Project no.: FP7-ICT-217077
Project full title: Heterogeneous 3-D Perception across Visual Fragments
Project Acronym: EYESHOTS
Deliverable no: D5.3b
Title of the deliverable: Report on the respective influence of motor and visual parameters on fragment location obtained from saccade adaptation data on monkeys.

Date of Delivery:	01 September 2010	
Organization name of lead contractor for this deliverable:	UNIBO	
Author(s):	S. Wulff, A. Bosco, G. Placenti, K. Havermann , M. Lappe and P. Fattori	
Participant(s):	UNIBO, WWU	
Workpackage contributing to the deliverable:	WP5	
Nature:	Report	
Version:	1.1	
Total number of pages:	16	
Responsible person:	Patrizia Fattori	
Revised by:	Silvio P. Sabatini	
Start date of project:	1 March 2008	**Duration:** 36 months

Project Co-funded by the European Commission within the Seventh Framework Programme		
Dissemination Level		
PU	Public	**X**
PP	Restricted to other program participants (including the Commission Services)	
RE	Restricted to a group specified by the consortium (including the Commission Services)	
CO	Confidential, only for members of the consortium (including the Commission Services)	

Abstract:

This deliverable reports data on the effect of the eye position on saccadic adaptation in a trained *Macaca fascicularis*. For that purpose the amplitude of reactive saccades of the monkey was modified by saccadic adaptation in one of five equally distributed starting positions. Afterwards adaptation of saccades with an identical amplitude vector was measured at all five possible starting positions. Since the continuous adjustment of the system by saccadic adaption is a requirement for the combining of fragments to a perception of the whole peripersonal space, the understanding of the process of saccadic adaptation is a necessity for the implementation of sensorimotor laws in an action-minded spatial representation.

Contents

1 Executive summary

This deliverable describes the research work performed by UNIBO and WWU in collaboration regarding task 5.3 (Motor description of fragment location) of Work Package 5 (Human behavior and neural correlates of multisensory 3D representation). This task is concerned with the study of the role of motor parameters in fragment location in humans, as described in deliverable 5.3a, and in monkeys. The goal is to provide specifications of the saccadic mechanism via the saccade adaptation paradigm so that the mechanism subsequently can be reproduced in the artificial system of Work Package 4. This artificial system will use estimated but not executed eye motor movements for the localization of fragments in the environment. Thus, the current experiment is designed to figure out which informations are used in humans and monkeys to create the parameters of motor signals. Until now, it is generally believed that there is no influence of an adapted saccade on saccades with an identical vector but different starting positions. In our experimental setup the amplitude of reactive saccades of a monkey was modified by saccadic adaptation and afterwards the gain change of saccades started in different positions was tested. This way we could show that the initial position of the eyes has an effect on the gain change at different starting positions. As it was foreseen a PhD student from WWU spent a period in the UNIBO lab to set up the stimulations and participate in the analysis of the experimental data.

2 Introduction

2.1 The visual system and saccadic adaptation

The visual system is regarded to be the most important sensory system in humans, since it provides far reaching three-dimensional information of high resolution of the environment. For an active exploration of the ambient scene, subjects make rapid eye movements called saccades which shift the direction of gaze from one target of interest to another. Saccades are so brief that no visual feedback can be given during the saccade. Therefore, the saccadic motor command have to be exactly prepared in advance to accurately aim the fovea at a new target. Due to growth, injury or muscle weakness in consequence of aging, the mechanical properties of the oculomotor plant are subject to alterations which would lead to an erroneous saccade based on the primal motor command. For this reason the motor command is continuously adjusted to the new requirements the way that the amplitude becomes shorter if the saccade consistently overshoot the target and the amplitude becomes longer if the saccade consistently undershoot the target. This effect is called saccadic adaptation. It can be activated in laboratory using the McLaughlin adaptation paradigm (McLaughlin 1967). If a subject is doing saccades, whose targets are systematically displaced during execution of the saccade, the amplitude will be adapted. In humans saccadic adaptation can usually be reached in less trials than in monkeys, however, it is normally incomplete in both species.

Whereas it is well known that there is an influence of an adapted saccade on the amplitudes of saccades made to larger or smaller target steps (Hopp and Fuchs 2004), it is generally believed that there is no influence of an adapted saccade on the amplitude of saccades with the same vector but different starting position (Semmlow et al. (1989), Albano (1996), Frens and Opstal (1994)). However, Markus Lappe already showed that this effect exists in humans (see Section 2.3) and in the current study we investigate the effect of the eye position in the beginning of the saccade on the transfer of adaptation to saccades with different starting positions in monkeys. Since we can specify additional characteristics of the process of saccadic adaptation this way, the results of the study could be used as an indication where to look for possible adaptation areas.

Furthermore, up to now plastic modulations to the visuomotor system are assumed to be coded in a purely retinal reference frame, but there are indications that additional information is needed since it is shown that synchronous amplitude adaptation in opposite directions at different positions in space is possible (Alahyane and Pelisson (2004)).

2.2 The role of fragments in action-perception coupling

In humans visual information is used to localize targets of interest to which then saccades are made to gain more visual information. Thus the visual system is a prime example of action-perception coupling. The perceived fragments of the environment are located reverting to information based on the interaction of motor and visual parameters. Hence, motor commands of the oculomotor system can be used to update egocentric relationships and object-to-object relationships in an action-minded spatial representation. The data we gained from our experiment allows to gather information about the process of origin of the motor command via the observation of its behavior during manipulation of the system by saccadic adaptation.

2.3 Eye position effects in humans

In a previous study the effect of the initial eye position on saccadic adaptation in humans has been analyzed (Haverman et al. (2010)). The subject's saccadic amplitude was adapted in one specific spatial location and then the transfered gain change to saccades with the same amplitude but different starting positions was measured. A schematic view of the spatial arrangement of fixation positions and target positions is depicted in Fig. 1.

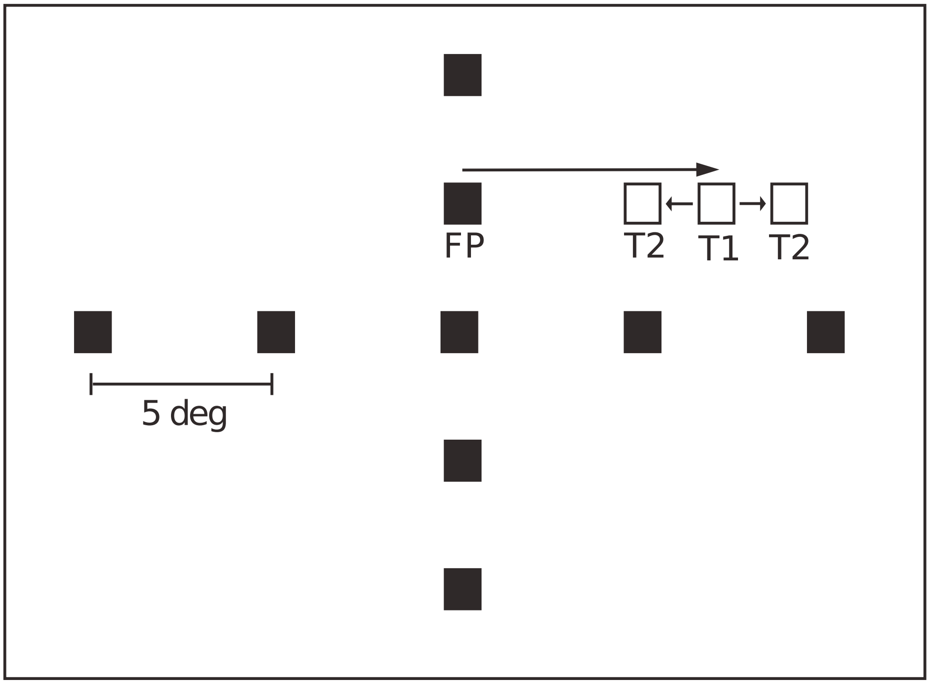

Figure 1: Schematic view of the possible position of the fixation point (filled). The fixation point appeared at one of five equally distributed fixation positions in a horizontal plane with a distance of five deg between adjacent fixation positions. In a second part of the study the fixation points appeared equally distributed in a vertical plane. The target (unfilled) is shown before (T1) and after the intrasaccadic target step (T2) for one possible fixation point (FP). Both target step directions, inward and outward were measured.

In the first part of the study the fixation points were equally distributed in a horizontal plane. The transfer of gain change was tested for inward as well as for outward adaptation for all five positions. In the second part of the study, the fixation points were equally distributed in a vertical plane. The amplitude of the adapted saccades as well as the test saccades was seven deg. The inward step was of the size of two deg and the outward step was doubled to four deg to reach a comparable amount of gain change. In one session the subjects were adapted in one spatial position in the horizontal or vertical plane and then the gain change was tested at the other four horizontal positions or vertical positions, respectively. Therefore, every subject had to accomplish ten sessions, five with inward adaptation and five with outward adaptation in the first part, and analogous ten sessions in the second part of the study.

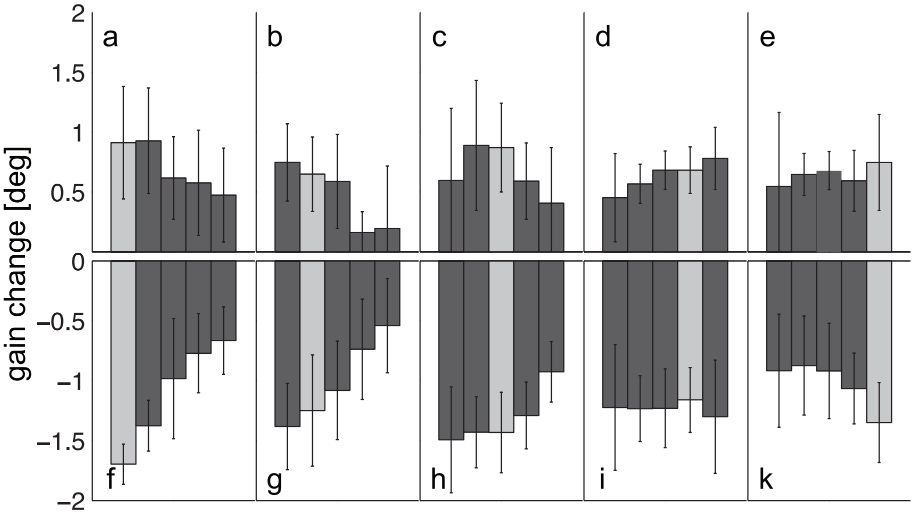

Figure 2: Gain change patterns with a horizontal arrangement of starting positions. Each panel shows the gain changes of all five test positions of one session in the spatial order of their appearance on the screen. The light grey bars show the adapted position, whose position is shifting from the most left position in a) and f) to the most right position in e) and k). Upper row: Outward adaptation, bottom row: Inward adaptation.

Fig. 2 shows the group results for the horizontal arrangement of initial eye positions. A clear dependence of the gain change on the eye position is visible. The adaptation behavior is quite similar for inward adaptation and outward adaptation. With increasing spatial distance from the adapted position, the adaptation decays. The gain change pattern appears to be quite linear, which leads to an increase in the adaptation in the most extreme positions after adaptation of the second most extreme positions. Furthermore, the steepness of the linear decay is flattened at the right side. The group results for the vertical arrangement of initial eye position can be seen in Fig. 3. A clear dependence of the gain change on the eye position is visible, too. And analogously to the horizontal setup, the adaptation behavior is quite similar for inward adaptation and outward adaptation. With increasing spatial distance from the adapted position, the adaptation decays.

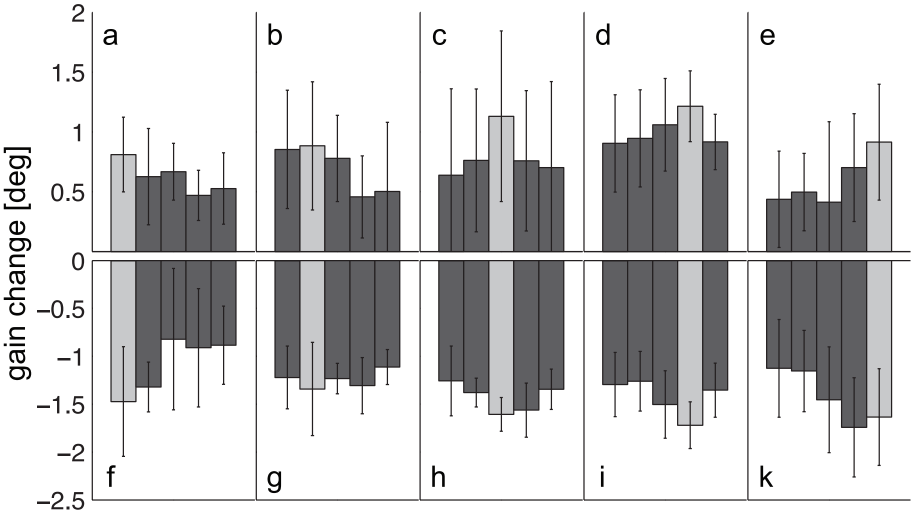

Figure 3: Gain change patterns with a vertical arrangement of starting positions. Each panel shows the gain changes of all five test positions of one session in the spatial order of their appearance on the screen, whereas the left bar position equals the bottom position on the screen. The light grey bars show the adapted position, whose position is shifting from the most left position in a) and f) to the most right position in e) and k). Upper row: Outward adaptation, bottom row: Inward adaptation.

The influence of the eye position on the measured gain change was analyzed for both parts of the study separately using a three factor repeated measures ANOVA. The adapt position was used as the first factor and the test position as a second factor. The direction of target step was included as a third factor to allow a comparison of inward and outward adaptation. Since the precondition for an eye position dependence is a dissimilar gain change at the different test positions, the effect would become evident if the gain change arising at a certain position would depend on the adapted position. Therefore, an interaction of the two factors adapt position and test position was determined. The interaction was significant for initial eye positions horizontally aligned (F(16,80) = 11.276 , p <.0001) as well as vertically aligned (F(16,64) = 5,271, p <.0001).

2.4 Study on eye position effects in monkeys

In our study the participating monkey performs reactive saccades following stimuli presented on a monitor placed in front of the animal. Analogously to the eye position study in humans, there are five equally horizontally distributed starting positions for the saccades. From these different initial positions saccades of 20 deg amplitude are made to targets which thus have all the same retinotopic coordinates when the monkey is fixating the corresponding fixation point. In each session the saccades in one selective position are adapted using the McLaughlin adaptation paradigm and the gain change of the saccades starting at the other four position is measured.
The results show an effect of the initial eye position on the gain change retrieved at the four testing positions including a dependency of the gain change at a certain test position on the distance from the adaptation position. With these findings we confirm the necessity of additional information used for the calculation of the motor signal beyond the pure retinal coordinates.

3 Materials and Methods

Experiments were approved by the Bioethical Committee of the University of Bologna and were performed in accordance with national laws on care and use of laboratory animals and with the European Communities Council Directive of 24th November 1986(86/609/EEC), recently revised by the Council of Europe guidelines (Appendix A of Convention ETS 123). A trained Macaca fascicularis performed a saccadic adaptation task with the head restrained. The head-restraint system was surgically implanted in asepsis and under general anesthesia (sodium thiopental, 8 mg/Kg/h, i.v.) following the procedures reported in (Galletti et al. (1995)). Adequate measures were taken to minimize pain or discomfort. A full program of postoperative analgesia (ketorolac trometazyn, 1 mg/Kg i.m. immediately after surgery, and 1.6 mg/Kg i.m. on the following days) and antibiotic care [Ritardomicina (benzatinic benzylpenicillin plus dihydrostreptomycin plus streptomycin) 1-1.5 ml/10 kg every 5-6 days] followed the surgery.

3.1 Recording of eye movements

During the recording sessions, signals from both eyes were recorded simultaneously with an infrared oculometer (ISCAN, Inc) at a sampling rate of 100Hz and a resolution of 1 deg. Before each experimental session, the monkey was required to perform a calibration task that allowed us to calibrate the signals from each eye seperately. In this task, the monkey fixated sequentially ten light emitting diodes (LEDs) that were mounted on a frontoparallel panel at a distance of 15 cm from the eyes. In front of each eye, there were five LEDs in a cross arrangement with the central one being aligned with the eyes primary position. The four peripheral LEDs were located at an angle of +/- 15 deg on left and right and on top and bottom of the central one. Calibration factors for each eye were extracted from the eye traces recorded in the calibration task.

3.2 Behavioural task

The monkey sat in a primate chair with its head restrained and faced a 17" monitor (Acer, AL 1716 As) with a visible display size of 33,5 cm x 26,8 cm. The viewing distance of 32 cm from the animal eyes to the screen resulted in a visual field of 55.3 cm x 45.4 cm. The display had a resolution of 1280 x 1024 pixels and a frame rate of 60 Hz. For stimuli presentation and data analysis we used MATLAB with the psychtoolbox extension (Brainard (2004)). In Fig. 4 the procedure of adaptation is explained. It shows the layout of a trial in the adaptation phase of the session. In addition we used pre-trials to define a baseline of the saccadic amplitude and test trials to measure the amount of adaptation. The two latter trial types will be explained below in detail.

To start a new trial the monkey had to press a button near its chest, out of the visual field, when the screen was all black. The button presses/releases were recorded by LABVIEW with 1 ms resolution. After the button press, a green fixation point was placed at one of five possible equally horizontally distributed saccadic starting positions, i. e. locations of the fixation point, at -10 deg, -5 deg, 0 deg, +5 deg or +10 deg gaze direction, see Fig. 5. All stimuli were presented along the screen horizontal line at the animal's eye level. The monkey had to establish and maintain fixation at this point. The monkey's eye position was monitored online by the tracker system the way that the direction of gaze had to enter and stay in a window of 5 deg x 5 deg centered around the fixation point. After a randomized time between 1000 ms and 1500 ms the fixation point was switched off and simultaneously a green target appeared 20 deg to the right with respect to the location of the fixation point (Fig. 4b). The monkey was trained to make a saccade towards the target as quickly

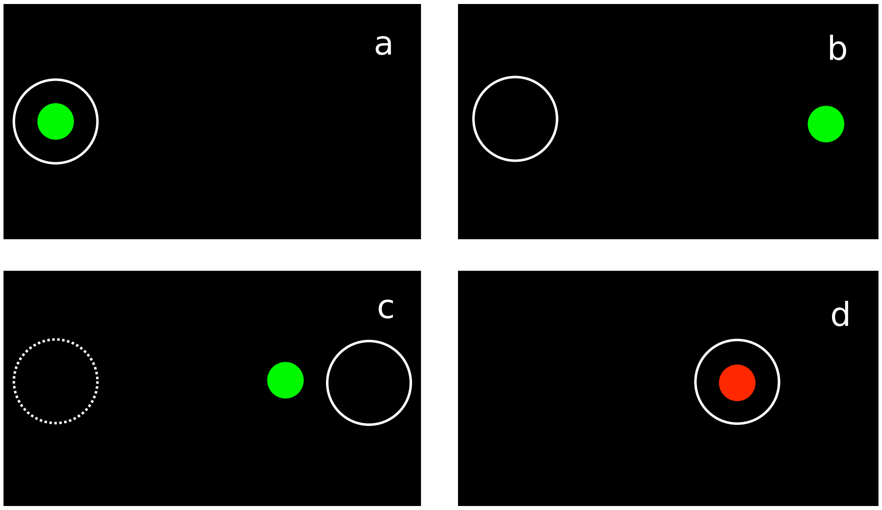

Figure 4: The experimental procedure for adaptation of reactive saccades. a) At the beginning of the trial the green fixation point is presented and the monkey's gaze (circle) is directed towards it. b) After a randomized time the fixation point is switched off and the green target appears 20 deg to the right with respect to the fixation point. c) As soon as the onset of the saccade is detected, the target is shifted 5 deg to the left. In consequence of the target back step, the saccade overshoots the target and thus a visual error is induced. The monkey makes a second saccade to land on the target. d) After a randomized time the target becomes red and the monkey releases the button to get its reward.

as possible and establish fixation at the green target. During the adaptation phase in every trial the target stepped back 5 deg as soon as the monkey left the window centered around the fixation point (Fig. 4c). In the initial trials of the adaptation phase this inward shift of the target caused a visual error at the end of the saccade since the target was now located in a certain distance to the landing point of the eyes (Fig. 4d). This leads to saccadic adaptation and thus to a decreased amplitude of the following saccades. The shifted target turned red after a randomized time between 600 ms and 1000 ms. This was the signal for the monkey to release the button. If the monkey reacted within a maximum time of 1000 ms, he was rewarded with a definite amount of water. In the case that the monkey released the button before the turning red of the target, i. e. already during the trial, or too late, the trial was aborted, the monkey did not get any reward and the screen turned black

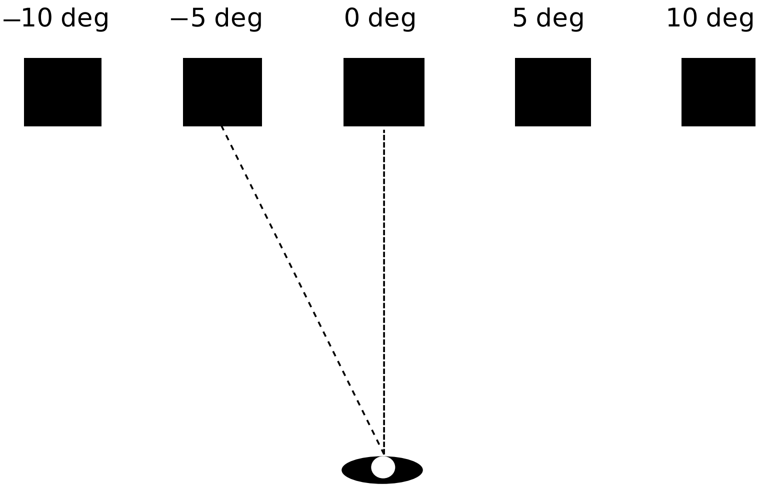

Figure 5: Schematic view on the possible positions of the fixation point. All positions are aligned with the screens horizontal line at the monkey's eye level.

so that a new trial could be started by the monkey pressing the button.
Every session consisted of 850 completed trials and was composed in the following way. The first part of each session consisted of 100 so called pre-trials which did not contain a target step. The pre-trials were used to measure the baseline of the saccadic amplitude in every possible saccade position. Hence there were five blocks of 20 pre-trials each, one block at each of the five positions. Afterwards the adaptations phase started in which 350 adaptation trials were performed by the monkey. During the adaptation phase all saccades were started at the same starting point and all trials contained an inward target step. After the adaptation phase, the monkey usually had achieved the maximal amount of adaptation so that the amplitude of the saccades did not decrease any more but stayed constant. At that time the test phase started. It consisted of 20 test saccades at each of the five possible positions in a randomized sequence. In a test trial the target is not stepped back when the onset of the saccade is detected but instead it is switched off for a time of 300 ms and than switched on again at the same position. Subsequently to the reappearance of the target it turned red after a randomized time so that the monkey could successfully fulfill its task and got rewarded. The target is switched off during the saccade to avoid that the target is seen when the saccade is finished and thus to reduce the error signal. In this way we tried to maintain the monkey's adaptation as complete as possible.

In addition, the test trials were interspersed with adaptation trials at the initially adapted positions in the ratio 1:2. Every test trial was followed by two adaptation trials. At the end of the session the last block consisted of 100 deadaptation trials to start extinguishing the monkey's adaptation.
The experiment consisted of five sessions which were performed by the monkey with a seperation time of 24 h between two of them. In every session the monkey's saccadic amplitude was adapted at one out of the five saccade positions and afterwards the amount of gain change was tested at all five positions.

4 Results

Our main interest was the detection of an influence of the initial eye position in the adapted saccades on the amount of gain change in the four test positions. To compare the gain change induced at the adaptation position to the gain change transfered to the other positions a pre-post-analysis was done. For that purpose the pre-trials were used to calculate an averaged unaffected amplitude at each test position including the adaptation position. Analogously, the test trials were used to calculate the average amplitude at each of the five positions after the succeeded adaptation in one position. The amount of gain change in every position in every single session was determined by subtracting the averaged amplitude gained from the pre-trials of that session in the relevant position from the averaged post amplitude gained from the test-trials of that session. Thus the gain change is the difference of averages of pre and post gains. The result is shown in Fig. 6.

Panels I-V correspond to the five experimental sessions and each panel shows the gain changes of all five test positions of one session. The position on the x-axis in every bar chart corresponds to the location of the test-saccade in the session the way that the outermost black bar on the left in every panel depict the gain change of the saccades started at -10 deg and the bar on the right depict the gain change of the saccades started at + 10 deg.
To test the effect of the eye position on the amount of gain change an unbalanced two factor ANOVA was done for the gain change measured in all test-trials with respect to the averaged preamplitude of the relevant pre-trials. Since an eye position effect on saccadic adaptation would lead to a dependence of the gain change achieved in a certain test position on the adaptation position, the two factors adaptation position and test position were introduced. The interaction of the two factors was found to be significant ($F(16,551) = 46.99$, $p < .0001$), what confirmed the existence of an eye position effect in the adaptation of reactive saccades.

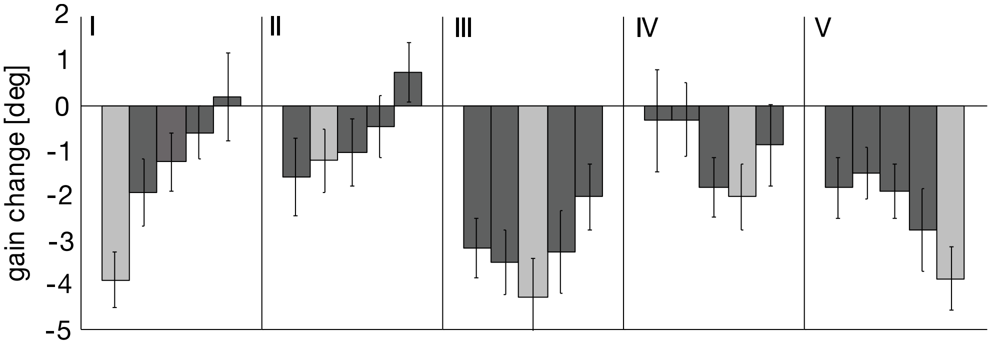

Figure 6: The gain change patterns of all five experimental sessions. Each panel shows the gain changes of all five test positions of one session in the spatial order of their appearance on the screen, from - 10 deg to + 10 deg in steps of 5 deg. In each session the adaptation was obtained for a different starting position: I) - 10 deg; II) - 5 deg; III) 0 deg; IV) + 5 deg; V) + 10 deg

5 Discussion

In this study we have shown that in monkeys the initial eye position has an influence on the amount of gain change transfered to saccades with the same amplitude but different starting positions. For that purpose a saccade of a certain starting position and amplitude was adapted and the amount of gain change was measured for four saccades with identical amplitude but different starting positions, as well as for the saccade at the adaptation position. The results show an unambiguous dependence of the initial eye position on the gain change. Hence, we proved that the plastic modulations to the visuomotor system required for saccadic adaptation cannot be coded in a purely retinal reference frame.
Furthermore, the results of our study on the effect of the initial eye position on saccadic adaptation in monkeys are consistent with the results from a previous study on humans, see Fig. 7.

To make further analysis of the results of the current study possible, including a detailed examination of the influence of any saccade direction specific effect, and to enhance the statistical significance of the study, data collection with a second trained animal will be indispensable. But since the data gained from the first monkey are in perfect agreement with the results of the study in humans, they can already give an indication which cortical areas could be involved in the process of saccadic adapta-

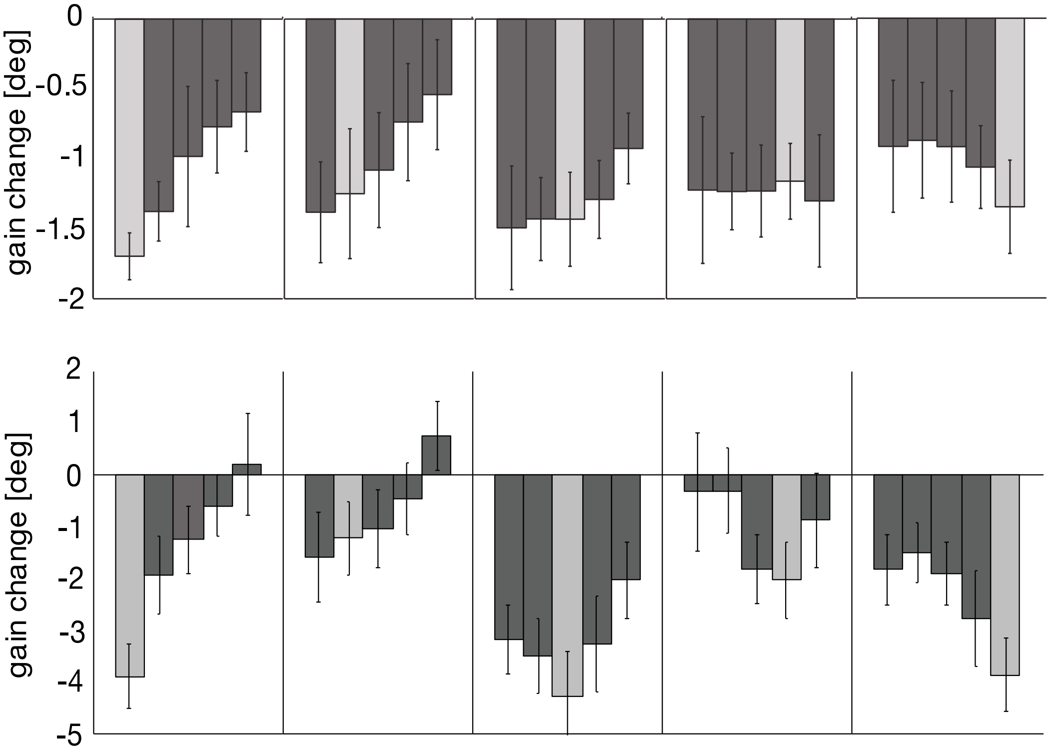

Figure 7: Comparison of gain change patterns with a horizontal arrangement of starting positions in humans and monkeys. Upper panels: Inward adaptation and testing of gain change at the five possible initial positions in humans. Lower panels: The data of the monkey's inward adaptation and testing of gain change at the five possible initial positions.

tion. The areas mainly discussed in the context of saccadic adaptation are the FEF, the LIP, the cerebellum, the superior colliculus, and the nucleus reticularis tegmenti pontis. In each of these areas a retinotopic arrangement of cells was observed, which, depending on their visual or movement related properties, show movement or receptive fields. Furthermore, in all these areas eye position modulation has been detected. To test, if one of these structures is causal for a detected gain change pattern, distinction criteria have to be defined for the different areas. One property, which is characteristic, is the alignment or anti-alignment of the receptive/movement field direction of any cell with the eye position sensitivity. In the colliculus, receptive field and eye position preference were found to be aligned, whereas the FEF shows an anti-alignment of receptive field and eye position preference (Cassanello and Ferrera 2007; Campos et al. 2006; Opstal et al. 1995). In our experiment only rightward directed saccades were tested in a spatial symmetric arrangement of initial eye positions. Therefore, an anti-alignment of retinal and eye position preference would lead to a specific asymmetry in the gain change patterns. In Fig. 7 it can be seen that the gain change patterns from our study, analogous to the patterns from the study on humans, show an asymmetry with respect to the distance between the initial eye position of the adapted saccade and the the initial position of the test saccades the way that more gain change was transfered to the test positions on the left than to the test positions on the right. Hence, our study rather points towards the FEF than to the colliculus as an area with anti-alignment of initial eye position and retinal target position to be the origin of the eye position dependent component of adaptation.

References

Alahyane, N. and Pelisson, D. (2004). Eye position specificity of saccadic adaptation. *Invest. Ophthalmol. Vis. Sci.*, 45(1):123–130.

Albano, J. E. (1996). Adaptive changes in saccade amplitude: oculocentric or orbitocentric mapping? *Vision Research*, 36(14):2087–2098. PMID: 8776475.

Brainard, D. H. (2004). The psychophysics toolbox. *Spat. Vis.*, 10(4):433–436.

Campos, M., Cherian, A., and Segraves, M. A. (2006). Effects of eye position upon activity of neurons in macaque superior colliculus. *J Neurophysiol*, 95(1):505–526.

Cassanello, C. R. and Ferrera, V. P. (2007). Computing vector differences using a gain field-like mechanism in monkey frontal eye field. *The Journal of Physiology*, 582(2):647–664.

Frens, M. A. and Opstal, A. J. (1994). Transfer of short-term adaptation in human saccadic eye movements. *Experimental Brain Research*, 100(2):293–306.

Galletti, C., Battaglini, P. P., and Fattori, P. (1995). Eye-position influence on the parieto-occipital area po (v6) of macaque monkey. *Eur. j. Neurosci.*, 7:2486–2501.

Haverman, K., Zimmermann, E., and Lappe, M. (2010). *Eye position affects saccadic adaptation.* In preparation.

Hopp, L. L. and Fuchs, A. F. (2004). The characteristics and neuronal substrate of saccadic eye movement plasticity. *Progress in Neurobiology*, 72:27–53.

McLaughlin, S. (1967). Parametric adjustment in saccadic eye movements. *Perceptual Psychophysics*, 2:359–362.

Opstal, A. J. V., Hepp, K., Suzuki, Y., and Henn, V. (1995). Influence of eye position on activity in monkey superior colliculus. *J Neurophysiol*, 74(4):1593–1610.

Semmlow, J. L., Gauthier, G. M., and Vercher, J. (1989). Mechanisms of short-term saccadic adaptation. *Journal of Experimental Psychology: Human Perception and Performance*, 15(2):249–258.