p > 0.1$) nor for the RTs ($F(1,15) = 0.1$, $p > 0.7$) of the subjects.

5.3.2. Eye-tracking results

Analysis of the eye-movement data revealed a very low occurrence of saccades with an average percentage of saccades across all conditions of 2.1% (range: 1.4-3.2%). Analysis of these data by a two-way RANOVA with the factors attention condition (Targets, Hold Attention, Switch Objects, Switch Space, Capture Across Objects and Capture Across Space) and side of stimulus-presentation (left vs. right visual field) did neither reveal any significant main effects of the experimental condition ($F(5,55) = 1.0$, $p > 0.3$) or of the side of stimulus-presentation ($F(1,11) = 2.2$,

$p > 0.1$), nor a significant interaction between both factors ($F(5,55) = 0.3$, $p > 0.7$). Because the percentage of eye-movements were considerably low and did not differ between conditions, activations observed in the fMRI analysis cannot be attributed to eye-movements made by the participants.

5.3.3. fMRI results

5.3.3.1. Group random-effects analysis

First, it was qualitatively explored if hemodynamic activations elicited by the different attention conditions occurred within the same or distinct brain-regions. Significant activations to all conditions were observed in several fronto-parietal, extrastriate visual, cerebellar, and thalamic regions (see Tab. 6 for MNI-coordinates and corresponding z-values). By superposing their SPM activation maps, the patterns of neural activations to the individual attention conditions (Hold Attention, Switch Objects, Switch Space, Capture Across Objects, and Capture Across Space; collapsed over both sides of stimulus-presentation) could be directly compared. The resultant color-coded maps (see Fig. 15) illustrate the number of conditions by which a particular region was significantly activated, thereby indicating an extensive activation-overlap between conditions within fronto-parietal areas. The local activation maxima of the different attention conditions lay in close proximity to each other (see Tab. 6), within those regions that showed the maximal activation overlap between conditions (illustrated in red in Fig. 15). With increasing eccentricity from these maxima the activation-densities declined, indicating a rather quantitative (in terms of activation magnitude), than qualitative difference between conditions. In line with this observation, a conjunction analysis revealed that the majority of regions that were activated by an individual attention condition were also significantly activated by the other conditions (see Tab. 6). Thus, the magnitude of these attentional modulations between conditions was compared in a ROI analysis. ROIs were centered within several fronto-parietal, extrastriate visual, and default-mode network regions at the local activation maxima observed in the overall effects of interest F-contrast of the group random-effects analysis that included all conditions of interest (see Tab. 5 for MNI-coordinates and corresponding z-values).

Tab.6: Local activation maxima of the different attention conditions and from the conjunction analysis

Anatomical structure	Hold Attention		Switch Object		Switch Space		Capture across Objects		Capture across Space		Conjunction analysis	
	MNI coordinates	Z- Max.	MNI coordinates	Z- Max.	MNI coordinates	Z- Max.	MNI coordinates	Z- Max.	MNI coordinates	Z- Max.	MNI coordinates	Z- Max.
FEF	L -34 -8 46	4.66	-34 -8 46	4.71	-34 -8 46	5.17	-32 -8 46	4.76	-34 -10 44	5.06	-34 -8 46	4.66
	R 24 -4 52	4.00	26 -6 50	4.41	26 -8 52	4.09	22 -4 50	3.40	24 -2 54	3.49	22 -4 52	3.36
FG	L -20 -76 12	3.35*	-22 -76 10	3.44	-22 -72 12	4.38	-18 -76 6	4.52	-14 -76 4	4.31	-	-
	R - - -	-	20 -62 6	3.26*	20 -72 0	4.12	-	-	24 -64 -2	4.70	-	-
fIPS	L -20 -62 38	4.96	-14 -62 42	4.97	-20 -70 38	5.44	-20 -70 42	3.99	-28 -74 34	4.40	-22 -68 40	3.70
	R 18 -58 30	4.85	16 -60 32	4.41	26 -72 34	4.26	32 -72 24	3.51	30 -70 36	3.44	20 -60 38	3.61
hMT	L -48 -72 20	5.21	-46 -68 18	5.62	-46 -70 20	5.26	-42 -78 26	5.17	-44 -74 24	4.75	-44 -60 20	4.65
	R 52 -64 18	5.25	50 -64 16	5.37	48 -64 16	5.45	46 -66 16	5.33	40 -70 26	5.75	48 -62 18	4.83
SMA	L -8 0 58	3.92	-8 2 56	4.22	-6 2 54	4.56	-8 2 56	4.03	-12 0 56	3.82	-10 0 58	3.50
	R 14 8 52	3.22*	12 8 52	4.51	12 8 52	4.27	10 6 54	3.51	8 6 54	3.24	12 8 54	3.08*
SPL	L -10 -62 56	4.55	-18 -54 -52	5.39	-20 -56 50	5.90	-18 -56 54	5.09	-22 -58 50	4.58	-22 -56 50	4.57
	R 16 -66 56	4.52	14 -64 54	4.58	14 -62 54	4.75	16 -58 44	4.68	14 -54 46	4.84	12 -60 54	5.45
Cerebellum	L -34 -62 -28	3.97	-26 -56 -28	3.93	-32 -64 -24	4.24	-30 -54 -30	3.29*	-	-	-	-
	R 32 -64 -32	3.16*	36 -64 -32	4.16	34 -66 -32	4.45	32 -70 -30	3.97	30 -64 -32	4.04	32 -64 -32	3.15*
TPJ	R 48 -42 20	5.06	48 -42 20	5.30	50 -44 22	5.48	50 -46 20	5.21	46 -48 24	6.12	50 -44 20	5.02
Lateral PFC	L -40 26 30	4.09	-34 34 26	4.83	-34 32 32	4.69	-36 30 32	4.39	-36 24 32	3.87	-38 24 30	3.80
Anterior Insula	L -32 24 0	4.59	-28 20 -4	5.49	-32 20 -2	5.50	-34 22 2	4.82	-32 24 8	4.24	-32 24 6	3.99
	R 32 28 0	3.99	34 24 0	4.29	34 28 2	4.27	34 28 2	4.12	38 26 4	3.38	32 32 14	3.71
Posterior PFC	L -42 23 0	4.70	-42 23 0	4.76	-42 23 0	4.81	-40 23 0	4.88	-36 23 0	4.60	-38 23 0	4.24
	R 44 23 2	4.41	44 23 0	4.43	44 23 0	4.31	44 23 2	4.46	44 23 2	4.12	44 23 2	4.10
Anterior IPS	L -44 -42 42	5.25	-44 -40 40	5.40	-46 -40 42	4.94	-48 -44 40	5.09	-52 -48 36	4.59	-44 -44 40	3.72
	R 36 -42 44	3.95	36 -42 44	5.62	36 -42 44	4.19	34 -44 50	4.27	34 -42 48	3.65	36 -42 46	3.68
Thalamus	L -8 -12 -2	3.32*	-12 0 -4	3.69	-8 -12 -2	4.31	-8 -18 -2	3.31*	-10 -14 8	3.26*	-8 -14 -2	3.06*
	R 12 -12 -2	3.55	14 -8 -2	5.78	14 -10 -2	5.00	12 -16 0	3.14*	12 -12 -2	4.34	12 -14 0	3.13*
Posterior PHG	L -42 -52 -2	4.56	-46 -56 -2	4.84	-42 -54 -2	5.42	-44 -56 -4	4.78	-38 -60 2	4.64	-44 -54 -4	4.18
	R 48 -52 -10	3.01	48 -56 -8	4.29	48 -56 -10	4.45	46 -58 -10	4.97	48 -48 -12	4.45	48 -52 -10	3.01*

Vales represent coordinates in millimeters in MNI-space and maximum z-values. Z-values marked with an asterisk display activations that did not survive the significance-threshold of $p < 0.01$, but survived at a whole-brain corrected false discovery rate (FDR) of $p < 0.05$. Abbreviations: FEF, frontal eye field; FG, fusiform gyrus; fIPS, fundus of the intraparietal sulcus; hMT, human analogue of the middle temporal area; SMA, supplementary motor area; SPL, superior parietal lobe; TPJ, temporo-parietal junction; PFC, prefrontal cortex; PHG, parahippocampal gyrus; L, left hemisphere; R, right hemisphere. Coordinates: x, left/right; y, posterior/anterior; z, inferior/superior in the reference frame of the MNI brain in SPM5.

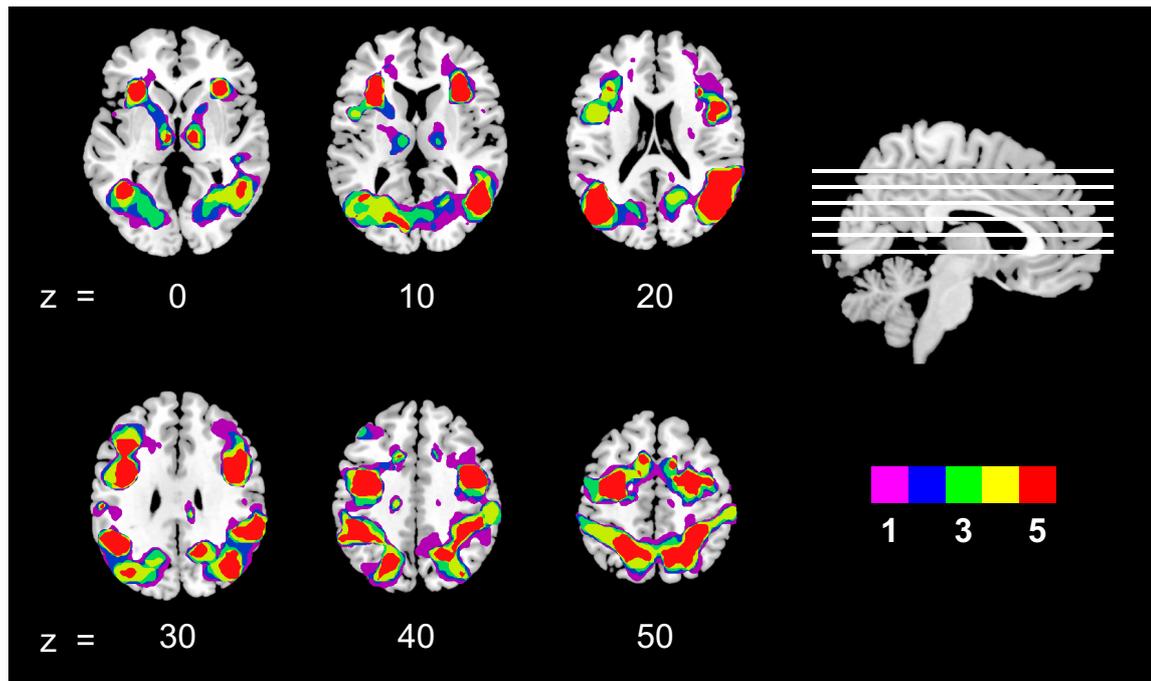


Fig. 15: ROI-density map showing the activation-overlap between conditions. SPM activation maps for all conditions (collapsed across stimulus-presentations to both visual fields) were concomitantly superimposed onto an anatomical template image. The resultant color-coded map indicates the activation density (number of overlapping statistical parametric maps) within each region (whole-brain FDR-corrected at $p < 0.01$). Numbers below slices represent z -coordinates in the MNI reference-frame. The extensive overlap between conditions highlights a common fronto-parietal network of attentional control.

5.3.3.2. Region of interest analyses

5.3.3.2.1. Modulations in dorsal fronto-parietal regions

To compare the activation magnitudes of the different attention conditions within source regions of top-down attentional control, activation estimates (beta-parameters) were extracted from ROIs located in the FEF, SMA, and SPL. The beta-parameters for each ROI were submitted to RANOVAs with the factors side of attention (ipsi-/contralateral to the ROIs) and attention condition (Hold Attention, Switch Objects, Switch Space, Capture Across Objects, and Capture Across Space).

The analysis of the data from the FEF and the SMA yielded similar results (for illustration see Fig. 16) in that both regions showed a main effect for the side of attention (FEF: $F(1,15) = 11.5$, $p < 0.001$; SMA: $F(1,15) = 20.8$, $p < 0.001$) indicating higher activity when attention was allocated contralateral to the ROIs' location. This is in line with previous reports of relatively small but consistent modulations within fronto-parietal regions, when stimuli are placed close to the fovea (Serences et al., 2005), while stimulation in the far periphery leads to more pronounced lateralization effects (Serences and Yantis, 2007). The present stimulus distance of 6.8° lateral from fixation lies in between of the eccentricities used in the aforementioned studies, which

might explain the rather small laterality effects observed here. In addition, both regions showed a main effect of attention condition (FEF: $F(4,60) = 13.5$, $p < 0.001$; SMA: $F(4,60) = 9.9$, $p < 0.001$), which did not interact with the side to which attention was directed (FEF: $F(4,60) = 0.4$, $p > 0.8$; SMA: $F(4,60) = 0.8$, $p > 0.5$). In the SPL (see Fig. 16), there was no significant effect of the side of attention ($F(1,15) = 0.7$, $p > 0.4$) but a main effect of attention condition ($F(4,60) = 19.7$, $p < 0.001$), which was significantly modulated by the side to which attention was directed ($F(4,60) = 6.2$, $p < 0.005$).

In summary, all dorsal fronto-parietal ROIs exhibited comparable patterns (see Fig. 16) for the different conditions: The modulations were higher for voluntary (Switch Space, Switch Objects) than for stimulus-driven attentional shifts (Capture Across Objects, Capture Across Space), with interjacent modulation-magnitudes during the maintenance of attention (Hold Attention).

5.3.3.2.2. Modulations in ventral fronto-parietal regions

Beta-parameter estimates were extracted from ROIs located in the right TPJ and the right IFG. Analysis of the data from the right IFG showed a significant main effect for the factor attention condition ($F(4,60) = 6.6$, $p < 0.001$), but not for the side to which attention was directed ($F(1,15) = 2.4$, $p > 0.1$) and no interaction between both factors ($F(1,15) = 2.0$, $p > 0.1$). The main effect for the factor attention condition was due to higher modulations during stimulus-driven (involuntary) reorienting towards an unattended surface (regardless whether the surface was located within the attended or unattended visual field; see Fig. 16). In contrast, for the right TPJ the analysis did not reveal any significant main effects (side of attention: $F(1,15) = 2.3$, $p > 0.1$; attention condition: $F(4,60) = 2.8$, $p > 0.05$) or interactions between factors ($F(1,15) = 1.4$, $p > 0.2$).

5.3.3.2.3. Modulations in extrastriate visual cortex

To compare the modulations within target regions of attentional control, beta-parameter estimates were extracted from ROIs located in extrastriate visual cortex, including FG, fIPS, and hMT. As for the fronto-parietal ROIs, activation estimates were analyzed by RANOVAs with the factors side of attention and attention condition.

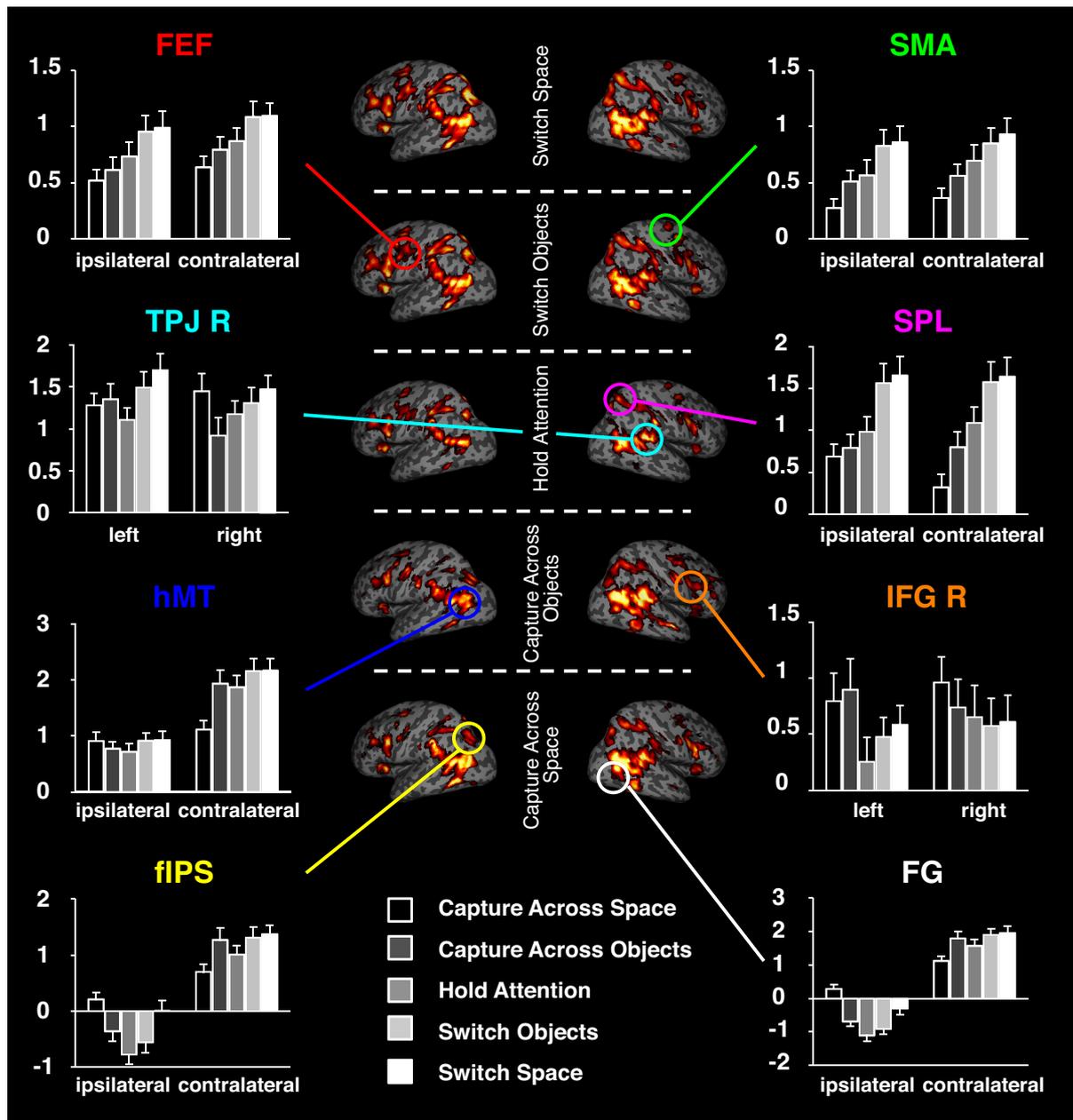


Fig. 16: Group-contrasts for the individual attention conditions and beta-parameter estimates of the fronto-parietal and extrastriate visual ROIs. For visualization purposes, statistical parametric maps for each attention condition (collapsed across both sides of attentional allocation) were superimposed on semitransparent surface-based representations of the MNI canonical brain. Activations are displayed at a whole-brain FDR-corrected threshold of $p < 0.01$, with a minimum cluster extent of $k = 20$ voxels. The bar charts depict the magnitude of the hemodynamic modulations to the different attention conditions. Mean beta-parameter estimates (\pm SEM) are separately depicted for attentional allocation ipsilateral and contralateral to the respective ROIs, except for the right TPJ and the right IFG, for which the absolute (left vs. right visual field) instead of the relative attended visual field is displayed (data averaged over subjects and both hemispheres for each ROI). The bar colors indicate the particular attention conditions. Abbreviations: FEF, frontal eye field; FG, fusiform gyrus; fIPS, fundus of the intraparietal sulcus; hMT, human analogue of the middle temporal area; IFG R, right inferior frontal gyrus; SMA, supplementary motor area; SPL, superior parietal lobe; TPJ R, right temporo-parietal junction.

For all ROIs, these analyses revealed significant main effects for the factors side of attention (FG: $F(1,15) = 109.6$; fIPS: $F(1,15) = 67.1$; hMT: $F(1,15) = 35.0$; $p < 0.001$ for all regions), and attention condition (FG: $F(4,60) = 10.0$, $p < 0.001$; fIPS: $F(4,60) = 7.2$, $p < 0.001$; hMT: $F(4,60) = 5.8$, $p < 0.005$), as well as significant

interactions between the factors (FG: $F(4,60) = 34.4$; fIPS: $F(4,60) = 30.4$; hMT: $F(4,60) = 16.0$; $p < 0.001$ for all regions). When separately analyzed for each side of attentional allocation (ipsi-/contralateral to the ROI), all regions showed a significant main effect for the factor attention condition when the contralateral visual field to the ROI was attended (FG: $F(4,60) = 10.9$, $p < 0.001$; fIPS: $F(4,60) = 11.9$, $p < 0.001$; hMT: $F(4,60) = 16.0$, $p < 0.001$). However, when attention was deployed to the ipsilateral aperture, a significant main effect of the attention condition was observed for the FG ($F(4,60) = 34.5$, $p < 0.001$) and the fIPS ($F(4,60) = 15.6$, $p < 0.001$), but not for hMT ($F(4,60) = 0.8$, $p > 0.5$).

In summary, all extrastriate visual regions showed a comparable activation pattern when attention was directed to the contralateral visual field (see Fig. 16), in that voluntary and stimulus-driven orienting towards an unattended object at the attended location elicited hemodynamic activations of comparable size. Smaller modulations were however observed when attention was initially in the ipsilateral and then captured to the contralateral visual field (Capture Across Space). A different pattern emerged when attention was directed to the ipsilateral visual field: While for MT all attentional modulations were of comparable magnitude, they differed significantly between conditions within the FG and fIPS. Increased activations were only observed when attention was involuntarily reoriented towards the ROIs' ipsilateral visual field (Capture Across Space), while almost no modulation was apparent during voluntary spatial orienting (Switch Space).

5.3.3.2.4. Modulations in the default-mode network

Increased activity to voluntary deployment of attention was observed within fronto-parietal and extrastriate regions, while default-mode network structures were more active during stimulus-driven orienting of attention (see Tab. 7 for MNI-coordinates and z-values and Fig. 17 for corresponding activation maps). The clusters of significant activation for both contrasts were located in close proximity to the local activation maxima identified in the effects of interest F-contrast from the group random-effects analysis (compare Tabs. 5 and 7). For direct comparison of modulations across attention conditions, a ROI analysis was performed within regions located in the LPC, MPFC, PCC, and bilateral temporal poles (see Tab. 5 for MNI-coordinates of activation maxima/ROIs and corresponding z-values).

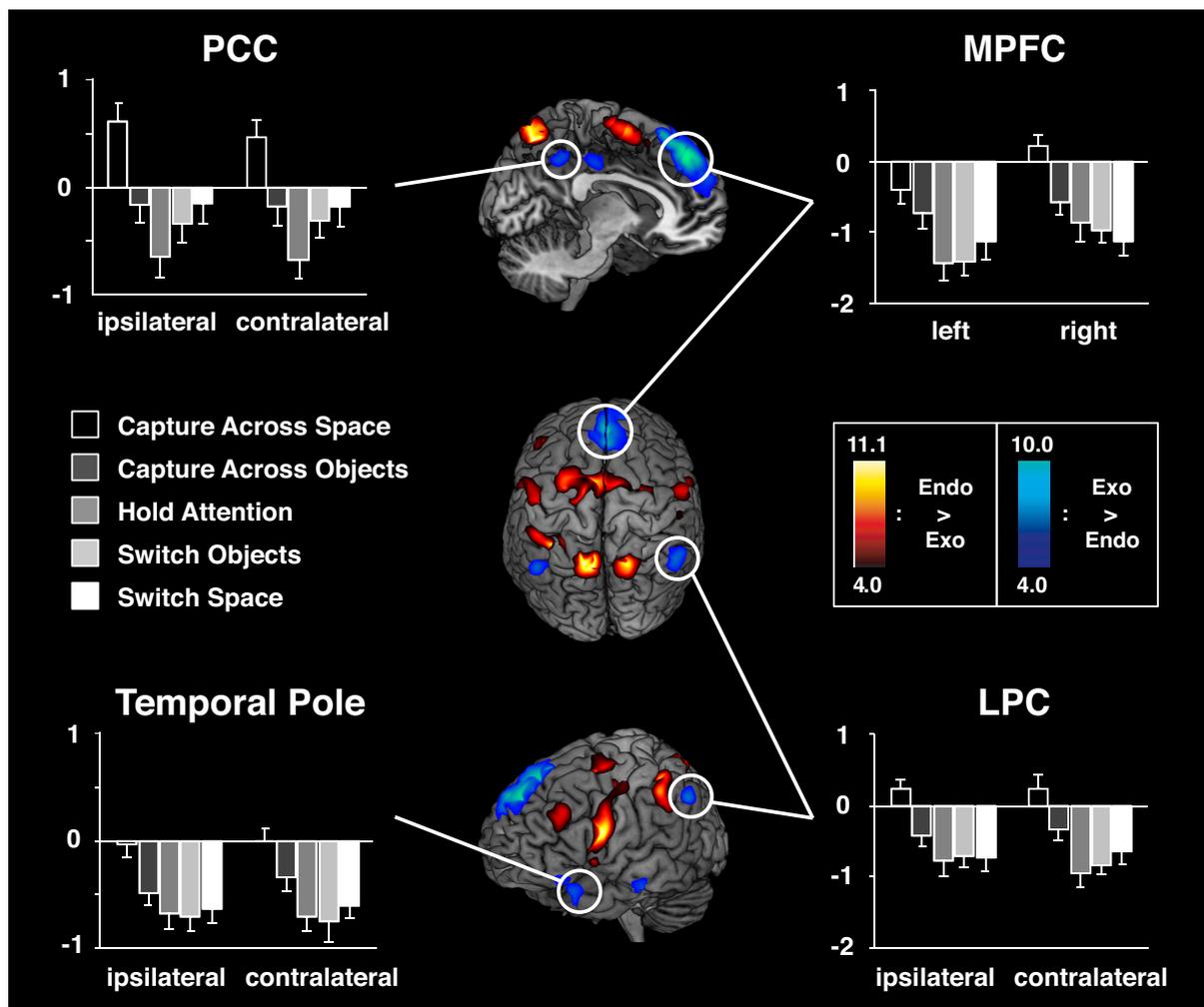


Fig. 17: Group-contrasts comparing stimulus-driven and goal-directed allocation of attention and beta-parameter estimates derived from the default-mode network ROIs. Warm colors (red-orange) depict regions that are more active during voluntary orienting, while cold colors (blue-green) depict regions that are more active during stimulus-driven attention. The scale at the right shows the corresponding t-values. Bar diagrams depict the magnitude of the hemodynamic modulations to the different attention conditions. Abbreviations: LPC, lateral parietal cortex; MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex.

Analysis of these data revealed a main effect for the side of attention only for the MPFC ($F(1,15) = 9.6$, $p < 0.01$), which was due to slightly more negative parameter estimates when attention was directed to the left in comparison to the right visual field (for illustration see Fig. 17). The other regions were not modulated by the attended side (LPC: $F(1,15) = 0.2$, $p > 0.6$; PCC: $F(1,15) = 2.3$, $p > 0.1$; and temporal pole: $F(1,15) = 0.4$, $p > 0.5$). Furthermore, all default-mode network regions showed a main effect for the factor attention condition (LPC: $F(4,60) = 19.7$; MPFC: $F(4,60) = 20.4$; PCC: $F(4,60) = 21.2$; and temporal pole: $F(4,60) = 16.7$; $p < 0.001$ for all regions), which did not interact with the attended side (LPC: $F(4,60) = 2.6$, $p > 0.05$; MPFC: $F(4,60) = 1.6$, $p > 0.1$; PCC: $F(4,60) = 1.2$, $p > 0.3$; and temporal pole: $F(4,60) = 1.2$, $p > 0.3$).

Tab. 7: Peak activation foci in the group random-effects analysis

Anatomical structure	Hemi-sphere	Endogenous > Exogenous				Exogenous > Endogenous			
		MNI coordinates (x,y,z)			Max. z-value	MNI coordinates (x,y,z)			Max. z-value
FEF	L	-24	-6	62	> 8	-	-	-	-
	R	28	-8	50	7.75	-	-	-	-
fIPS	L	-18	-60	40	5.23	-	-	-	-
	R	22	-56	30	6.35	-	-	-	-
IFG	R	-	-	-	5.49	44	22	22	5.49
LPC	L	-	-	-	-	-46	-60	42	6.66
	R	-	-	-	-	50	-52	40	7.18
Medial PFC	L	-	-	-	-	2	38	42	> 8
hMT	L	-50	-62	10	3.68	-	-	-	-
	R	46	-58	16	4.88	-	-	-	-
PCC	L	-	-	-	-	-8	-46	38	6.12
	R	-	-	-	-	8	-50	42	7.42
SMA	L	-12	-6	62	> 8	-	-	-	-
	R	8	-6	66	7.28	-	-	-	-
SPL	L	-12	-62	58	> 8	-	-	-	-
	R	14	-64	58	> 8	-	-	-	-
Temporal Pole	L	-	-	-	-	-42	20	-24	6.78
	R	-	-	-	-	32	20	-30	6.83
Cerebellum	L	-34	-64	-24	3.53	-	-	-	-
	R	68	-30	22	4.88	-	-	-	-
Lateral PFC	L	-42	30	36	5.34	-	-	-	-
Anterior Insula	L	-28	18	4	4.59	-	-	-	-
Posterior PFC	L	-50	2	20	> 8	-	-	-	-
	R	58	4	28	6.15	-	-	-	-
Anterior IPS	L	-36	-48	50	> 8	-	-	-	-
	R	40	-3	42	5.32	-	-	-	-
Thalamus	L	-10	-12	4	3.73	-	-	-	-
Precuneus	L	-40	-52	26	4.74	-	-	-	-
	R	22	-56	30	> 8	-	-	-	-
Striatum	L	-20	8	6	6.21	-	-	-	-
	R	20	14	-4	4.45	-	-	-	-

Abbreviations: ACC, anterior cingulate cortex; FEF, frontal eye field; FG, fusiform gyrus; fIPS, fundus of the intraparietal sulcus; PFC, prefrontal cortex; SFG, superior frontal gyrus; SMA, supplementary motor area; SMG, supramarginal gyrus; SPL, superior parietal lobe; hMT, human analogue of the middle temporal area.

Summarizing, the response pattern in default-mode regions differed substantially from fronto-parietal and extrastriate cortex (compare Figs. 16 and 17): For one, the attentional modulations were mainly independent of the attended side and the highest modulations were observed during involuntarily orienting towards a previously unattended spatial location (Capture Across Space), while all other

conditions elicited negative beta-parameter estimates (deactivation of the default-mode network). Moreover, within MPFC, LPC, and temporal pole, these deactivations were significantly stronger when attention was under voluntary control. Finally, the PCC exhibited higher modulations when attention was oriented towards an unattended spatial location but not towards a different object at the same location, and was deactivated stronger during voluntary maintenance of attention.

5.4. Summary

In Experiment 4, hemodynamic activations were observed within several fronto-parietal, extrastriate visual, and default-mode network regions that showed an extensive overlap between the different attention conditions. Within dorsal fronto-parietal cortex the modulations were of higher magnitude when attention was oriented in a goal-directed fashion. A partially opposing pattern was found for ventral fronto-parietal regions, whose activations either were higher during stimulus-driven orienting (IFG), or which were not differentially modulated across the attention conditions (TPJ). In analogy to the pattern observed in the IFG, default-mode network regions showed the highest hemodynamic response during stimulus-driven spatial reorienting, while they were consistently deactivated during voluntary orienting.

6. General discussion

The results from Experiments 1-4 will be discussed in separate chapters, one devoted to each experiment (Chapters 6.1-6.4), while a general summary and a correspondent outlook will be given in the final chapter of this General discussion (Chapter 6.5).

6.1. Feature-selective modulation of hemodynamic activity in hMT

Experiment 1 aimed to investigate the validity of the feature-similarity gain hypothesis at the population-level by analyzing hemodynamic modulations as a function of feature-based attention and motion coherence. Therein, the results from Experiment 1 provide support for the feature-similarity gain hypothesis by demonstrating that activity in hMT is positively correlated with a stimulus' coherence when its motion-direction is attended (resembling the subjects behavioral performance), while it displays an inverse relationship when the stimulus' motion is opposed to the attended direction. Importantly, out of all investigated regions, hMT is the only to exhibit this specific pattern: Activity in the fIPS and the thalamus shows a positive linear correlation with motion-coherence irrespective of feature-based attention, while attentional control regions display an activation pattern opposed to the one observed in hMT.

In agreement with neurophysiological investigations in primates, previous fMRI studies in humans have also demonstrated feature-based attentional modulations in hMT. These modulations were observed when a moving transparent surface was attended as opposed to an overlapping stationary stimulus (O'Craven et al., 1997), or even in absence of direct visual stimulation (Chawla et al., 1999). Furthermore, feature-based attention can spread to moving stimuli outside the focus of spatial attention if they match the attended feature (Saenz et al., 2002). These neuroimaging studies have repeatedly demonstrated attention-related changes of activity in area hMT; nevertheless, none of the studies specifically investigated attentional modulations as a function of individual changes within a single feature dimension. To date, with the exception of two studies that employed classifiers (Kamitani and Tong, 2006; Serences and Boynton, 2007), fMRI studies have failed to show direction selectivity, a hallmark of MT neurons in neurophysiological measurements. The most plausible explanation is that the native responses of hMT neurons to different motion-directions are too small in view of the spatial and temporal resolution of the employed

methods. The two recent fMRI studies that used pattern-classification algorithms could show that attention influences direction-selective activity within multiple stages of the visual cortex (Kamitani and Tong, 2006; Serences and Boynton, 2007). The interpretation of these results, however, requires some caution because the neural processes underlying classification accuracy are not entirely understood (Bartels et al., 2008). It has to be kept in mind that although direction-selective information could be decoded from multiple stages throughout the visual hierarchy, the results do not necessarily imply the existence of direction-selective neuronal populations within all of these visual areas (Serences and Boynton, 2007).

The results from Experiment 1, however, clearly demonstrate such direction-selective modulations using conventional fMRI analysis techniques. The results are consistent with the feature-similarity gain hypothesis, which posits that an individual neuron's response is modulated according to the similarity between a currently attended feature and the feature-preference of that neuron (Treue and Martinez Trujillo, 1999; Martinez-Trujillo and Treue, 2004). The present results strongly support this notion, by demonstrating that feature-based attention also enhances direction-selective activity within cortical area hMT on the level of an integrated population-response. Notably, responses to stimuli moving in the attended direction are enhanced, while for opposite directions they are suppressed (see Fig. 2). In this way the difference between stimuli moving into the attended versus opposite to the attended direction is increased in relation to native hMT-responses when no direction is specifically attended. Thus, the current results suggest that the integration of direction-selective responses (multiplicatively scaled by feature-based attention) occurs in cortical area hMT in dependence of the signal-to-noise characteristics of the presented stimuli, thereby enhancing their neural representations according to the current perceptual goals of the observer.

The pattern of hemodynamic modulations in fronto-parietal, in contrast, is opposed to the one observed in hMT regions (see Fig. 3B): their activations correlate negatively with motion-coherency when the direction of the stimulus is attended, while it shows a positive linear relationship with stimulus-coherence for stimuli moving opposed to the attended direction. From a signal-detection point of view, stimuli of lower coherence contain more noise, thus imposing increased perceptual demands on identifying the prominent direction of a movement. Within this framework, the activation-pattern from fronto-parietal regions is consistent with earlier observations

that their activation magnitude varies as a function of the attentional requirements of a task (Culham et al., 2001; Jovicich et al., 2001; Lavie, 2005). Thus, endogenous signals about the subjects' current goals (e.g., the attended motion-direction) are complemented with information about actual stimulus-contingencies to provide optimal top-down signals to bias the processing of appropriate stimulus features and locations in early visual regions (Corbetta et al., 2008).

In conclusion, the results from Experiment 1 demonstrate that feature-based attention modulates hemodynamic activity within hMT in a direction-selective manner. These modulations and corresponding behavioral performance were positively correlated with motion-coherency, whereas intraparietal and thalamic activations were independent of the attended feature. Attentional control regions, in contrast, displayed an activation pattern opposed to the one observed in hMT, matching the predictions drawn from a signal-detection theory perspective. These results provide strong support for the feature-similarity gain hypothesis (Martinez-Trujillo and Treue, 2004) and suggest that feature-based attention improves behavioral performance by modulation of direction-selective population-activity within area hMT.

6.2. The timing of global direction-selective modulations

Experiment 2 used simultaneous EEG/MEG recordings to quantify the magnitude and latency of ERPs and ERMFs in dependence of the similarity between the motion-direction of a spatially unattended in relation to that of an attended surface. In line with the results from Experiment 1, the data from Experiment 2 demonstrate a feature-based attentional modulation of ERP and ERMF amplitudes that parametrically depends on the similarity between the motion-directions of the attended and unattended surfaces. The field distributions and the current-source reconstructions of these activations suggest them to originate within left middle occipito-temporal cortex, likely corresponding to area hMT. Moreover, the time courses of the ERP and ERMF waveforms indicate that this attentional enhancement occurs comparatively late, not starting before ≈ 200 ms after stimulus onset. These findings once more provide support for the feature-similarity gain hypothesis by demonstrating that feature-based attention parametrically modulates direction-selective population activity in a global manner, and that it does so within the cortical module that processes the physical attributes of the presented stimuli.

Previous studies indicated that the selection of task-relevant features is initiated in the time range between 120 and 180 ms after stimulus onset (Harter and Aine, 1984; Kenemans et al., 1993; Motter, 1994; Anllo-Vento and Hillyard, 1996; Smid et al., 1999; Torriente et al., 1999; Kenemans et al., 2000; Martinez et al., 2001; Beer and Roder, 2004, 2005). Within the motion-domain this selection process is reflected by an enhanced negativity over centro-posterior electrodes in the ERP (the so-called selection-negativity) starting around 150-160 ms after stimulus onset (Anllo-Vento and Hillyard, 1996; Torriente et al., 1999; Beer and Roder, 2004, 2005). In accordance with these results, the current study also observed an enhanced negativity over centro-posterior electrodes within the EEG, whose magnitude parametrically depended on the similarity between the motion directions of the attended and the unattended surfaces (see Fig. 5). This graded negativity was accompanied by corresponding modulations of ERMF amplitudes over occipito-temporal sensors. Comparisons of the field distributions and source analyses nevertheless suggest that these modulations could be attributed to the same neural generators located in middle occipito-temporal cortex (most likely corresponding to area hMT) as described before (Schoenfeld et al., 2003a; Beer and Roder, 2005; Schoenfeld et al., 2007).

The onset latency of the feature-selective modulations within the current study was slightly later (≈ 200 ms) than previously reported. One possible explanation for this inconsistency relies on the paradigmatic differences in the experimental designs. For example, if a spatially attended feature dimension (e.g., a stimulus' motion) has to be selected from another one (e.g., a stimulus' color), the attentional enhancement begins as early as 100 ms after stimulus onset (Schoenfeld et al., 2007). If, on the other hand, the selection occurs within a single feature dimension (e.g., selecting one motion direction from another), the enhancement starts about 50 ms later (Hillyard and Munte, 1984; Anllo-Vento and Hillyard, 1996; Karayanidis and Michie, 1996; Lange et al., 1998). Thus, the electrophysiological signs of feature-selection within the focus of attention can be observed quite early, i.e., in the range of the N1-component (100-180 ms after stimulus onset). If, in contrast, a feature is task-irrelevant and is selected only because it is part of an attended object, the feature-specific modulations occur considerably later. Such modulations have been shown to start within 230-240 ms when the irrelevant feature belongs to an object presented at an attended location (Schoenfeld et al., 2003b), and not until 270 ms after stimulus-onset if it is part of an attended object presented to the unattended visual field (Boehler et al., 2010). The

onset-latencies in the present study lie in between the ones described above, with the earliest modulations starting around 190-200 ms (see Fig. 5). These data suggest that the access to feature information within its specific cortical processing module proceeds at different speeds in dependence of the particular selection-process engaged. The fastest modulations are observed when relevant features are presented within the spotlight of attention, i.e. ≈ 100 ms for attentional selection between feature-dimensions and ≈ 150 ms for selection between feature-values. These results further highlight the outstanding importance of spatial selection, which can bias the processing of other visual attributes (Hillyard and Munte, 1984; Klingstone and Klein, 1991; Handy et al., 2001) and leads to higher attentional modulations than feature-based selection alone (Stoppel et al., 2007). If, in contrast, attention operates on features presented at unattended locations (as in the present study), this selection-process takes somewhat longer (≈ 200 ms). While demonstrating that feature-based attention operates in a spatially global manner, the current data thus also show that the spread of feature-selective modulations to the unattended visual field is a time-consuming process.

In conclusion, the results of Experiment 2 demonstrate a parametric direction-selective modulation of ERP and ERMF amplitudes by feature-based attention, supporting the validity of the “feature similarity gain model” on the level of an integrated population response (Treue and Martinez Trujillo, 1999; Stoppel et al., 2011). Since these direction-selective modulations (localized to cortical area hMT) occurred in response to spatially unattended stimuli, the current data also put further emphasis on the global nature of feature-based attentional selection (Treue and Martinez Trujillo, 1999; Saenz et al., 2002; Kamitani and Tong, 2006; Serences and Boynton, 2007). However, a comparison of onset latencies between studies suggests, that the timing of the feature-based attentional modulations might vary in dependence of the particular attentional demands during task-execution.

6.3. Interaction between space- and feature-selective modulations

While Experiments 1 and 2 specifically addressed the neuronal substrates, as well as the timing of feature-based selection within a single feature-dimension, Experiment 3 was conducted to investigate the functional relationship between feature-based and location-based selection using fMRI in human observers. To this end, hemodynamic activity elicited by physically identical stimuli (colored moving

transparent surfaces) was compared, while attention was either directed towards or opposed to their spatial location and their constituent features. The highest hemodynamic activations were observed when attentional selection was based on a stimulus' spatial location, regardless of whether its color was attended or not. Positive, though relatively smaller, modulations also were seen for stimuli comprising the attended relative to the unattended color when their spatial location was attended, while - for stimuli presented at unattended locations - an increased feature-selective response was only observed in motion- but not in color-sensitive regions.

More precisely, robust attentional modulations of hemodynamic activity occurred in ventral (FG and LG) and dorsal (hMT, anterior IPS and fIPS) visual stream areas, as well as in the FEF (see Fig. 8). These findings are in line with the literature reporting that regions that process the physical attributes of the presented stimuli exhibit increased neuronal activity regardless of the particular selection mechanism (space or feature-based) that is engaged (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Yantis and Serences, 2003; Maunsell and Treue, 2006). The highest modulations were found during space-based attentional selection, i.e., when stimuli were presented contralateral to the location of the particular cortical regions (either in the cS+ or cS+F+ contrast). This result, in accordance with previous findings, highlights the outstanding importance of spatial attentional selection. Previous electrophysiological investigations clearly point out that spatial selection is faster than feature-based (Schoenfeld et al., 2007), and studies using combined expectancies have shown that location-based selection not only precedes but also biases the processing of other visual attributes (Hillyard and Munte, 1984; Kingstone, 1992; Handy et al., 2001). Thus, spatial attention appears to be the fastest and most efficient selection-mechanism in vision.

Given that in the current study spatial selection led to the highest attentional modulations, it is important to note that the hemodynamic activations were of comparable magnitude, regardless of whether the particular stimuli comprised the attended (cS+F+) or unattended feature (cS+). At first glance this finding seems to contradict the intuitive assumption that a concurrent modulation by space- and feature-based selection should have an additive effect, and therefore elicit higher modulations than space-based selection on its own. In view of these results, it is tempting to speculate that location-based selection leads to a ceiling effect, thus preventing a further response increase by concomitant occurrence of an attended

feature. This would be well in line with the idea that increased processing resources are assigned to all features presented to spatially attended locations, regardless if their specific feature-value is attended or not (Heinze et al., 1994).

In contrast to the present results, however, a recent SSVEP study – which employed a similar design as the present one – found that concurrent manipulation of spatial and color-selective attention had independent and largely additive effects on the magnitude of SSVEPs recorded from early visual areas (Andersen et al., 2009). One possible explanation for this inconsistency relies on one major paradigmatic difference in the experimental designs that were employed. Within the current experiment, attended and ignored features were presented one at a time (i.e., only one of the dot populations executed a short coherent movement during each trial), which minimized the direct competition between both feature values. In the study by Andersen and colleagues, in contrast, only trials that did not include the presentation of a motion-onset were analyzed. Thus, SSVEPs to the four RDKs (each flickering at an individual frequency) were compared under conditions of simultaneous competition between the attended and ignored feature-value, while trials only differed with respect to the particular feature (color) and location that were attended. Such direct competition between stimuli has been shown to markedly affect attentional selection: The magnitude of both spatial (Luck et al., 1997) and feature-based modulations (Saenz et al., 2003; Zhang and Luck, 2009) is increased if attended, and ignored stimuli must compete for access to perceptual processing resources. The absence of direct competition between stimuli within the current study thus might have diminished such independent and additive modulations during concurrent manipulation of spatial and feature-based attention, rendering them too small to be resolved with classical fMRI analysis techniques.

Besides the spatial attentional modulations discussed above, feature-based selection on its own (i.e., comparison of attended vs. unattended feature-values both presented at a spatially attended location; F+) led to a robust response increase throughout all ROIs. This finding is in line with the literature reporting enhanced hemodynamic activations or an increased gain of single feature-selective neurons upon the occurrence of an attended feature (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Yantis and Serences, 2003; Maunsell and Treue, 2006; Schoenfeld et al., 2007), thus also resembling the observations from Experiment 1. At unattended locations, however, feature-selective modulations (RFE) could only be

observed in motion- but not in color-sensitive regions (compare Figs. 10 and 12). While this finding further supports the global nature of feature-based attentional selection (as already highlighted in Experiment 2), it also indicates that at unattended locations a stimulus' motion might either be of higher bottom-up saliency (Treue and Martinez Trujillo, 1999; Nothdurft, 2002), or able to capture attention to a much higher degree than a stimulus' color (Hillstrom and Yantis, 1994; Abrams and Christ, 2003; Franconeri and Simons, 2003; Rauschenberger, 2003). Both possibilities, however, fit well into the concept of a higher biological relevance of moving stimuli in the visual world, since motion onset might yield a substantial survival benefit (as a powerful cue to animacy) by indicating the appearance of a living and perhaps dangerous being.

6.4. One unitary network for the control of goal-directed and stimulus-driven attention-shifts between objects and locations

The first three Experiments examined how stimulus processing is modulated by feature- and/or location-based attentional selection. Experiment 4, in contrast, sought to investigate the control signals that bias attentional orienting during voluntary and stimulus-driven shifts between objects and locations. For this purpose, observers were cued to either voluntarily maintain their attention at a currently attended object, switch to another object presented at the same spatial location, or to shift their attention to an object located in the opposite visual field. Besides these voluntary conditions, target-like movements occurring within one of the unattended objects (either within the attended or the unattended aperture) captured the subjects' attention in a stimulus-driven manner.

Consistent with current theories on attentional control, hemodynamic activations to the different attention conditions were observed within several fronto-parietal, extrastriate visual, and default-mode network regions. Since these activations showed an extensive overlap between conditions (see Fig. 15), these results support the hypothesis that a distributed network of fronto-parietal regions controls the allocation of attentional resources regardless of the particular perceptual domain (Corbetta et al., 2008; Chiu and Yantis, 2009). This domain-independent account has originally been postulated based on the observation that different attention-shifts (e.g., between features (Liu et al., 2003), objects (Serences et al., 2004), or locations (Hopfinger et al., 2000; Yantis et al., 2002)) recruit a common network of fronto-parietal regions across studies. Recently, this notion has repeatedly been supported

by studies that employed within-subject designs to directly compare the mechanisms of attentional control between different types of attentional operations (Giesbrecht et al., 2003; Peelen et al., 2004; Shomstein and Behrmann, 2006; Greenberg et al., 2010). The current results further add to this notion by showing a substantial activation-overlap between multiple types of attention-shifts, in which modulations only differ in magnitude between conditions.

A more detailed look at these differences in the magnitude of hemodynamic modulations between the individual attention conditions revealed substantial differences in the activation-pattern between the ventral and the dorsal part of the attention-network. These findings are in line with current theories on attentional control postulating two interacting systems that mediate the allocation of attentional resources to environmental events (Corbetta et al., 2008). Within the dorsal part of the network higher modulations were observed for voluntary orienting, which is in accordance with its well-known role in the generation of endogenous signals that bias the processing of particular features, objects, or spatial locations, according to the expectations and current goals of an observer (Kastner et al., 1999; Corbetta et al., 2000; Hopfinger et al., 2000). The ventral fronto-parietal cortex, in contrast, is recruited when attention is involuntarily oriented towards behaviorally relevant events (e.g. targets or target-like stimuli) that occur outside the focus of attention (Kincade et al., 2005; Indovina and Macaluso, 2007), whereas it usually remains inactive during voluntary attentional orienting or task preparation. Consistent with this notion, the present data show that target-like movements elicited increased activity within the right IFG if they were executed by an object located in the unattended visual field, but also – and more importantly – if these movements occurred within an unattended object that was presented at a spatially attended location. These data once more support the notion that the IFG is one of the core regions of the so-called “saliency network” (Sridharan et al., 2008), which initiates the key control signals in response to salient unexpected events (as e.g. infrequent/invalidly cued targets; Linden et al., 1999; Kincade et al., 2005), even if they occur within the focus of spatial attention (Asplund et al., 2010).

Besides these modulations within dorsal and ventral fronto-parietal cortex, foci of significant activation also were observed within several default-mode network areas. The functional connectivity of this network is known to correlate negatively with the activation state of attentional control regions located in dorsal fronto-parietal cortex (He et al., 2007). On this account, a push-pull relationship between the two networks

has been suggested (Sridharan et al., 2008). The current findings are in line with this proposal, in that default-mode regions were deactivated during voluntary deployment of attention, in contrast to the increased activations observed within dorsal fronto-parietal cortex. More importantly, however, the highest response across all default-mode regions occurred during stimulus-driven spatial orienting. One possible explanation for this pattern is that the detection of stimuli matching the current attentional set (contingent capture) might be accomplished automatically through activation of ventral fronto-parietal cortex, sparing the redistribution of processing resources between dorsal fronto-parietal and default-mode network regions. On the other hand, a lack of deactivation within the default-mode network during stimulus-driven spatial orienting (and concurrent activation of dorsal fronto-parietal cortex) might also simply reflect a failure to suppress distractive information and thus to deploy attentional resources to the current task (Rule et al., 2002). This view is supported by the observations that attentional capture induces performance costs (Folk et al., 2002; Serences and Yantis, 2007) and that reduced default-mode deactivations are associated with momentary lapses in attention (Weissman et al., 2006) or slower and less accurate performance in other tasks (Lawrence et al., 2003; Polli et al., 2005).

Taken together the results of Experiment 4 suggest that the allocation of attentional resources is mediated by a complex interplay within one unitary network of fronto-parietal and default-mode network regions, in which processing-resources are dynamically distributed in dependence of the particular attentional demands.

6.5. Summary

Testing the validity of the feature-similarity gain hypothesis at the population level with fMRI and EEG/MEG, Experiments 1 and 2 could demonstrate that feature-based attention modulates hemodynamic activity in hMT (Experiment 1) and comparable electromagnetic indices (Experiment 2) in a direction-selective manner. Concerning the timing of the electromagnetic activity-modulations, Experiment 2 showed that these feature-selective effects arise comparatively late, i.e., not until 200 ms after stimulus-onset. Thus, the data from both Experiment 1 and 2 provide strong support for the validity of the feature-similarity gain hypothesis on the level of an integrated population response. By investigating the direct functional relationship between feature- and space-based attentional selection, thereby extending the

subject of investigation into the spatial domain, Experiment 3 revealed that spatial selection leads to higher hemodynamic modulations than feature-based attention. These location-based effects were independent of the concurrent feature-content of the particular stimuli. Moreover, feature-selective modulations for stimuli presented at unattended locations were only observed in motion- but not in color-sensitive regions. These findings support the notion that space-based attentional selection appears to be the most efficient selection-mechanism in vision. Furthermore, they indicate that global feature-based attention is more effectively directed towards a stimulus' motion than to its particular color, thus highlighting the high biological priority of moving stimuli in natural biological settings. Finally, by investigating how the control of voluntary and stimulus-driven re-/orienting between objects and locations is implemented within the human brain, Experiment 4 indicates that different types of attentional transitions are mediated by a complex interplay within one unitary network of fronto-parietal and default-mode network regions, in which processing-resources are dynamically distributed in dependence on the particular attentional demands.

Taken together the present data in concert with findings from previous studies show that attentional selection operates in a highly flexible manner. For one, the units that are selected for preferential processing encompass spatial as well as non-spatial (feature- and object-based) attributes of our visual world. On the other hand, visual attention is also flexible within the temporal domain, in that the timing of object-, location- and feature-based selection can be adaptively adjusted in dependence of the particular situational requirements.

7. Bibliography

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8. Curriculum vitae

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8.2. School education

1986-1990 Grund- und Hauptschule Dettingen
1999 Abitur at the Alexander-von-Humboldt Gymnasium Konstanz
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8.3. Community service

1999 - 2000 Mobile social service at the Arbeiterwohlfahrt Konstanz

8.4. University education

2000 - 2007 **Medicine**
Medical faculty of the Otto-von-Guericke-University, Magdeburg

- Summer 2002 Pre-diploma (Grade: „sehr gut“)
- WS 02/03 - SS 03 2 research semesters
- Autumn 2007 2. ÄP (Grade: „sehr gut“)
- State Examination 13.11.2007 (Final grade: 1,5)
- Approbation as Physician 16.11.2007

2002 - 2007 **Neural Sciences**
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04/2008 MD (Dr. med.) thesis at the Otto-von-Guericke University

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Title: „Charakterisierung des Einflusses von Somatostatin auf die Furchtgedächtnisbildung der Maus “

Since 01/2008 Ph.D. Thesis at the Faculty of Natural Sciences at the Otto-von-Guericke University Magdeburg

Since 01/2008 Medical assistant at the Clinic for Neurology of the Otto-von-Guericke University Magdeburg

8.5. Scholarships

2002 - 2003 **Doctorate scholarship of the graduate school 253** „Biological foundations of central nervous systems diseases“ from the German Research Foundation (DFG) at the Otto-von-Guericke University Magdeburg

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8.6. Publications

C. Stoppel, A. Albrecht, H.-C. Pape, O. Stork: *Genes and neurons: molecular insights to fear and anxiety*. Genes Brain Behav. 2006; 5 Suppl 2: 34-47.

C. Stoppel, H. Bielau, B. Bogerts, G. Northoff: *Neurobiologische Grundlagen depressiver Syndrome*. Fortschr Neurol Psychiatr. 2006; 74(12): 696-705.

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C. Kluge*, **C. Stoppel***, C. Szinyei, O. Stork, H.-C. Pape: *Role of the somatostatin system in contextual fear memory and hippocampal synaptic plasticity*. Learn Mem. 2008; 15(4): 252-60. *shared first-authorship

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C. Eckart, **C. Stoppel**, J. Kaufmann, C. Tempelmann, H. Hinrichs, T. Elbert, H.-J. Heinze, I.-T. Kolassa: *Structural alterations in lateral prefrontal, parietal and posterior midline regions of individuals with chronic PTSD*. J Psychiatry Neurosci. 2011; 36(3): 176-86.

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C.N. Boehler, J.-M. Hopf, R.M. Krebs, **C.M. Stoppel**, M.A. Schoenfeld, H.-J. Heinze, T. Noesselt: *Task-load-dependent activation of dopaminergic midbrain areas in the absence of reward*. J Neurosci, 2011; 31(13): 4955-4961.

T. Hassa, M.A. Schoenfeld, C. Dettmers, **C.M. Stoppel**, C. Weiller, R. Lange: *Neural correlates of somatosensory processing in patients with neglect*. Restor Neurol Neurosci. 2011; 29(4): 253-63.

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Erklärung

Hiermit erkläre ich, Christian Michael Stoppel, dass ich die von mir eingereichte Dissertation zu dem Thema:

„ Neural Mechanisms of Attentional Selection in Vision:

Locations, Features, and Objects”

selbständig verfasst, nicht bereits als Dissertation verwendet habe und die benutzten Hilfsmittel und Quellen vollständig angegeben wurden.

Weiterhin erkläre ich, dass ich weder diese noch eine andere Arbeit zur Erlangung des akademischen Grades doctor rerum naturalium (Dr. rer. nat.) an anderen Einrichtungen eingereicht habe.

Magdeburg, den 29.07.2011

Dr. med. Christian Michael Stoppel