Behavioral and neural correlates of human visual processing as assessed by psychophysics and functional magnetic resonance imaging

PhD thesis summary

Lajos R. Kozák, MD

János Szentágothai PhD School of Neurosciences
Semmelweis University

Supervisor: György Karmos, MD, PhD (MTAPI, Budapest)
Consultant: Miguel Castelo-Branco, MD, PhD (IBILI, Coimbra)

Opponents: Imre Szirmai, MD, DSc
Gábor Jandó, MD, PhD

PhD Theoretical Exam Committee:
Chair: Anita Kamondi, MD, PhD
Members: Péter Barsi, MD, PhD
Róbert Bódizs, MD, PhD

Budapest

2009

I. INTRODUCTION

This thesis, like any other PhD thesis, is a summary of research done over years, and there are numerous ways to order and present someone's work. As my focus shifted from color vision to motion perception over the years, I decided to introduce the studies in chronological order. All of the studies included deal with different aspects of vision, thus the common background is set by the way visual information is processed in the brain from the retina to the cortex.

1. Disease-related changes in color vision

1.1. Glaucoma

Glaucoma is a chronic, degenerative optic neuropathy (most often associated with elevated intraocular pressure) leading to a progressive loss of retinal ganglion cells and their axons. There is a current controversy in glaucoma research on the degree of relative damage across pathways, in particular regarding the parvo- and koniocellular systems.

It is widely believed that glaucoma is predominantly associated with tritan-like defects and substantial damage has also been extensively reported for the magnocellular system partly from indirect evidence that large fibers are preferentially affected early on in this disease. These findings have formed the basis for the so-called preferential damage hypothesis. There is, however, increased awareness that detectable impairment in a visual pathway also depends on its internal degree of redundancy, the less redundant pathways being more vulnerable.

1.2. Best's vitelliform macular dystrophy (VMD) study

Best disease is an autosomal dominant disorder with variable expressivity characterized by the accumulation of a yellowish lipofuscin-like material within and beneath the retinal pigment epithelium (RPE). It is believed that most hereditary forms of macular disease, such as VMD and Stargardt disease, exhibit type I red-green deficits.

2. Experiments on visual motion perception

2.1. Center-surround interactions in visual motion integration and segmentation

The rules governing peripheral contextual influences on the interpretation of ambiguous central motion stimuli are largely unexplored to date. Collinear configurations, spatial proximity, and common fate are believed to impose grouping of contour segments into spatially extended objects through predominant feedforward processing. However, it remains unclear into which extent local-global feedback mechanisms can modulate such bottom-up processes. In other words, it remains unclear how perceptual organization influences the dynamics of binding, and how the visual system partitions the visual scene into individuated entities such as surfaces and objects.

2.2. Neural correlates of real and illusory motion perception

It is well known that modulation of activity in visual area hMT^+ is related to the perception of global motion and that response levels also depend on attentional modulation. However, it is still an open question whether net blood oxygenation level dependent (BOLD) responses to motion aftereffects (MAE) reflect global motion adaptation-related responses or shifts in arousal and/or specific attentional modulation.

2.3. Learning-induced changes in motion processing

Developing perceptual expertise is essential in many situations, from an air traffic controller monitoring complex video displays to a radiologist searching for a tumor on an x-ray. With practice, these complex tasks become much easier, a phenomenon referred to as *perceptual learning*. Previous functional neuroimaging research in humans has focused on the role of training in increasing neural sensitivity for task-relevant visual information. However an ideal observer should also attenuate task-irrelevant sensory information that interferes with the processing of task-relevant information. The implementation of this optimal strategy is supported by the observation that training leads to much stronger learning effects when task-relevant information is displayed in a noisy environment. However, previous studies have not examined how training influences the neural representation of task-irrelevant information to facilitate learning.

II. AIMS

1. Disease-related changes in color vision

1.1. Glaucoma study

To assess the relative vulnerability of color pathways during the course of glaucoma by using a novel psychophysical approach based on luminance noise. Also, to investigate the relationship between color vision deficits and standard clinical markers of disease progression.

1.2. Best disease study

To quantify chromatic dysfunction in Best disease by using a novel methodological approach based on luminance noise. Also, to reassess the classic categorization of chromatic damage by investigating correlations between color vision and standard clinical markers of disease progression.

2. Experiments on visual motion perception

2.1. Center-surround interactions in visual motion integration and segmentation

To study how visual context influences visual motion integration and segmentation in the center. Also to assess the interaction of suppression and facilitation mechanisms related to congruence and incongruence between center and surround percepts.

2.2. Neural correlates of real and illusory motion perception

To study illusory and real motion processing in visual area hMT^+ using fMRI, with special focus on the effects of attention and the interactions between motion signals. Also, to investigate whether there is a genuine motion aftereffect signal in hMT^+.

2.3. Learning-induced changes in motion processing

To study how perceptual learning changes the processing of relevant and irrelevant visual motion signals.

III. METHODS

1. Disease-related changes in color vision

1.1. Patient Selection and Classification

1.1.1. Glaucoma study

One hundred and ninety-two subjects participated in this study. The individuals were divided into three different groups based on a complete ophthalmic examination: patients with primary open-angle glaucoma (POAG; $n = 51$ eyes) or ocular hypertension (OHT; $n = 95$ eyes) and control subjects ($n = 46$ eyes). The patient and control groups were age matched.

1.1.2. Best disease study

We included 17 patients (34 tested eyes) in this study. Disease staging was done according to the Fishman criteria. Patient distributions across stages were as follows: stages 0/I, 6 eyes; stages II/III, 14 eyes; and stage IV, 14 eyes. A population of 21 normal-sighted controls (41 eyes) was selected for statistical comparisons. Patient and control populations were age matched.

1.2. Psychophysical Methods and Data Analysis

We followed a strategy of parallel interleaved staircase stimulus presentation using a slightly modified version of the Cambridge Color Test (Cambridge Research Systems Ltd, Rochester, England) to evaluate the degree of differential impairment of parvocellular and koniocellular function in patients and compare them with those of normal age-matched subjects. The experiments were conducted at the Institute of Biomedical Research on Light and Image, Faculty of Medicine, University of Coimbra, Portugal.

We have extracted the following quantitative parameters from the color test results: confusion line length, ellipse length, and axis ratio. Further statistical analyses (factorial and repeated measures ANOVA, with the post hoc Fisher PLSD correction; multiple linear regression) were performed using StatView (SAS, Cary, NC, USA).

2. Experiments on visual motion perception

2.1. Center-surround interactions in visual motion integration and segmentation

2.1.1. Participants

Nine subjects participated in Experiments 1 and 2, fifteen in Experiment 3, and nine in Experiment 4, all with normal or corrected-to-normal visual acuity, and good fixation abilities. The experiments were conducted at the Institute of Biomedical Research on Light and Image, Faculty of Medicine, University of Coimbra, Portugal.

2.1.2. Stimuli

Observers were asked to give continuous on-line report whether they perceived non-transparent or transparent plaid motion within the 5° central circular region of the 20° diameter plaid display. Stimuli were presented under three distinct overall luminance/contrast sets: high luminance high contrast (HLHC), high luminance low contrast (HLLC), and low luminance (LL). Behavioral responses (perceptual decisions) were continuously recorded during the motion period by means of mouse button presses.

In experiment 1 stimuli were presented in subject-initiated 12-second blocks containing 2 seconds fixation and 10 seconds plaid movement. Eleven center conditions were defined for each luminance/contrast sets: eight were obtained by varying the luminance of grating intersections and three by applying local dynamic texture on the gratings. Surround conditions were defined as either no surround, or as a 20-degree diameter moving plaid patch surrounding the central patch, having similar spatio-temporal properties as the central stimulus, but biased either towards non-transparent or transparent motion. The spatiotemporal parameters of plaid movement were kept constant throughout the experiment, only luminance parameters, texture, and the presence or absence of the surround patch were varied across conditions.

In experiment 2 we have analyzed the effect of stimulus size on coherency decisions by varying the size of plaid stimuli.

In experiment 3 we have investigated the modulation of highly ambiguous center stimuli during longer stimulus presentation periods: stimulus blocks were presented for 72 seconds, with 12 seconds static fixation and 60 seconds plaid movement.

In experiment 4 pattern motion of the central patch was kept vertical whilst pattern movement in the surround could follow any of the four cardinal directions. The stimuli were presented in subject initiated 22-second blocks (2 seconds period for fixation, 10 seconds plaid motion period and 10 seconds intermixed static plaid rest period)

2.1.3. Data analysis

The continuous recording of responses allowed to estimate the overall duration of single percept types (transparent or nontransparent), the relative ratio of these perceptual states during the presentation periods, and the number of perceptual switches as a possible measure of percept stability.

2.2. Neural correlates of real and illusory motion perception

2.2.1. Participants and data acquisition

Experiment 1 was performed at the Department of Neuroradiology, University Hospital Maastricht, The Netherlands on 4 subjects at 1.5 T. **Experiment 2a** was performed at Ginoeco S.A, Porto, Portugal on 4 participants (only one of which had participated in Experiment 1) at 1.5T. **Experiment 2b** was performed at the Maastricht Brain Imaging Center, Maastricht, the Netherlands on 8 participants (only two of which had participated in Experiments 1 and 2) at 3T. All functional scans were acquired using standard head coils and gradient echo echo-planar imaging (EPI) sequences. High resolution T1 weighted anatomies were also collected in all cases.

2.2.1. Visual stimuli and paradigms

In experiment 1 subjects viewed moving plaids separated by fixation baseline or stationary plaid rest conditions. Subjects performed either an *angle task*, where they had to report whether the angle of the fixation cross (changing every 2 s) was larger or smaller than the plaid angle, or a *color task* where they had to report whether the fixation-cross (changing every 2 s) had the same or different color from the curve outlining the stimulus aperture.

In experiment 2a epochs of plaid motion and static plaids were combined and presented in a block design manner. Motion blocks had either constant direction of motion (adapting *fixed motion conditions*) or the direction changed in every two seconds (non-adapting *mixed motion conditions*). There were motion and static blocks with and without overlaid apparent motion (AM). Subjects had to track speed changes of

the apparent motion stimulus superimposed on the moving and static plaids.

In experiment 2b stimulus properties were similar to Experiment 2a, except for the inclusion of a real motion (RM) condition using similar stimuli as in the AM condition overlaid on top of the MAE period.

2.2.2. Data Analysis

Data analysis was performed using BrainVoyager 2000 and BrainVoyager QX (Brain Innovation B.V., Maastricht, The Netherlands) with standard preprocessing steps. Percent signal change was calculated for each condition separately in hMT^{+}, based on the average activation level of the immediately preceding fixation period.

2.3. Learning-induced changes in motion processing

2.3.1. Participants and stimuli

Fourteen subjects participated in the main experiment and four in a control experiment. In all experiments, moving dots were presented within a 20 deg circular field centered on the fixation square, with a 1.6 deg circular blank region around the fixation point. Dots subtended 0.15 deg in diameter, and had a limited lifetime of seven frames. Behavioral responses were collected by means of mouse button presses.

2.3.2. Experimental procedure

The experiment protocol consisted of a training phase and two testing phases, one before and another after training. Each observer underwent four different testing steps before training: a retinotopic mapping session, a psychophysical testing session, an EEG session, and an fMRI scanning session. The same set of experiments (except retinotopic mapping) was repeated after training to evaluate training induced changes in performance and brain activity. EEG data are not presented in this thesis.

Training comprised six one-hour sessions of psychophysical testing during which subjects performed a series of 2-interval forced choice speed discrimination tasks, while instructed to attend to dots moving in one of the directions (+45° or -45° relative to the upward direction, task-relevant direction) and ignore dots moving in the orthogonal direction (task-irrelevant direction). The speed of the task-relevant direction was fixed for one of the two intervals and varied using a QUEST adaptive staircase procedure for the other interval.

2.3.3. Testing motion coherence detection threshold

Motion coherence thresholds were acquired before and after training for three motion directions within the same block, two directions similar to those of the training and a third, downward control direction. Motion coherence was varied independently using QUEST procedures.

2.3.4. fMRI experiments

Subjects performed a 2-interval forced choice speed discrimination task during scanning. Subjects were instructed to indicate which of the two intervals contained faster motion. The speed was fixed for one of the intervals at 6 $deg \cdot s^{-1}$ while for the other it was adjusted so that subject's performance was around 75% correct during scanning.

MRI data acquisition was performed at the MR Research Center, Szentágothai Knowledge Center, Semmelweis University, Budapest, Hungary on a 3 Tesla Philips Achieva scanner (Philips Healthcare, Best, The Netherlands). All functional scans were acquired using an 8 channel SENSE head coil and gradient echo EPI sequences. High resolution T1 weighted anatomies were also collected in all cases. Data analysis was performed using BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands) and custom time series analysis routines written in Matlab (MathWorks Inc., Natick, MA).

Region of interest analysis was done in retinotopic visual areas (V1, V2, V3, V4v, V3a) mapped by the standard traveling wave method. and in area hMT^+ identified using a localizer scan and GLM analysis.

We extracted time course data locked to stimulus onset and averaged over blocks from each ROI and for each condition. In order to be able to compare activations between different scanning sessions (before and after training) we derived normalizing factors for each area and scanning session. For statistical analysis of the difference between response magnitudes in different conditions we used repeated-measures ANOVA with test session, task relevance, and ROI as factors.

IV. RESULTS

1. Disease-related changes in color vision

1.1. Glaucoma study

1.1.1. Color discrimination deteriorates during the course of disease

We found robust evidence for early chromatic dysfunction in glaucoma as shown both by color discrimination ellipse and color confusion vector parameters. Color confusion vectors seem to be better measures than the length of discrimination ellipses in differentiating control subjects from patients with hypertension. While the tritan discrimintation axis seems to be the most affected, there is a clear-cut global increase across all axes showing that concomitant early damage is already present in patients with hypertension, regarding the konio- and parvocellular systems.

1.1.2. Deterioration of chromatic function correlates well with C/D and MD measures

The cup-to-disc (C/D) ratio correlated significantly with almost all our measures of chromatic performance. Moreover, we also found strong and significant correlations regarding perimetric assessment. Not surprisingly, this correlation is mostly explained by the pattern of loss within the glaucoma group. Interestingly, no significant correlation was found with tritan axis length, suggesting that in spite of more prominent tritan loss, this measure is less correlated with field loss once glaucoma is established.

1.2. Best disease study

1.2.1. Color discrimination deteriorates substantially in all cone pathways during the course of disease

We found a steady elongation of the major axis of discrimination ellipses across the stages, which was accompanied by a significant enlargement of ellipses. The increased axis ratio suggests that although all axes are affected, there is some pattern of preferential damage.

Comparison of chromatic loss along the 3 main confusion lines showed substantial functional impairment with more prominent protan and deutan loss, but this effect was not significant on post hoc analyses,

suggesting that the classic notion of a predominant red-green deficit has to be revised.

1.2.2. Deterioration of chromatic function correlates well with clinical parameters

Strong and significant negative correlations were found between confusion vectors and visual acuity (VA). Ellipse variables were also strongly and significantly correlated with VA (the ellipse length being better correlated than the axis ratio). Furthermore, significant correlations were found between lesion size and chromatic dysfunction.

2. Experiments on visual motion perception

2.1. Center-surround interactions in visual motion integration and segmentation

2.1.1. Transparent surrounds impose stronger modulation on central percepts than non-transparent surrounds

We found that reported central percepts significantly depended on the types of contextual surrounds used. Comparison of context types revealed asymmetric dependence on the type of surround perceptual bias: component surrounds (transparent) being either textured or luminance defined evoked significant modulatory effects, while pattern (non-transparent) surrounds did not yield significant effects when compared to absent surrounds. This effect was present across all non-textured center conditions on all of the luminance/contrast sets.

Textured component surrounds provided stronger modulation than luminance-defined component surrounds. This effect was likely due the fact that they were inherently more biased for transparent motion due to the disambiguation provided by local dots. On the other hand textured stimuli were not prone to be modulated by surround. This novel and intriguing finding suggests that disambiguation provided by local texture is sufficient to render contextual modulation non-effective.

2.1.2. Patch size do not explain the observed modulation

Increasing the stimulus size decreased the observed transparency regardless of stimulus type suggesting that size effects cannot explain the surround modulations observed using component stimuli.

2.1.3. The pattern of modulation is consistent across viewing times

Increasing the presentation time did not change the pattern of mosulation: component surrounds had a highly effective and congruent modulatory effect in contrast to pattern surrounds which, in general, had a more variable effect. Moreover, we found that the described contextual effects are independent of the direction of the coherent plaid motion.

Regarding switch dynamics, we found that transparent-biased surrounds induced more switches and coherent-biased surrounds induced fewer switches than what was observed without surround modulation. Also, at the single percept level component surrounds enhanced the duration of single congruent percepts and reduced the duration of incongruent percepts, while pattern surrounds had a marked facilitatory effect on congruent percepts and no significant suppression on incongruent percepts.

2.1.4. The interactions between local and global context modulate observed transparency

The perceived transparency was, in general, similar when surround motion was in similar or in opposite direction to the center movement. This rule was, however, broken when surround patches moved so that only one (no less and no more) set of the local moving grating contours of the surrounds was constantly collinear with one of the center component gratings. Then, we observed an enhancement of transparent motion percepts in the central plaid patch, caused by the coherent pattern surrounds. The resulting percept was phenomenally striking due to the contrasting perceptual interpretations of center and surround regions. This incongruence was highly significant and occurred under both high and low contrast conditions.

2.2. Neural correlates of real and illusory motion perception

2.2.1. MAE-related motion signal is present when attention is focused on motion independent features

Activity levels in hMT^+ were increased upon plaid motion adaptation, even if disparate motion independent tasks keeping attention stably away from stationary plaid features (color task) or from moving plaid features (spatial comparison task) were used to control for attention. The effect therefore appears to be general across motion independent tasks.

2.2.2. MAE-related motion signal is absent when attention is focused on concurrent independent motion features

A net MAE related signal could be observed upon motion adaptation without any other motion signal overlaid on the static plaid period. However, this effect is abolished when subjects have to selectively attend either overlaid AM or RM during the test period.

Motion interactions during the plaid movement period were additive, proving that adapting plaid motion alone does not saturate hMT^+ responses. Superposition of AM on the adapting plaid motion signal does not completely cancel motion adaptation, but nevertheless decreases the saliency of MAEs, and the BOLD response related to them.

2.3. Learning-induced changes in motion processing

Speed discrimination thresholds gradually improved as a result of training, showing a significant learning effect.

2.3.1. Training decreased sensitivity to motion in task-irrelevant (distractor) direction

We investigated how training on a speed discrimination task affects perceptual sensitivity to different motion directions by measuring motion detection thresholds for three different directions.

The results revealed that training had a strong effect on the observers' performance: motion coherence threshold for the task-relevant direction became significantly lower than the threshold for the task-irrelevant direction after training.

The observed effect is explained by the following changes: thresholds for the irrelevant direction increased significantly while thresholds for the task-relevant direction decreased non-significantly as compared to those before training. Moreover, the threshold for the control direction also underwent a non-significant decrease, further supporting the observation that training decreased sensitivity to motion in a direction that was continuously present as a task-irrelevant distractor during training.

2.3.2. Training decreased fMRI responses to motion in task-irrelevant direction in extrastriate visual areas

Before training, the magnitude of the fMRI responses evoked by the two motion directions was similar. However, after training, fMRI

responses evoked by the task-irrelevant direction were smaller than responses evoked by the task-relevant direction. This difference was significant in V2, V3, V3A, hMT^+.

Normalized data showed a trend of increased neural responses in the early visual cortical areas in the case of task-relevant direction after training compared to that before training; however, this difference was significant only in the primary visual cortex. On the other hand, a comparison of the fMRI responses to the task-irrelevant direction before and after training showed that learning resulted in a significant reduction of the fMRI responses in areas hMT^+ and V4v.

V. CONCLUSIONS

1. Disease-related changes in color vision

1.1. Glaucoma study

The present study shows that a concomitant involvement of multiple chromatic pathways within the central retina is present in the natural history of glaucoma earlier than previously believed. This provides an advance over previous studies not including ocular hypertension, or detailing changes along the tritan axis, only.

We found that progression of chromatic damage proved to be significantly good predictor of clinical and perimetric changes, which is in agreement with a recent finding that development of glaucoma may actually be best predicted by a change in the length of the protan discrimination axis.

Our findings of early dysfunction of both parvo- and koniocellular systems in glaucoma favor the functional-redundancy hypothesis in comparison to the preferential-loss model.

Taken together, our findings suggest that earlier detection of functional damage can be achieved in both the red-green and blue-yellow chromatic pathways than previously believed. Optimized psychophysical procedures based on luminance noise may allow for the establishment of new clinical correlations that are useful to quantify disease progression and to define subpopulations of patients with ocular hypertension that may evolve into glaucoma.

1.2. Best disease study

We found that substantial damage occurs in all cone pathways in Best disease, even in a subset of patients with relatively preserved visual acuity. These results are compatible with the now almost consensual postulate that the primary disturbance occurs in the retinal pigment epithelium.

Our findings challenge the view that chromatic deficits in VMD are type I red-green (as is the current view in Stargardt disease, as well). This is only true for stage IV, moreover tritan deficits actually become statistically significant earlier than protan and deutan deficits, whereas

the latter become more prominent only when the lesion size has increased or foveal involvement has emerged.

As all of our quantitative variables showed statistically significant correlations with visual acuity, proved to be reliable in quantifying relative damage and in predicting disease progression, and correlated significantly with staging and the size of the retinal lesion, we can conclude that psychophysical color testing provides a safe, efficient and non-invasive means for Best disease patient follow-up.

2. Experiments on visual motion perception

2.1. Center-surround interactions in visual motion integration and segmentation

We showed that the dynamics of central motion integration significantly depended both on the type of motion perception in the contextual peripheral surround and on the presence of local motion disambiguation cues. Transparently perceived surrounds evoked more consistent effects as compared to non-transparent surrounds.

The modulation was stronger using textured surrounds in line with the fact that they are inherently unambiguous. Indeed, unambiguous feature motion provided by overlaid random dots completely determines the perceived direction of local contours, and thereby provides a solution to the aperture problem. This rendered textured peripheries to have a powerful contextual influence. On the same token, textured centers escaped from modulation regardless of their inherent perceptual bias or the surrounds used.

Potential MT-V1 feedback analogous the model of Bayerl and Neumann, 2004 might explain the observed effect, producing an imbalance of early response distributions producing more robust shifts towards transparent (component) than coherent interpretations on the population level. A model like this would explain the differential contextual modulation of surface integration processes for pattern (non-transparent) and component (transparent) motion conditions.

Using surround with pattern motion direction orthogonal to that of the centers we showed that collinear facilitation does not necessarily result in motion integration but may even cause segmentation. This represents an unusual instance of Gestalt “good continuation” and

common fate rules, since it leads to center-surround perceptual incongruence. This phenomenally striking effect can be explained by causal contour capture mechanism, where collinearly moving grating elements at center-surround borders dynamically capture local contours in the center thus helping to segment it into separate surfaces while the surrounding context remains unsegregated.

The presented study extends the knowledge on low-level contextual influences on the perception of local visual stimuli and integration of form and depth information in extracting surface representations in early visual areas, by demonstrating a role of peripheral perceptual bias in global surface segmentation/segregation processes and the role of enhancement/suppression mechanisms in this process. Moreover, we showed that these processes can be differentially influenced by local information and common fate mechanisms in adjacent regions of the visual field. Our findings support the notion that the brain uses a hierarchy of precedence rules in attributing motion to different segments of the visual scene and in this case being "local" confers a high rank in the scheme of priorities.

These observations have strong basic and clinical research implications. First, they suggest that the shifting balance between the coherent and transparent (two-surface) percepts are attributed to processing stages before any integration or combination of local motion signals occur, in agreement with previous work. Second, these findings are also clinically relevant because motion may often become ambiguous in different visual disorders, e.g. central ambiguity occurs more frequently in patients with macular diseases, implying that the surround might have a more powerful effect, which may be used clinically in rehabilitation approaches.

2.2. Neural correlates of real and illusory motion perception

We conclude that the neural substrate of illusory motion aftereffect perception can be identified in conditions requiring selective attention to concomitant non-motion features and is masked by concurrent apparent/real motion tasks. In other words, hMT^+ sensitivity to MAE can be differentially modulated by selective attention to various non-motion and motion features. Finally, superimposed real and apparent motion may lead to additive adaptation effects without saturation of area hMT^+

responses, while the interaction of apparent motion and MAE reflects interference effects.

We do believe that our results do reconcile the apparently contradictory results of Tootell et al., 1995 and Huk et al., 2001 by showing that selective attention can suppress motion-adaptation related activity in area hMT^+, if and only if it is focused on concomitant motion features, regardless of whether they are apparent or real.

2.3. Learning-induced changes in motion processing

Our findings provide evidence that learning results in increased detection thresholds for task-irrelevant features during training. This learning-induced sensitivity decrease was specific for the feature that served as a distractor during training since the detection threshold for a control direction that was not present during training slightly decreased (rather than increased) after training.

We also found that learning results in decreased fMRI responses evoked by the task-irrelevant motion direction compared to the task-relevant motion direction throughout visual cortex. The strongest learning effects were observed in extrastriate visual cortical areas V2, V3, V3a and hMT^+, the latter two of which are known to be involved in visual motion processing,

We propose that the learning-induced modulation of fMRI responses might be a combined effect of increased neural responses to the task-relevant direction and decreased neural responses to the task-irrelevant direction after training. Importantly, we also suggest that learning-induced modulation of neural responses to task-relevant and task-irrelevant directions is not restricted to the trained task condition, but affects processing of these directions generally, in a task independent manner.

Taken together, learning-induced suppression represents an important mechanism underlying more efficient distractor exclusion after training, and should be incorporated into models of perceptual learning.

THE CANDIDATE'S BIBLIOGRAPHY

Publications related to the thesis

1. Castelo-Branco M, Faria P, Forjaz V, **Kozak LR**, Azevedo H (2004): Simultaneous comparison of relative damage of chromatic pathways in ocular hypertension and glaucoma: correlation with clinical measures, *Invest Ophthalmol Vis Sci* 45(2):499-505. ***IF:3.577*** *Cited: 13 times*
2. Campos SH, Forjaz V, **Kozak LR**, Silva E, Castelo-Branco M (2005): Chromatic dysfunction in Best's macular dystrophy: a model for new quantitative strategies of phenotyping and clinical staging, *Arch Ophthalmol* 123(7):944-949. ***IF: 3.274*** *Cited: 3 times*
3. **Kozak LR** and Castelo-Branco M (2009): Peripheral influences on motion integration in foveal vision are modulated by central local ambiguity and center-surround congruence, *Invest Ophthalmol Vis Sci* 50(2):980-988. ***IF: 3.528***
4. Gál V, **Kozák LR**, Kóbor I, Bankó ÉM, Serences JT, Vidnyánszky Z (2009): Learning to filter out visual distractors Eur J Neurosci 29(8):1723-1731 ***IF: 3.673***
5. Castelo-Branco M*, **Kozak LR***, Formisano E, Backes WH, Teixeira J, Xavier J, Goebel R (2009): The type of featural attention differentially modulates hMT+ responses to illusory motion aftereffects, *J Neurophysiol* (Aug 26, 2009, * shared first authorship) ***IF: 3.648***
6. ***Kozak LR****, Lima B, Neuenschwander S, Muckli L, Castelo-Branco M: Motion coherence is differentially affected by local-global common fate between center and surround components, under rev. in Percept Psychophys*

Publications unrelated to the thesis

1. Eke A, Hermán P, Kocsis L, **Kozak LR** (2002): The fractal characterization of complexity in temporal physiological signals, *Physiol Meas*, 23(1): R1-R38**.** ***IF: 1.160*** *Cited: 46 times*
2. **Kozák LR**, Hegyi M, Barsi P, Rudas G (2009): Clonazepam can facilitate sensorimotor functional mri examinations in status epilepticus during sleep, (in Hungarian), *Ideggyogy Sz 62(3-4):130-135*
3. Hegyi M, Siegler Zs, Barsi P, Rudas G, Lengyel Zs, Szakáll Sz, Bognár L, **Kozák LR**, Neuwirth M, Fogarasi A (2009): Surgically cured resistant epilepsy – caused by hemispherical dysgenesis a case report (in Hungarian), *Ideggyógy Sz 62(5-6):185-189*
4. **LR Kozák**, M Bangó, M Szabó, G Rudas, Z Vidnyánszky, Z Nagy (2009): Using Diffusion MRI for Measuring the Temperature of Cerebro-spinal Fluid within the Lateral Ventricles In-Vivo, *Acta Paediatrica* (Oct 20, 2009) ***IF: 1.517***

Citable abstracts related to the thesis

1. Castelo-Branco M, **Kozak LR**, Teixeira J, Xavier J (2007): The role of visual area hMT/V5 in dissociating perceptual decision from veridical stimulus properties, ECVP, Arezzo, Italy, *Perception* 2007; 36:135-135.
2. Gál V, **Kozák LR**, Kóbor I, Bankó E, Serences J, Vidnyánszky Z (2007): Perceptual and neural mechanisms of visual attentional suppression, ECVP, Arezzo, Italy, *Perception* 2007; 36:115-115.
3. **Kozak LR**, Lima B, Neuenschwander S, Muckli L, Castelo-Branco M (2005): Contextual modulation of bistable plaid motion perception, ECVP, A Coruña, Spain, *Perception* 2005; 34: 163-163 Suppl. S,
4. **Kozak LR**, Formisano E, Backes W, Teixeira J, Xavier J, Goebel R, Castelo-Branco M (2005): Neural correlates of illusory motion perception: the influence of apparent motion on plaid motion aftereffects, VSS, Sarasota, FL, USA, *J Vis* 5(8):666a.
5. **Kozak LR**, Formisano E, Backes W, Teixeira J, Xavier J, Goebel R, Castelo-Branco M (2005): Human neural responses to overlaid real and apparent motion: implications for mechanisms of illusory motion perception, ARVO, Fort Lauderdale, Fl, USA, *Invest Ophthalmol Vis Sci* 2005; 46: E-Abstract 5657.
6. **Kozak LR**, Formisano E, Goebel R, Castelo-Branco M (2004): Interactions between visual attention and illusory motion perception, European EVER, Vilamoura, Portugal; *Ophthal Res 36 (S1):168 [abstract No: 2421]*
7. Castelo-Branco M, Forjaz V, Campos SH, **Kozak LR**, Silva E (2004): Chromatic adaptation in Best's macular dystrophy: implications for quantitative phenotyping and clinical staging, ARVO, Fort Lauderdale, FL, USA; *Invest Ophthalmol Vis Sci* 2004;45: E- 4334.
8. Castelo-Branco M, Faria P, Forjaz V, Campos SH, **Kozak LR** (2003): Quantification of relative damage of chromatic pathways in diseases involving the central or peripheral retina, EVER, Alicante, Spain, *Ophthal Res 35 (S1):195 [abstract No: 2363]*
9. Faria P, Castelo-Branco M, Forjaz V, **Kozak LR**, Azevedo H (2003): Early and late damage of parvo and koniocellular function in ocular hypertension and glaucoma: correlation with clinical markers of disease progression, EVER, Alicante, Spain, *Ophthal Res 35 (S1):204 [abstract No: 2444]*
10. Forjaz V, Campos SH, **Kozak LR**, Silva E, Castelo-Branco M (2003): Chromatic deficits in Best's macular dystrophy: insights for the development of new clinical tools, poster, EVER, Alicante, Spain, *Ophthal Res 35 (S1):43 [abstract No: 261]*
11. Castelo-Branco M, Faria P, Forjaz V, Campos S, **Kozak LR** (2003): Early quantification of chromatic pathway involvement in central and peripheral retinal disorders (Quantificação precoce do envolvimento relativo das vias cromáticas em doenças da retina central ou periférica), SPO, Vilamoura, Portugal, *Oftalmologia* 27(4):5

Citable abstracts unrelated to the thesis

1. **LR Kozak**, I Gyuricza, T Gyorke, L Szidonya, J Gyebnar, T Kovacs, G Rudas, P Barsi (2009): Medial temporal lobe atrophy score: a locally derived measure with strong global implications, European Society of Neuroradiology Meeting, Athens, Greece, *Neuroradiology, 2009;51 Suppl1 S30*
2. I Gyuricza, **LR Kozak**, T Gyorke, L Szidonya, J Gyebnar, T Kovacs, G Rudas, P Barsi (2009): Cerebral MR-volumetric examinations in the diagnosis of Alzheimer disease, European Society of Neuroradiology Meeting, Athens, Greece, *Neuroradiology, 2009;51 Suppl1 S62*
3. **LR Kozak**, G Rudas, Z Vidnyanszky, Z Nagy (2009): Pulse triggering can improve the quality of diffusion tensor imaging data in neonatal subjects, European Society of Neuroradiology Meeting, Athens, Greece, *Neuroradiology, 2009;51 Suppl1 S96-97*
4. **LR Kozak**, M Hegyi, P Barsi, G Rudas (2009): Clonazepam can assist performing sensorimotor functional mri examinations in status epilepticus during sleep, European Society of Neuroradiology Meeting, Athens, Greece, *Neuroradiology, 2009;51 Suppl1 S140*
5. **LR Kozák**, G Rudas, Z Vidnyánszky, Z Nagy (2009): Examining the Need for Pulse Triggering When Collecting Diffusion Tensor Imaging Data from Neonatal Subjects, Pediatric Academic Societies Annual Meeting, Baltimore, MD, USA, 2009
6. Bangó M, Kelen D, **Kozák LR**, Róka A, Szabó M, Rudas G (2008): Serial proton MR spectroscopy measurement of cerebral metabolites in asphyxiated infants during the first week of life, International Congress of the UENPS, Rome, Italy, *Early Hum Dev, 2008;84:S57-S57.*
7. **Kozák LR**, Barsi P, Erőss L, Vidnyánszky Z, Rudas G (2008): Optimization of clinical functional MRI protocols at 3 Tesla, ESNR, Krakow, Poland, *Neuroradiology, 2008, 50 Suppl1: A2:2:2*
8. **Kozak LR**, Szatmary G, Vidnyanszky Z (2007): Neural and behavioral mapping of the visual field in true and simulated visual field deficits, EVER, Portoroz, Slovenia, *Acta Ophthalmol Scand* 2007;85(s240):0-0.
9. Nagy Z, **Kozák LR**, Bangó M, Szabó M, Rudas G, Vidnyánszky Z (2007): Measuring the CSF temperature using diffusion MRI: a possible method to monitor the brain temperature of cooled babies, ESPR, Prague, *Acta Paediatr* 2007;96:47-47.
10. Castelo-Branco M, **Kozak LR**, Teixeira J, Xavier J (2007): The role of visual area hMT/V5 in dissociating perceptual decision from veridical stimulus properties, ECVP, Arezzo, Italy, *Perception* 2007;36:135-135.
11. Kóbor I, Gál V, Bankó E, Körtvélyes J, **Kozák LR**, Vidnyánszky Z (2007): ERP correlates of decision making in a motion direction discrimination task, ECVP, Arezzo, Italy, *Perception* 2007;36:142-142.
12. Vidnyánszky Z, Gál V, Kóbor I, **Kozák L**, Serences J (2007): Attentional suppression spreads throughout the visual field, VSS, Sarasota, FL, USA, *J Vis*, 7(9):787a
13. **Kozak LR**, Castelo-Branco M, Read JCA (2004):Physiologically-realistic circuitry underlying the motion aftereffect, VSS, Sarasota, FL, USA, *J Vis* 4(8):486a,
14. **Kozak LR**, Castelo-Branco M, Karmos G, Read JCA (2004): A computational model of the motion aftereffect, ARVO, Fort Lauderdale, FL, USA; *Invest Ophthalmol Vis Sci* 2004;45: E-4366.