LMU LUDWIG-MAXIMILIANS-UNIVERSITÄT MÜNCHEN

CAS LMU CENTER FOR ADVANCED STUDIES

PROGRAM

2-DAY WORKSHOP

Lateralized attention in the brain: Top-down versus bottom-up biases in human search behavior

Keynote: Steven J. Luck (Davis, USA)

Speakers: Nancy Carlisle (Leicester, UK), Clayton Hickey (Rovereto, IT), Jens-Max Hopf (Magdeburg, D), Veronica Mazza (Rovereto, IT), Thomas Töllner (Munich, D), Rolf Verleger (Lübeck, D), Edmund Wascher (Dortmund, D), Iris Wiegand (Copenhagen, DK)

THURSDAY, MARCH 26, 2015

09.30 – 09.45	Welcome address
	Session I
09.45 – 10.30	Edmund Wascher: "*N1, N2pc and re-entrant processing in the visual system"*
10.30 – 11.15	Nancy Carlisle: "*Examining the interactions of working memory and attention*"
11.15 – 11.45	*Tea & Coffee*
11.45 – 12.30	Clayton Hickey: "*Incentive salience in human vision*"
12.30 – 14.00	*Lunch & Walk in the English Garden*
	Session II
14.00 – 14.45	Thomas Töllner: "*Orienting attention to locations in visual versus mental space: Same or different mechanisms?*"
14.45 – 15.30	Veronica Mazza: "*Electrophysiological correlates of object individuation in the enumeration process*"
15.30 – 16.00	*Tea & Coffee*
16.00 – 16.45	Jens-Max Hopf: "*Neural mechanisms of global feature-based attentional selection in humans*"
17.00 – 18.30	**Poster session**
19.30	Workshop Dinner at Restaurant "Reitschule"

FRIDAY, MARCH 27, 2015

	Session III
09.30 – 10.15	Iris Wiegand: "*EEG markers of attention parameters based on Bundesen's Theory of Visual Attention*"
10.15 – 11.00	Rolf Verleger: "*Can left and right be separated? Hemisphere-specific N2pcs and the advantage of the left visual field in rapid serial presentation*"
11.00 – 11.30	*Tea & Coffee*
11.30 – 12.45	Steven J. Luck (Keynote address)**:** "*Lateralized Electrical Signatures of Attention in the Human Brain: A 25 Year Retrospective*"
12.45	*Snack*

ABSTRACTS

TALKS: SESSION 1

Edmund Wascher (Dortmund, D): N1, N2pc and re-entrant processing in the visual system

Due to limited capacities in the human information processing system, the distinction of relevant and irrelevant signals is one of the most important cognitive functions. Biologically plausible theories assume that this selection takes place in early sensory areas, controlled by supervising executive functions. Based on a change detection task with partially competitive information, we were able to demonstrate the dependency of exogenously driven spatial coding (as reflected in the N1) and subsequent attentional allocation mechanisms. The latter are reflected in posterior asymmetries in the N2 range (N2pc) or even later (sPCN). Inefficient early scene segmentations have to be compensated by intentionally driven allocation mechanisms. Assumed that information is repetitively processed in the visual system until signal to noise ratio reaches a level sufficient for conscious perception, we were able to show that posterior asymmetries re-appear until a decision can be made. Thus, posterior asymmetries in the EEG provide insight into the time course of the generation of aware representations.

Nancy Carlisle (Leicester, UK): Examining the interactions of working memory and attention

In this talk, I will highlight two studies investigating the relationship between working memory and attentional control. These studies use Event-Related Potentials (ERPs) to examine a proposal from Biased Competition Theory (Desimone & Duncan, 1995) that working memory is both necessary and sufficient for attentional control. In the first study, we measure the lateralized N2pc index of attention and show that merely holding a representation in working memory is not sufficient for attentional control, but that a goal must also be associated with the working memory representation. In the second study, we examine the N2pc and the lateralized CDA index of working memory and find that working memory representations can be used to guide search when the target frequently changes. When the target stays the same across trials, the CDA decreases quickly suggesting that working memory is no longer needed to perform efficient search. These two studies suggest that working memory is neither necessary nor sufficient for visual search, and highlight the utility of lateralized ERP components in addressing fundamental questions concerning attention.

Clayton Hickey (Rovereto, IT): Incentive salience in human vision

We use outcome feedback to guide strategic preparation for future interactions in our visual environment and this involves attentional control settings that subsequently modulate visual processing. When foraging for food, a sweet red berry will accordingly motivate the strategic establishment of attentional set for these objects and their features. However, rewarding outcome also appears to have a unique, non-strategic impact on perception and selection, causing stimuli to become salient and attention-drawing even when this is strategically counter-productive. Thus when the berry bush is plucked bare, and it is time to look for bananas, a bias for berries and berry-like features can sustain until further experience overwrites this prime. In this talk I will present results from an array of studies investigating this phenomenon, including behavioural, ERP, fMRI, and stimulation data.

TALKS: SESSION 2

Thomas Töllner (Munich, D): Orienting attention to locations in visual versus mental space: Same or different mechanisms?

The human visual working memory (WM) system enables us to store a limited amount of task-relevant visual information temporally in mind. One actively debated issue in cognitive neuroscience centers around the question of whether attentional orienting to locations in WM may reflect the same mechanisms as those that mediate attention shifts to locations in external visual space. In this talk, I will present two event-related lateralization (ERL) studies that used the retro-cue paradigm to explore people's ability to access WM representations as a function of dimensional context (study 1) and task set (study 2). Our findings show that both factors selectively influence WM access: whereas cross-relative to intra-dimensional WM targets gave rise to amplified ERL waves, localization relative to identification task demands yielded speeded ERL and manual response times. As these dimension-based findings are not reconcilable with contemporary feature- and/or object-based accounts of WM, I will introduce an alternative view that is based on and extends the hierarchical feature-bundle model. Finally, results will be discussed in relation to recent visual search data, according to which retro-cue-synchronized ERL waves may be equivalent to feedback-driven stimulus identification (SPCN/CDA) rather than feedforward-driven attentional selection (N2pc/PCN) processes.

Veronica Mazza (Rovereto, IT): Electrophysiological correlates of object individuation in the enumeration process

The ability to process concurrently multiple visual objects is fundamental for a coherent perception of the world. A prototypical example of this ability is represented by enumeration at a glance, in which the elements to be enumerated need to be analyzed as distinct entities, so that each element is counted once and only once. How does the visual system cope with the presence of multiple objects to be enumerated? What is the core component that allows for the exact enumeration of small quantities?

I will discuss recent electrophysiological findings on enumeration and consider three responses of the EEG signal that are modulated by object numerosity, and which are associated respectively with perceptual modulation, attention selection, and working memory. Together with other lines of research, these results indicate that the lateralized neural response associated with attention selection shows the hallmarks of an object individuation mechanism, including the property of simultaneous individuation of a limited number of objects thought to underlie the behavioral subitizing effect. The findings support the view that the core component of exact enumeration is an attention-based individuation mechanism that provides a stable representation of a limited set of relevant objects. The resulting representation is made available for subsequent cognitive operations.

Jens-Max Hopf (Magdeburg, D): Neural mechanisms of global feature-based attentional selection in humans

In this talk I will review a series of electromagnetic brain recording studies that aim at characterizing the spatiotemporal dynamics of neural modulations underlying global feature-based attention (GFBA) in human observers. GFBA refers to the observation that attention to an item feature prioritizes the selection of that feature even outside the spatial focus of attention. Focusing on the color and orientation domain, we will observe that GFBA is mediated by a series of modulation phases in multiple cortical areas that propagate in reverse hierarchical direction through the ventral extrastriate visual cortex. We will learn that early phases in higher-tier areas reflect a feature bias due to the mere task-relevance of an attended feature, while later phases in lower-tier areas rather reflect the actual discrimination of the feature. We will further explore the influence of feature competition on the different modulation phases, and finally discuss preliminary evidence that the sequence of reverse hierarchy modulations map onto a coarse-to-fine evolution of categorical selectivity in visual cortex.

TALKS: SESSION 3

Iris Wiegand (Copenhagen, DK): EEG markers of attention parameters based on Bundesen's Theory of Visual Attention

The "Theory of Visual Attention" (TVA) is a computational theory of selective attention in vision. TVA is based on the principles of biased competition and integrates large parts of the theoretical and empirical knowledge on visual perception, attention and short-term memory. The theory's central equations have been interpreted on the neuronal level; thus, the formal model incorporates a direct link between psychological and neurobiological perspectives on cognitive processes.

TVA partitions visual attention functions into mathematically independent parameters, such as processing speed, short-term storage capacity, and attentional selection. The parameters can be precisely assessed for an individual subject using simple psychophysical whole- and partial-report tasks. We combine TVA-based assessment with EEG to isolate neural correlates of these distinct attentional components. On the one hand, this approach permits investigating the neural mechanisms underlying visual attention functions on a micro-level. On the other hand, it provides a strong tool to derive neuro-cognitive markers of individual differences, and age- and disease-specific changes in cognitive core abilities.

Rolf Verleger (Lübeck, D): Can left and right be separated? Hemisphere-specific N2pcs and the advantage of the left visual field in rapid serial presentation

Everyday experience suggests that people are equally aware of events in both visual hemi-fields. However, when two streams of stimuli are rapidly presented left and right, containing two targets (T1 and T2) the second target is better identified in the left than in the right visual field. Evidence we have collected in variations of this task points to a right-hemisphere advantage in reactively directing attention to relevant events as the responsible mechanism for this asymmetry.

Both the salient T1 (distinct by its color) and the unique T2 (distinct by its category: digit among letters) evoke N2pc components. Measuring these N2pcs is challenging in how to do this separately for left and right stimuli and how to separate N2pc from potentials evoked by the ongoing background of distractor stimuli and by preceding stimuli. When sides of the upcoming targets are known in advance, effects of this knowledge differ between T1 and T2: For T1, such knowledge lowers N2pc amplitudes and does not affect identification rates, whereas for T2, knowledge does not affect N2pc but improves identification rates. This dissociation may reflect how attention works in this task.

Dovetailing with the pathological asymmetries of attention after right-hemisphere lesions and with asymmetries of fMRI-measured brain activation when healthy participants shift their attention, the present results extend that body of evidence by demonstrating unusually large and reliable behavioral asymmetries for attention-directing processes in healthy participants.

Steven J. Luck (Davis, USA): Lateralized Electrical Signatures of Attention in the Human Brain: A 25 Year Retrospective

The N2pc component, a lateralized index of the focusing of attention, was first reported in 1990. Over the ensuing 25 years, the use of this component to study various aspects of attention has increased exponentially. For example, the number of papers citing the N2pc component has increased from approximately 1 per year from 1990-1994 to approximately 200 per year from 2010-2014. Other lateralized attention-related components have also been discovered (e.g., PD, SPCN, CDA). In this

presentation, I will describe how these components were discovered, review some of the ways in which they have been used to answer important questions about attention, discuss our evolving understanding of the neurocognitive processes they reflect, and describe some of the underappreciated difficulties in linking neural measures with specific cognitive processes.

POSTERS

Barbara Berger & Paul Sauseng (Munich, D): Top-down allocation of attention in visual working memory by EEG cross-frequency synchronisation

Working memory (WM) consists of various cognitive processes like maintaining and manipulating information no longer available in the environment. Individual processes are co-ordinated by a central monitoring component ensuring their efficient interaction. This central component is strongly linked to top-down attention processes. On cortical level, frontal-midline theta (FMT, a slow medial-prefrontal EEG frequency) was found as prime candidate for serving as such top-down attention/monitoring component. FMT has been shown to orchestrate local activity as well as distant brain areas in visual WM by synchronising fast oscillations (gamma, 30-80 Hz) in posterior task-relevant brain areas into specific phases of a FMT cycle.

The current study investigates whether this fronto-parietal theta-gamma synchronisation reflects voluntary top-down allocation of attention in WM. We designed a delayed-match-to-sample EEG experiment where participants retained four Gabor patches (two per hemifield) simultaneously. Importantly, a cue immediatedly preceding the patches indicated which side the participant needed to prioritise, i.e. to which hemifield to allocate more attention. We found that over right posterior-parietal areas – an area specialised in visuo-spatial processing – gamma activity was locked to the excitatory phase of FMT when participants prioritised the left hemifield. In contrast, when participants prioritised the right hemifield gamma over the right posterior-parietal cortex was locked near the inhibitory FMT phase.

Our results indicate that voluntary top-down attentional processes in visuo-spatial WM are implemented in the human brain via very selective coupling between medial-frontal and task-relevant posterior-parietal cortical areas. Furthermore, this process seems to be more engaged with the right hemisphere than the left.

Markus Conci, Kathrin Finke, Thomas Töllner, Kornelija Starman, Hermann J. Müller, & Iris Wiegand (Munich, D): Global form suppression declines with age: Evidence from event-related EEG lateralizations

Visual selection of illusory 'Kanizsa' figures, an assembly of local elements that induce the percept of a whole object, is facilitated relative to configurations composed of the same local elements that do not induce a global form – an instance of 'global precedence' in visual processing. Selective attention, i.e., the ability to focus on relevant and ignore irrelevant information, declines with increasing age; however, how this deficit affects selection of global vs. local configurations remains unknown. On this background, the present study examined for age-related differences in a global-local task requiring selection of either a 'global' Kanisza- or a 'local' non-Kanisza configuration (in the presence of the respectively other configuration), by analyzing event-related lateralizations (ERLs). Behaviorally, older participants showed a more pronounced global-precedence effect. Electro-physiologically, this effect was accompanied by an early (150–200 ms) 'positivity posterior contralateral' (PPC), which was elicited for older, but not younger, participants, when the target was a non-Kanizsa configuration and the Kanizsa figure a distractor (rather than vice versa). In addition, timing differences in the subsequent (250–500 ms) posterior contralateral negativity (PCN) indicated that attentional resources were allocated faster to Kanisza, as compared to non-Kanisza, targets in both age groups. Our results suggest that the enhanced global-local asymmetry in the older age group originated from less effective suppression of global distractor forms on early, pre-attentive processing stages – indicative of older observers having increased difficulties with disengaging from the global default and switching to the required local state of attentional resolution.

Tina Schwarzkopp, Ulrich Mayr, & Kerstin Jost (Aachen, D): Visual working memory and filtering out distractors: Evidence for an age-specific delay in filtering

Working memory (WM) capacity varies across individuals and declines with age. Whereas the ability to filter out irrelevant information has proven critical for general individual differences in visual WM, other factors seem to be responsible for the age-related differences in WM. We present data of a series of experiments that support earlier findings of an age-related delay in filtering. In a visual short-term memory task (i.e., change-detection task) targets were presented along with distractors. The contralateral delay activity of the EEG measured during the retention interval was used to track the number of stored items and to assess filtering efficiency. The data suggest that older adults do not have a general impairment in filtering, but that efficient filtering is delayed. Moreover, this filtering delay is specific for older adults and is not observed in WM-equated younger adults. A detailed analysis of the N1 revealed that older and younger adults already differed during early processing of targets and distractors. Older adults seem to initially encode distractors into WM and then need to suppress them after the fact, during the course of maintenance. This is consistent with the view that older adults' proactive control over attentional settings is less

efficient and that they rely more on reactive control strategies.

Heinrich R. Liesefeld, Anna M. Liesefeld, Thomas Töllner, Michael Zehetleitner, & Hermann J. Müller (Munich, D): Reliable electrophysiological evidence of attentional capture in visual search

Whether a salient distractor can capture attention in the presence of a less salient target is a central question in the debate on top-down versus bottom-up guidance of visual attention. Hickey et al. (2006) were the first and hitherto only to report the key piece of evidence of such attentional capture: with target and singleton distractor presented on opposite sides of a visual-search display, event-related potentials (ERPs) indicated that attention was directed first to the distractor and only then to the target. A re-analysis of that data (McDonald et al., 2013), however, revealed that this pattern was not reliable, so that hard evidence of attentional capture is still lacking. In light of the dimension-weighting account (DWA, e.g., Müller et al., 2009), it would appear critical that, in these studies, distractor and target were defined in different (color and shape) dimensions. DWA predicts that people can prevent bottom-up capture of attention by strategically down-weighting the distractor and/or up-weighting the target dimension. By contrast, selective weighting would be less effective when target and distractor are defined within the same dimension. Consistent with this, the present study demonstrated attentional capture by distractors defined within the same dimension as the target (orientation): the observed ERPs indicated that attention was initially allocated towards the distractor and subsequently re-allocated towards the target. Capture was evident not only on trials with slow but also trials with fast behavioral responses. This pattern provides robust neuro-physiological evidence of attentional capture by irrelevant objects.

Silvia Pagano, Elisa Fait, Alessia Monti, Debora Brignani, & Veronica Mazza (Rovereto, IT): Neural correlates of multiple object processing in healthy aging

The ability to enumerate multiple items is crucial in our everyday life and it may undergo age-related decline. Previous studies suggest that in order to enumerate objects we first need to individuate them as separate entities and then to maintain those representations active in visual working memory (VWM). However, so far it is unknown whether the changes in enumeration performances associated to aging are due to a diminished ability to individuate items as separate individuals or to a decline in VWM capacity. In order to address this question in the present electrophysiological study we compared a group of young (M=24.8) and old (M=69.7) adults while counting a varying number of targets (1-6) presented among distractors. We measured two posterior ERP components, N2pc and CDA, that have been associated respectively to individuation and VWM. To further characterize the age-related changes in enumeration we computed theta (4-7 Hz) and alpha (8-12 Hz) synchronization, a measure associated to memory encoding. Our results show that old participants performed worse than the younger in the enumeration task. Electrophysio-logical data showed that both components were modulated by target numerosities independently of age. However, N2pc was suppressed in the old group over the whole numerosity range (1-6) while CDA showed a suppression only for the largest set (4-6), suggesting that aging influences individuation and simultaneously diminishes the capacity of VMW. Finally, older adults showed higher theta and alpha synchronization over frontal electrodes than the younger, suggesting that to enumerate successfully the aged group required more memory resources that were recruited from frontal sites.

Dragan Rangelov, Hermann J. Müller, & Thomas Töllner (Munich, D): Efficiency of attentional selection is continuous rather than categorical

The distinction between efficient and inefficient attentional selection is a cornerstone of any modern theory of attention. Efficient visual search implies that the first item to be selected is always the target, irrespective of the number of distractors (or the display density). Whether or not a target is found efficiently seems to primarily depend on what the target is: if the target is the only item of its kind, i.e., a singleton, the search will be efficient. In other words, efficiency is usually assumed to vary in a categorical (either/or) way predicting efficient search whenever the target is a singleton. However, here we found an inefficient singleton search implying that search efficiency is continuous. On every trial, several diamond-shaped items missing either the top or the bottom corner were briefly presented. One was always different in color from the others (e.g., a red target amongst green distractors) and the task was to report the missing corner of the target. Also, on every trial one of distractors (foil) was an orien-tation singleton, i.e., the missing corner was either on the left or the right. On different blocks of trials either sparse (4 items) or dense (36 items) displays were used. Analyses of the response times (RTs) and the PCN ERP component locked to the target (indexing the speed of attentional selection) showed both slower RTs and a delayed PCN in sparse relative to dense displays. Critically, the foil-locked PCN was significant only in sparse displays. This demonstrates that the foil, rather than the target, was frequently the first item to be selected, i.e., that selecting a color singleton was inefficient. Our results call for a modification of the current models of spatial attention and the development of new tests of search efficiency. Finally, since many studies investigating early vision used singleton search tasks with sparse displays, the present findings question whether these studies truly investigated only early vision.

Kamila Śmigasiewicz & Rolf Verleger (Lübeck, D): Unequal distribution of stimulus-driven orienting of attention as reflected in N2pc-like activity. Evidence from rapid serial visual presentation.

In dynamically changing environments visual spatial attention is not equally distributed across the visual field. For example, when presenting two streams of distractors at horizontal midline, the second target (T2) is better identified in the right (RVF) than in the left visual field (LVF). In the first experiment (E1) we show that this imbalance was related to weaker orienting of stimulus-driven attention toward the RVF than the LVF: the RVF disadvantage was largely decreased with salient task-irrelevant valid cues and increased with invalid cues. In the second experiment (E2) where an additional stream was presented in the top of vertical midline, we show that this LVF bias appeared already in response to salient task-irrelevant cues: cues in the LVF impaired the identification of T2 at vertical midline more than cues in the RVF. These behavioral results were confirmed by event-related EEG potentials: N2pc-like negativity evoked by cues appeared earlier at the right than at the left hemisphere in E1 confirming that even for salient task-irrelevant cues attention is directed faster toward the LVF. In E1 and E2, cues effectively influenced target selection by slowing down the latency of N2pc evoked by T2 after invalid cues as compared to valid cues. Furthermore, T2 in the LVF was selected faster than in the RVF, as reflected in earlier latencies of N2pc evoked by left than by right T2. These results suggest that the hemisphere-specific N2pc component is a useful tool to study faster stimulus-driven orienting of attention toward the LVF.

Matthew D. Weaver, Wieske van Zoest, & Clayton Hickey (Rovereto, IT): Covert selection and suppression as determinants of oculomotor behaviour

In a concurrent eye-tracking/EEG study we explored how mechanisms of attention in visual cortex contribute to oculomotor control. Participants made eye movements to a line-segment target embedded in a search display also containing a salient distractor. Target and distractor salience was manipulated by varying degree of orientation offset from a homogenous background. Results show that successful saccades to less-salient targets were preceded by a.) a target-elicited contralateral negativity (N2pc), reflecting the deployment of covert attention to the target, and b.) a distractor-elicited contralateral positivity (Pd), reflecting distractor inhibition. When the eyes were mis-deployed to the distractor, these components were absent or reduced. Counter-intuitively, overt and covert selection of the target was predicted by increased amplitude of high alpha band activity (12 - 17 Hz) in the pre-stimulus interval. Pre-stimulus alpha thus improved task accuracy, possibly by slowing saccadic response and thus allowing for the establishment of control. Our results demonstrate the contribution of pre-saccadic visuo-cortical mechanisms in the control of oculomotor selection and establish the utility of concurrent eye tracking/EEG recording in directly linking selection performance with neural mechanisms.

Agnieszka Wykowska (Munich, D): Higher-order social cognition influences early mechanisms of perceptual selection, as evidenced by early visual ERP components.

In a series of studies, we examined the impact of higher-order social cognition on early mechanisms of perceptual selection. With the use of a gaze-cueing paradigm, we either manipulated participants' beliefs about the gazer [1] or we embedded the gaze cueing procedure in a complex action scenario [2]. In [1], beliefs were manipulated either by cue identity (human or robot, Experiment 1), or solely via instruction (Experiment 2) with cue identity (robot) remaining identical across conditions. ERP results and behavior showed that participants' attention was guided by gaze only when gaze was believed to be controlled by a human. Specifically, the P1 was more enhanced for validly cued, relative to invalidly cued, trials only when participants believed the gaze behavior was the result of a mind, rather than of a machine. This shows that early mechanisms of perceptual selection can be influenced by higher-order (task-irrelevant) beliefs about the observed scene.

Our study reported in [2] extended these findings by examining how gaze cueing effects and their ERP correlates are influenced by expectations participants have regarding successive action steps of an observed agent. In this experiment, photographs of naturalistic scenes were presented to participants and an agent gazed at objects that could either be congruent or not with the expectations of participants regarding where the agent should look, given the action sequence the agent was involved in. Again, gaze cueing effects were modulated by higher-order cognition: when the agent's gaze behavior was not in line with participants' expectations, participants did not orient attention to the object at which the agent gazed, as evidenced by validity effects observed only in congruent and neutral (but not in incongruent) conditions. This behavioral result was reflected by a similar pattern of validity effects on the N1 ERP component.

In sum, our series of studies show that orienting attention in response to social stimuli – gaze in this case – relies (at least partially) on a top-down component originating in higher-order cognition and modulating early stages of perceptual selection.

[1] Wykowska, A., Wiese, E., Prosser, A., Müller, H.J. (2014). Beliefs about the minds of others influence how we process sensory information. *PLOS ONE*, 9 (4), e94339

[2] Perez-Osorio, J., Müller, H., Wykowska, A. (in prep.). Electrophysiological evidence for modulatory effects of action-related expectations on early mechanisms of perceptual selection.