ERNI-HSF workshop

**Orienting of attention:**
**Neural implementation, underlying mechanisms and clinical implications**
Tuebingen 2-3.11.2012
Organizers: Dr. Daniela Balslev and Prof. Hans-Otto Karnath

Scientific report

**1) Summary (up to 1 page)**

The limited capacity for information processing allows that only a part of the sensory input becomes available to awareness and action. Surprinzingly, the tremendous progress in uncovering the neural mechanisms that support visual attention in the healthy brain has only had limited impact in understanding the pathophysiology of the clinical conditions characterized by a breakdown of this selection process. This workshop aimed to present recent progress in the field of visuospatial attention from the perspective of the challenges raised by the observations in patients with spatial attention disorders such as neglect or extinction.

The workshop had 2 subthemes:

1. Neuro-implementation of spatial attention
2. Mechanisms steering the allocation of attention

Subtheme 1 addressed how the prioritization of space is implemented in the brain. What is the anatomy and which are the ways to reconcile the apparently contradictory evidence from neglect showing a lateralized, inferior parieto-fronto-temporal system and fMRI in humans showing a bilateral superior parietal network involved in visuospatial attention ? Are the selection processes implemented within a dedicated brain area, in the timing of the neural oscillations or in the pattern of connectivity between brain areas?

Subtheme 2 attempted to define attention from a theoretical, computational perspective and discuss the mechanisms that determine how attention is allocated. Observations in neglect patients show that body posture impacts on which locations are selected for processing. Which sensory, motor, intentional or emotional signals lie behind location selection ? Which internal representations of space support this selection ?

The workshop was attended by 107 participants from 27 countries. The programme included 12 talks given by speakers from Germany (6), EU (4), and the USA (2). We had a poster session with 41 posters preceded by a poster blitz session, where the participants briefly presented their main findings in plenum. We were able to award 8 travel bursaries to support student and postdoc poster presenters. The selection of the awardees was based on the quality of their submitted abstracts and on the need for funding according to their motivation letters (e.g. the need for financial support).

## 2) Description of the scientific content of and discussion at the event (up to 4 pages)

A summary of the talks is provided below:

### Subtheme 1. Spatial attention. Neural implementation

*Neural basis of visual attention in the primate brain*
Sabine Kastner

Our natural environments contain too much information for the visual system to represent. Therefore, attentional mechanisms are necessary to mediate the selection of behaviorally relevant information. Much progress has been made to further our understanding of the modulation of neural processing in visual cortex. However, our understanding of how these modulatory signals are generated and controlled is still poor. In the first part of my talk, I will discuss recent functional magnetic resonance imaging and transcranial magnetic stimulation studies directed at topographically organized frontal and parietal cortex in humans to reveal the mechanisms underlying space-based control of selective attention. In the second part of my talk, I will discuss recent monkey physiology studies that suggest an important function of a thalamic nucleus, the pulvinar, in controlling the routing of information through visual cortex during spatial attention. Together, these studies indicate that a large-scale network of high-order cortical as well as thalamic brain regions is involved with the control of space-based selection of visual information from the environment.

*Anatomy of spatial attention − Evidence from stroke patients*
Hans-Otto Karnath

Homologous neural networks seem to exist in the human left and right hemispheres tightly linking cortical regions straddling the sylvian fissure. It is argued that in humans these perisylvian networks serve different cognitive functions, a representation for language and praxis in the left hemisphere and a representation for processes involved in spatial orienting in the right. The tight perisylvian anatomical connectivity between superior/middle temporal, inferior parietal and lateral prefrontal cortices might explain why lesions at these distant cortical sites around the sylvian fissure in the human right hemisphere can lead to the same disturbance of orienting behavior, namely to spatial neglect. It will be argued that for undisturbed attentional orienting the functioning of the perisylvian cortical areas is critical, not the mere disconnection of their white matter interconnections. Moreover, it will be demonstrated that the physiological changes and corresponding interhemispheric imbalance detected by fMRI BOLD in acute neglect patients − particularly those observed close to the lesion border − may not necessarily reflect changes in the neural function, nor necessarily influence the individuals' attentional behavior.

*Functional dissociations within parietal cortex: Patient lesion studies and fMRI of the intact brain*
Rik Vandenberghe

On the basis of a series of behavioral and fMRI studies in cognitively intact individuals and patients with focal lesions following stroke, we will illustrate how human lesion studies continue to provide invaluable insights into the critical contribution of specific parietal regions to attentional processing (selection between competing stimuli and spatial shifting). In our presentation we will mainly focus on the cross-talk between 'multiple single-case' studies and models of functional specialization of parietal cortex for selective attention. A critical feature of such single-case studies in the modern era is the use of both structural and functional measures to thoroughly document the anatomical extent as well as the functional consequences at a network level. We will also emphasize the utility of a subtractive approach when cognitive functions are studied in patients, akin to the subtraction methodology that is common in functional imaging studies. Finally, we will put forward a model of functional specialization in parietal cortex that is firmly grounded in empirical evidence from patients and studies of the intact brain.

*Primate models for disorders of spatial attention*
Melanie Wilke

The intact visual awareness of space around us is am emergent property of activity in the two brain hemispheres. Following a damage to certain regions in one hemisphere, the perception and action in the contralesional hemispace are impaired, leading to spatial neglect syndrome. The dominant model of spatial neglect, the interhemispheric opposition, or rivalry theory, postulates mutually suppressive interactions between two hemispheres that are in equilibrium in the normal state, and whose balance is disturbed following the lesion. This theory is corroborated by stimulation studies showing that inhibition of the healthy hemisphere may alleviate neglect symptoms. However a direct neuronal evidence for the proposed interhemispheric suppression is still largely missing. The study of basic neglect mechanisms in human patients is hindered by large and variable lesions, lack of pre-lesion "baseline" data, and medical considerations.
Using local reversible pharmacological inactivation of MRI-targeted brain areas, we are studying the basic mechanisms of spatial disorders and recovery in a monkey model. Since pharmacological agent action is limited to several hours, inactivation experiments in combination with fMRI or electrophysiological recordings can be performed repeatedly in the same subject, both in normal and lesioned states. Using this technique, we are hoping to gain insight into the dynamic interactions between areas within each hemisphere and between hemispheres that underlie spatial neglect and recovery.

*Spatial attention networks studied with large-scale high-resolution electrocorticography*.
Pascal Fries

Activated neuronal networks typically engage in rhythmic synchronization. We have hypothesized that synchronization subserves efficient communication. In particular, in the visual system, multiple simultaneously present stimuli activate multiple neuronal groups, but only the behaviorally relevant, attended signals are communicated to higher brain areas. I will show that this selective communication is supported by selective interareal gamma-band synchronization. This routing between visual areas is most likely controlled by top-down influences from frontal and parietal areas. I will show that these top-down influences are subserved by beta-band synchronization between corresponding brain areas. The experimental results were obtained with large-scale high-resolution electrocorticography, which combines millimeter spatial and millisecond temporal resolution with coverage of large parts of a hemisphere.

**Subtheme 2. Spatial attention: Underlying mechanisms**

*Computational models of spatial attention and visual stability*
Fred H. Hamker

Cells in many visual areas are retinotopically organized and thus shift with the eyes, posing the question of how we construct our subjective experience of a stable world. While predictive remapping (Duhamel et al., Science, 1992, 255, 90-92; Melcher & Colby, Trends in Cog. Sci., 2008, 12, 466-473) and the corollary discharge (CD) to move the eyes (Sommer & Wurtz, Nature, 2006, 444, 374-377) have been proposed to provide a potential solution, there exists no clear theory let alone a computational model of how CD and predictive remapping contribute.
After a brief overview of attentional models and how they relate to behavioral and physiological observations, I introduce a realistic systems neuroscience model of area LIP, using CD of eye displacement and proprioceptive eye position as inputs. I show that predictive remapping emerges within a model of coordinate transformation by means of the interaction of feedback and CD. Moreover, I demonstrate the influence of predictive remapping on visual stability as objectified by a suppression of saccadic displacement task (Deubel et al., Vis Res, 199, 36, 985-996). The model predicts that an absent CD signal leads to a bias negative to saccade direction in SSD. Remapping

introduces a feedback loop which stabilizes perisaccadic activity and thus leads to the typical increase in displacement detection threshold.

*The body's functional space in allocation of attention*
Catherine Reed

Theories of embodied cognition emphasize the importance of sensorimotor experience and the interaction of the body with the world. Our own bodies perform important everyday movements and actions. It stands to reason that the actions of bodies may also prioritize specific regions of space to help us respond to important events. One of the primary functions of spatial attention is to select objects and locations in space that are functionally relevant to what an organism's current and future actions. However, most theories do not address the role of the body's and its actions on spatial attention. In this talk we present research demonstrating that the functions of the hand and body influence the allocation of attention. Attention is influenced not only by current actions but also by intended actions. Further, the allocation of attention can be altered when the perceived function of the hand is changed. These results, in addition to EEG studies, suggest both bottom-up and top-dow n influences of the body's actions and intended actions on attention. An embodied model of attention that integrates current biased competition models of visual attention with multisensory body-based inputs provides a theoretical framework to account for these findings.

*Motor intention and the allocation of attention*
Heiner Deubel

It is now well established that goal-directed movements are preceded by covert shifts of visual attention to the movement target. I will first review recent evidence in favour of this claim for eye movements, manual reaching movements, and combined eye-hand movements, demonstrating that the planning of some of these actions establishes multiple foci of attention which reflect the spatial–temporal requirements of the intended motor task. Recently our studies have focused specifically on how finger contact points are chosen in grasp planning, and how this selection is related to the spatial deployment of attention. Subjects grasped cylindrical objects with thumb and index finger. A perceptual discrimination task was used to assess the distribution of visual attention prior to the execution of the grasp. Results showed enhanced discrimination for those locations where index finger and thumb would touch the object, as compared to the action-irrelevant locations. A same-different task was used to establish that attention was deployed in parallel to the grasp-relevant locations. Interestingly, while attention seemed to split to the action-relevant locations, the eyes tended to fixate the centre of the to-be-grasped object, reflecting a dissociation between overt and covert attention. A separate study demonstrated that a secondary, attention-demanding task affected the kinematics of the grasp, slowing the adjustment of hand aperture to object size. Our results highlight the import role of attention also in grasp planning. The findings are consistent with the conjecture that the planning of complex movements enacts the formation of a flexible “attentional landscape” which tags all those locations in the visual lay-out that are relevant for the impending action.

*Update on the premotor theory of attention*
Daniel Smith

The Premotor theory of attention (Rizzolatti, Riggio & Sheliga, 1994) has been enormously influential and contributed significantly to the understanding of the mechanisms underlying spatial attention. However, some of the claims of the Premotor theory are also highly controversial. In particular, the claim that covert spatial attention (the ability to orient attention independently of gaze direction) is dependent on motor preparation has been hotly debated. In this talk I will present data from a series of behavioural and neuropsychological experiments which investigate the role of motor preparation in spatial attention. These studies show that oculomotor preparation is required for exogenous attention, but independent from covert endogenous attention. It is argued that although the Premotor theory offers a reasonable account of exogenous attention, the relationship between motor control and endogenous attention is better understood in terms of a biased competition model of attention. In this model activity in the motor system contributes to competition between different sensory representations, biasing the cognitive system towards the saccade goal. However, contrary to the predictions of the Premotor theory, motor activation does not guarantee attentional selection and the absence of motor preparation does not necessarily rule out the possibility of attentional selection.

*The impact of eye position on the prioritization of visual space*
Daniela Balslev

Spatial attention can be defined as the selection of a location for preferential processing. The last decades of neuroscientific research have established that this function is implemented at cortical level by networks linking the posterior parietal cortices, frontal eye fields and the right temporo-parietal junction. The somatosensory cortex, which processes sensation from the body, is not among the nodes of these networks. Therefore it is intriguing that repetitive transcranial magnetic stimulation (rTMS) over the postcentral gyrus alters visual detectability to favor some visual targets over others, despite their equal retinal eccentricity (Balslev et al., JoCN, 2011). In my talk I will present evidence that a somatosensory gaze direction signal, eye proprioception, shapes the allocation of attention in space and discuss possible mechanisms for this effect.

*Controlling spatial attention in a multisensory world*
Charles Spence

The last 30 years or so have seen a rapid rise in research on attentional orienting from a crossmodal perspective. The majority of this research has tended to focus on the consequences of the covert orienting of attention (either to a sensory modality or spatial location) for both perception and neural information processing. The results of numerous studies have highlighted the robust crossmodal links that exist in the case of both overt and covert, and both exogenous and endogenous spatial orienting. I will highlight how such laboratory-based research findings are increasing informing the design of multisensory warning signals and interfaces in real-world settings (including driving, air traffic control, and military applications). Neuroimaging studies have now started to highlight the neural circuits underlying such crossmodal effects. Researchers are now using transcranial magnetic stimulation in order to temporarily lesion putative areas within these networks; their aim being to determine whether attentional orienting is controlled by supramodal versus modality-specific neural systems. The available research demonstrates that crossmodal attentional orienting (and multisensory integration – from which it is sometimes hard to distinguish) can affect the very earliest stages of information processing in the brain.

*Emotion, attention and neglect*
Patrik Vuilleumier

Past research on attention and its disorders (such as spatial neglect) indicates that spatial orienting is controlled by both endogenous top-down signals related to task goals and exogenous bottom-up effects driven by stimulus saliency, but evidence suggests that attention may also be modulated by affective factors related to intrinsic or learned value of stimuli. Functional neuroimaging and behavioral studies show that attention is preferentially biased towards emotionally significant information (e.g. either threat or reward related), with enhanced activation of perceptual processing at various stages along sensory pathways. These effects may persist in patients with damage to fronto-parietal systems involved in the control of patient and may depend on distinct modulatory signals from limbic systems that boost, or interact, boost, or compete with other modulatory signals from fronto-parietal networks. In particular, the amygdala appears to play a central role in such affective influences on attention through both direct projections to sensory areas as well as indirect influences on fronto-parietal systems.

3. **Assessment of the results and impact of the event on the future direction of the field (up to 2 pages)**

## Subtheme 1 Spatial Attention: Neural Implementation

This section addressed the current status on the anatomy of spatial attention. The discussion at the workshop highlighted the following unresolved issues and directions of future research:

First, there is a striking discrepancy between a) the results of lesion studies in neglect patients showing a spatial attention network that is lateralized to the right hemisphere and that consists of the superior and middle temporal cortices, inferior parietal cortex and inferior frontal cortex and b) the results of neurophysiological studies in the monkey and fMRI studies in humans that identify a spatial attention network the intraparietal sulcus and the premotor cortex in both brain hemispheres. The discussions at the workshop highlighted the dissimilarity of the tasks used to test spatial attention in the two populations as a possible reasons for this discrepancy. Whereas fMRI studies in humans and neurophysiological studies in the monkey use cueing, the tests for spatial attention in patients rely on visual search. When the tasks are similar – e.g. only Posner tasks are used in both populations - then the results of the lesion studies and fMRI converge. A critical difference between the tasks may relate to the frame of reference for spatial selection. Visual search tasks require eye movements, and therefore test for spatial attention in a body- or object-centered reference frame. In contrast, cueing tasks are performed while the eyes fixate, so they do not require a transformation between retinotopic and body-centered coordinates. In this condition, retinotopic salience maps would be sufficient and mechanisms that select locations in body-centered space redundant. Whereas the retinotopic salience maps have been successfully identified in the human brain, the location and the eye position input for their non-retinotopic counterparts is a topic for future research.

Another emerging idea is that of an interplay between brain areas that implement spatial selection. This interplay is emphasized by the synchronization of the neural oscillations in various frequency bands to convey top-down influence or to select among multiple visual stimuli.

Finally, new research underscores the modulatory influence of the subcortical structures such as the pulvinar on visual processing. It remains a challenge for the future to uncover the connectivity within this cortical-subcortical network and how a breakdown of function in one of the nodes affect the function of the whole network.

## Subtheme 2. Spatial attention: Underlying mechanisms

This subtheme focused on the factors that determine how attention is allocated. The discussion at the workshop highlighted the following unresolved issues and directions of future research:

First, voluntary control or stimulus salience are well-established factors that control the allocation of attention. Beyond top-down and bottom-up mechanisms however, evidence is accumulating for the idea that spatial selection is embodied, involuntarily controlled by the organism's movement plans, posture or emotion. Whereas behavioral results and computational models presented at the workshop document the role of posture, movement or emotion in the prioritization of space, understanding how these factors impact on the activity or connectivity of the brain's attention network represents a major future challenge.

Second, there is consensus that spatial attention and eye movements are tightly coupled. New evidence suggests that this may not always be the case (e.g. covert endogenous attention is independent of eye movements) or that the coupling is not restricted to eye movements or oculomotor areas (the focus of attention can shift with perceived eye position and the eye proprioceptive area in the somatosensory cortex plays a role in spatial selection. Characterizing which behavioral components of the spatial selection process are affected by predictive and re-afferent oculomotor signals remains thus a future challenge.

**Conclusion**

Thus, to support an integrative approach in spatial attention research that combines the insight from healthy and clinical populations and to facilitate the translation of the findings in cognitive neuroscience into efficient rehabilitation programmes, the worskshop has highlighted the following strategies:

a) An increased consensus between the behavioral paradigms used in healthy and clinical populations to investigate the anatomical substrate of spatial selection

b) The need to address not only the contribution of the individual neural attention nodes to behavior, but also their connectivity, and the effect that a lesion in one area has of the function of the whole network.

c) A better understanding of the "embodied" aspect of spatial selection, namely how sensorimotor or emotional signals impact behavior as well as the activity or the connectivity in the brain's attention networks

## 4. Final programme of the meeting

### Friday, 02 Nov 2012

08:15 Registration

08:45 - 09:00 Opening Remarks

**Spatial Attention: Neural Implementation**

09:00 - 09:45
**Neural mechanisms of spatial attention control in the primate brain**
Sabine Kastner *(Department of Psychology, Princeton University, USA)*

09:45 - 10:30
**Anatomy of spatial attention: evidence from stroke patients**
Hans-Otto Karnath *(Center of Neurology, University of Tuebingen, Germany)*

10:30 - 11:00 Coffee break

11:00 - 11:45
**Spatial attention deficits in humans after parietal lesions**
Rik Vandenberghe *(Department of Neurology, University Hospitals Leuven, Belgium)*

11:45 - 12:30
**Primate models for disorders of spatial attention**
Melanie Wilke *(Department of Cognitive Neurology, University of Medicine Goettingen, Germany)*

12:30 - 14:00 Lunch break

14:00 - 14:45
**Attentional selection through brain-wide synchronization networks**
Pascal Fries *(Ernst Strüngmann Institute (ESI) for Neuroscience in Cooperation with Max Planck Society, Frankfurt, Germany)*

14:45 - 15:30
**(Spatial) attention - computational modelling**
Fred Hamker *(Department of Computer Science, Chemnitz University of Technology, Germany)*

15:30 - 16:00 Coffee break

16:00 - 18:00 **Poster blitz: 1 min plenum intro into each poster followed by a poster session**

18:00 Guided walking tour of Tübingen

20:00 Social dinner

**Saturday, 03 Nov 2012**

## Spatial Attention: Mechanisms

09:00 - 09:45
**The body's functional space in allocation of attention**
Catherine Reed *(Department of Psychology, Claremont McKenna College, Claremont, USA)*

09:45 - 10:30
**Motor intention and allocation of attention**
Heiner Deubel *(Department of Psychology, Ludwig-Maximilians-University Munich, Germany)*

10:30 - 11:00 Coffee break

11:00 - 11:45
**Update on the premotor theory of attention**
Daniel Smith *(Wolfson Research Institute, Durham University, Stockton-on-Tees, UK)*

11:45 - 12:30
**The impact of eye position on the prioritization of visual space**
Daniela Balslev *(Center of Neurology, University of Tuebingen, Germany & Department of Psychology, University of Copenhagen, Denmark)*

12:30 - 14:00 Lunch break

14:00 - 14:45
**Cross-modal interactions in spatial attention**
Charles Spence *(Department of Experimental Psychology, Oxford University, UK)*

14:45 - 15:30
**Emotion, attention and neglect**
Patrik Vuilleumier *(Department of Neuroscience, University Medical Center & Department of Neurology, University Hospital, Geneva, Switzerland)*