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Oculomotor signals and their role in the perception of visual space

Okulomotorische Signale und deren Rolle in
der visuellen Raumwahrnehmung

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Chapter 1

1 General Introduction

1.1 Visual processing

Light enters the eye through the cornea and then passes the lens. Cornea and lens form a compound lens and project an inverted image onto the retina. The retina consists of two photoreceptor types, which transform light into electric impulses. The two photoreceptors are called rods and cones. Rods are primarily located in the periphery of the retina. Cones are located in the fovea centralis, a small pit in the center of the retina. The fovea covers about 2 degrees of visual angle and is the part of the retina where visual acuity is maximal. This is because the foveal pit allows cone receptors to be more densely packed. Another reason is that in the fovea every photoreceptor is connected to a single ganglion cell, which transmits visual information to the brain. In the periphery many photoreceptors converge onto one ganglion cell. Visual acuity decreases as a function of distance from the fovea. The axons of the ganglion cells pass through the retina at the optic disc and thereby create a scotoma in the visual field, which has been termed the blind spot. One needs to distinguish the retinal image from the visual field. The visual field is the view which is seen by both eyes when the head is not moved. The human field of view of each eye extends 90 deg in temporal and 60 deg in nasal direction and 60 deg above and 75 deg below the horizontal meridian. Light in the left visual hemifield is projected onto the nasal hemifield of the left eye and the temporal hemiretina of the right eye. Light in the right visual hemifield is projected onto the nasal hemiretina of the right eye and the temporal hemiretina of the left eye. The electric impulses from the retina are transmitted to the brain via the optic nerve, which contains over one million fibers. Fibers coming from the nasal part of the retina cross to the contralateral side in the opticum chiasm. Since fibers from temporal hemiretina do not cross the left optic tract relays information from the right visual hemifield and the right optic tract from the left visual hemifield. The sensory signals from the eye are relayed to subcortical structures before they reach the visual cortex. Two pathways from the retina to the visual cortex exist:

The retinogeniculo-striatal pathway projects through the thalamus to the cortex. In the thalamus the axons of the optic nerve reach the lateral geniculate nucleus (LGN), which is a small area composed of six layers. Every layer receives information from only one eye and contains a retinotopic map of the contralateral visual field. Fibers from the LGN end in the striate cortex, Brodman Area 17 of the visual cortex. Lesions in this pathway lead to impairments of conscious vision. Even without conscious vision due to lesions in the visual cortex patients are nevertheless able to use visual information. This phenomenon called blindsight highlights the relevance of additional visual pathways.

In the retinotectal pathway information from the retina is sent to the superior colliculus, which in turn projects through the pulvinar, a nucleus in the thalamus, to a broad area of the visual cortex. The colliculus superior is organized in three layers. The superficial layers receive input from retinal ganglion cells and contain a map of the contralateral visual field.

1.2 Eye movements

There are five types of eye movements: Drift and microsaccades are short eye movements (< 1 deg), which occur involuntarily during fixation. Their

function is still a matter of debate. They are believed to correct displacements in eye position produced by drifts to prevent the retinal image from fading or to maximize information intake during fixations (Melloni et al., 2009). During smooth pursuit the eye follows a moving object ($<$ 50 deg / sec). The oculomotor system therefore must keep smooth eye velocity close to the velocity of the moving object in order to avoid retinal image motion. The nystagm is a combination of a smooth pursuit and a saccade. Depending on how they are elicited two kinds of nystagm can be observed: The optokinetic nystagm will be executed when observing a large moving surface, e.g. a train. The vestibular nystagm is the reaction to a rotation of the own body. The role of the nystagm is to keep perception stable. Convergence and divergence are disjunctive movements, where the eyes move in opposite directions. These movements are performed to fixate on near or distant objects.
Saccades are fast (in humans up to: 600 deg/sec) and brief (in humans: 20-50 ms) rotations of the eye. Saccades are pre-programmed and when they are on flight visual feedback cannot guide the saccade to the target. They have therefore been described as ballistic, although sometimes the trajectory can be modified online. Their function is to quickly bring the fovea on interesting regions of the visual field. During normal vision humans perform ∼3 saccades per second.

1.3 Eye movement generation

Eye movements are the most frequent movements humans and monkeys perform. In order to generate eye movements accurately and quickly the oculomotor system faces several problems: It first has to select a saccade target based on the visual information provided by the visual system. In several computational models it is assumed that behavioral saliency determines saccade target selection (Koch and Ullman, 1985; Findlay and Walker, 1999; Clark, 1999; Itti and Koch, 2000). Behavioral saliency is a combination of visual saliency and behavioral relevance of the stimulus. After saccade target selection the next problem consists in the transformation between different coordinate systems. Since the eyes are located in the head and the head can move relative to the rest of the body retinal coordinates must be combined with head-centered coordinates to calculate the relative contributions of eye and head movements. When the saccade target coordinates are calculated a neural controller must send a go-signal to initiate the movement. In order to finally move the eye the spatial code of the saccade target position must be transformed into a rate code, which represents the duration and firing rate of neurons that drive the eye muscles. When the eye movement has been generated a controller should monitor the accuracy of the motor command. If deviations between the actual and the intended movement occur the controlling mechanism should be able to adjust the motor command. Figure 1 shows the pathways which are involved in saccadic eye movement generation. How the central structures of these pathways contribute to the above mentioned problems of eye movement generation will be discussed in the next sections. The order in which the structures are discussed reflects the way from saccade target selection to eye movement execution.

1.3.1 Parietal Cortex

The parietal cortex is crucially involved in visuospatial orientation (Husain and Nachev, 2007). Patients with lesions in this brain structure have problems in orienting to the contralesional parts of the field of view.

The parietal cortex contains neurons which are active before saccade execution. Movement fields in the parietal cortex are very large. The movement

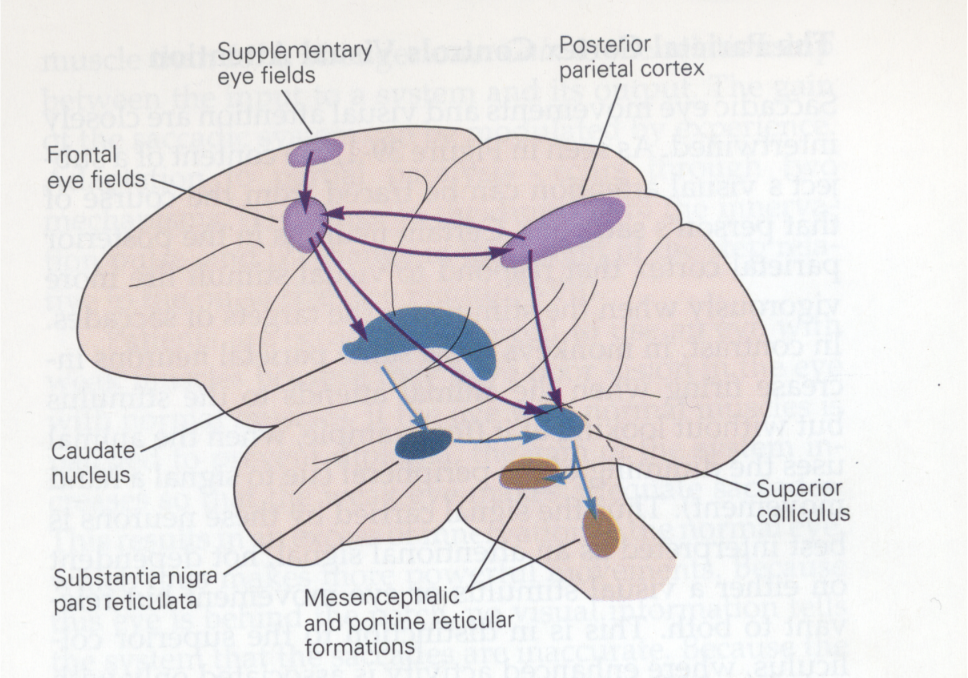

Figure 1: Pathways involved in the generation of saccadic eye movements. Cortical contributions to saccade generation are shown in purple, subcortical parts in blue and the brainstem burst generator in brown. Saccade targets are selected in the cortical areas which in turn relay their information to the superior colliculus. To generate saccadic eye movements the superior colliculus sends commands to the brainstem burst generator which controls the eye muscles. Figure taken from Kandel et al. (2000).

field of a neuron is that area of the visual field in which stimulation drives the neuron to trigger a saccade. The neurons do not contain precise information about size and direction of the saccade. They rather deliver the go-signal to initiate a saccade (Mountcastle et al., 1975). Neurons in the parietal cortex can also be activated just by visual stimulation even when subjects are instructed to ignore them (Robinson et al., 1978). This activation is enhanced when subjects are instructed to attend the stimulus. When a saccade to a remembered target location has to be performed neurons are active in the delay period between target extinction and saccade execution (Gnadt and Andersen, 1988). The combination of neurons that react to visual information and neurons that are linked to saccade preparation suggests that the parietal cortex is a likely candidate for sensorimotor transformation. After lesions in the parietal eye field (PEF), which is located in the intraparietal sulcus (Müri et al., 1996), reactive and memory-guided saccades into the contralesional field of view become inaccurate (Pierrot-Deseilligny et al., 1991a). The PEF projects to the superior colliculus in the parieto-tectal pathway (Lynch et al., 1985). This pathway probably triggers the generation of unpredictable reactive saccades (Gaymard et al., 1998).

1.3.2 Frontal eye field and superior colliculus

Neurons that represent saccade goals have been found in the frontal eye field (FEF) and in the superior colliculus (SC). Both structures are able to initiate saccadic eye movements. When one of these structures was ablated in monkeys no serious limitation in eye motility had been observed (Schiller et al., 1980). However, when both structures were lesioned eye movements were heavily impaired. Lesion studies in human provide information about the functional differences between the FEF and the SC:

In humans the FEF lies in the caudal part of the middle frontal gyrus. The FEF contains neurons that can be activated by visual stimuli (Mohler et al., 1973). These neurons have very large receptive fields. The neuronal response to visual stimuli is enhanced when a saccade will be performed to the target (Goldberg and Bushnell, 1981). However, the FEF also contains neurons that only respond to visual targets and movements neurons that do not respond to visual stimuli at all (Bruce and Goldberg, 1985). Another type of neurons has been found which is activated before voluntarily triggered saccades which are executed in the absence of any visual saccade target (Schlag and Schlag-Rey, 1985). Movement neurons in the FEF have movement fields. These movement fields represent targets irrespective of eye position in the orbita. They are thus not retinotopically but place-coded. The FEF does not represent movement vectors, but saccade goals (Russo and Bruce, 1994). Electrical microstimulation in the FEF can produce saccade eye movements (Bruce and Goldberg, 1985). Two pathways from the FEF trigger saccade generation. One pathway projects through the SC to the premotor circuitry. Projections from the FEF to the SC start in FEF layer V and terminate in intermediate SC layers (Fries, 1984; Komatsu and Suzuki, 1985; Huerta et al., 1986; Stanton et al., 1988; Leichnetz et al., 1981; Shook et al., 1991). The second pathway goes from the FEF immediately to the brainstem (Huerta et al., 1986; Stanton et al., 1988; Leichnetz et al., 1984b,a; Schnyder et al., 1985; Shook et al., 1990). However, it was not possible to elicit saccades with microstimulation of the FEF, following reversible deactivation of the SC (Hanes and Wurtz, 2001). This result suggests that the pathway from the FEF through the SC to the brainstem is the dominant pathway for saccade generation.

The SC is a laminated structure in the dorsal mesencephalon. The superficial layers receive information from the visual cortex (Robinson and Brettler, 1998). The intermediate and deep layers of the superior colliculus are involved in oculomotor control (Wurtz and Albano, 1980; Schlag-Rey and Schlag, 1989). Visuomotor neurons in the intermediate layers are active before execution of a saccade. These layers have a retinotopic map of the contralateral visual field, which is specific for saccade amplitude size and direction (Schiller and Koerner, 1971). The deeper layers fire before saccades of specific directions and amplitudes. These signals are sent to oculomotor regions of pons and midbrain. The SC is involved in saccade target selection (McPeek and Keller, 2004), most likely in connection with the pre-frontal and the parietal cortex (Schall and Thompson, 1999; Burman and Segraves, 1994;

Kim and Shadlen, 1999; Olson et al., 2000; Hasegawa et al., 2000; Platt and Glimcher, 1997; Shadlen and Newsome, 2001; Goldberg et al., 2002; Schiller and Chou, 2000; Schiller and Tehovnik, 2003).

1.3.3 Brainstem

The processing of neuronal signals that command the extraocular muscles is done in the brainstem (Moschovakis et al., 1996; Scudder et al., 2002). Motor neurons which directly control the eye muscles can be found in the formatio reticularis, the pons and the medulla oblongata. The horizontal component of an eye movement is processed in the paramedian pontine reticular formation (PPRF) and the rostral medulla. Neurons in the central mesencephalic reticular formation (cMRF) control the vertical component. Tonic neurons are active during the time of saccadic eye movements. Their discharge frequency is correlated with the position of the eye in the orbita and the velocity of the eye. Long lead burst neurons are active before saccades. They have a peak of activity immediately before saccade onset and their activity stops at saccade start. Short lead burst neurons are active before and after saccades. Burst neurons are selective for the direction of a saccade. Pause neurons stop their activity only during saccades. It is still unclear how the brainstem burst generator (BBG) accomplisehs the transformation from a spatial code of the saccade target coordinates into a rate code which can drive the eye muscles. It has been hypothesized that the SC sends a fixed command specifying the size, direction and partly velocity of the saccade to the burst generator. Saccade size in turn is encoded in the number of spikes in the burst of excitatory and inhibitory burst neurons (Gisbergen et al., 1987).

1.3.4 Cerebellum

The brainstem saccade generator is fine-tuned by the cerebellum (Robinson and Fuchs, 2001). Since saccades are initiated by a pre-planned motor command that cannot be modified online a structure is needed which monitors movement accuracy. If the eye motility changes which might, for instance be due to muscle weakening the motor command does not bring gaze to the target correctly. The function of the cerebellum is to compensate motor commands when they lead to consistently inaccurate movements. Saccade accuracy and smoothness are maintained by the cerebellum. Lesions of the cerebellum makes saccades slow, inaccurate, rough and variable (Vilis and Hore, 1981; Robinson et al., 1993). The role of the forebrain is to control the "where" and "when" of saccade generation. Whereas the where signal needs goal coordinates to drive the eye rotation, the "when" signal just consists in a go-signal, when to start the movement.

1.3.5 Eye muscles

Three pairs of antagonistic extraocular muscles rotate the eye in the orbit. Eye movements can be classified on the basis of the three axes of rotation: horizontal, vertical and torsional. The rectus medialis and the rectus lateralis muscle move the eye in horizontal direction. Eye movements in vertical direction are controlled by the rectus superior and the rectus inferior muscle. Torsional movements are controlled by the obliquus superior and obliquus inferior muscle.

1.4 Saccade types

1.4.1 Reactive saccades

Saccade types differ depending on how they are elicited. Reactive saccades are triggered by a suddenly appearing salient visual stimulus in an unpredictable location. These saccades are the most common saccade types used in laboratory studies. Reactive saccade latencies, i.e. the duration between onset of the saccade target and eye movement initiation, range between 180 - 250 ms.

1.4.2 Voluntary saccades

Saccades which are performed in normal situations are usually self-paced to a prespecified goal. These saccades are called voluntary saccades. Various experimental setups have been created which are supposed to measure voluntary saccades. One of them is the overlap paradigm, in which a fixation point and a saccade target are presented simultaneously (their presentation time overlaps). Since the saccade target is visible from trial start on saccades executed in the overlap paradigm are driven by an internal go-signal rather than visually driven by target appearance. Saccade latencies in the overlap paradigm usually range between 250 - 350 ms.

Another variant of voluntary saccades are scanning saccades which we perform when reading or watching scenes. Studies which investigated scanning saccades presented several saccade targets simultaneously. Subjects then scan these targets by fixating on them sequentially. Scanning saccade latencies range between 300 - 500 ms.

Antisaccades are an artificial saccade type invented to experimentally dissociate visual and motor components of saccade production. In an antisaccade task a saccade target is presented in one visual hemifield and the subject has to perform a saccade in the opposite hemifield. The oculomotor system therefore has to inhibit the disposition to execute a saccade to the target and must then voluntarily perform a saccade in the opposite direction. Latencies in the antisaccade task are highly variable.

Memory-guided saccades are executed to a remembered target location. In experimental setups a saccade target is presented and extinguished after several milliseconds. The subject is instructed to wait some specified amount of time after target extinction and to then perform the saccade to the position where the target was. Latencies in this paradigm depend on how long the subjects is instructed to wait until saccade execution.

Lesion studies revealed that reflexive and voluntary saccades are controlled in separate locations. Deficits in the parietal eye field (PEF) impair reflexively generated saccades into the contralesional hemifield, leaving voluntary saccades intact. Conversely, impairments of the frontal eye field (FEF) have influences only on intentionally initiated saccades (Pierrot-Deseilligny et al., 1991b; Rivaud et al., 1994; Heide and Kompf, 1998; Gaymard et al., 1999).

1.4.3 Corrective saccades

Saccades do not always reach their target accurately. In many cases saccades either land before their target, which is called saccade undershoot, or the saccade lands behind the target, which is called saccade overshoot. In both cases a second saccade will be executed to correct this error. These saccades are called corrective saccades.

1.5 Saccade adaptation

A systematic displacement of the target during the saccade, which goes unnoticed by the subject for reasons of saccadic suppression, leads to a gradual adaptive change of saccade amplitudes. This process has been termed saccadic adaptation and can be induced experimentally using the double step paradigm (McLaughlin, 1967; Deubel et al., 1986). Depending on the direction in which the target is displaced saccade amplitudes can be decreased or increased. Saccade adaptation is specific for the direction of the saccade, i.e. when a rightward saccade is adapted a leftward saccade remains unadapted. Saccade adaptation is also limited to the target amplitude. Saccades that differ in amplitude are gradually less affected by saccade adaptation. This spatial boundedness has been termed adaptation field (Frens and Van Opstal, 1994). The time course of saccade adaptation may depend on various factors as the setup and the size of the target displacement. In humans inward saccade adaptation is usually reached within not more than $\sim$ 100 trials (Deubel et al., 1986). For reasons which are still unknown adaptation in monkeys needs $\sim$ 1000 trials (Straube et al., 1997b). Outward adaptation is slower and needs 200-400 trials in humans (Miller et al., 1981; Straube et al., 1997b; Noto et al., 1999; Bahcall and Kowler, 2000; Robinson et al., 2003). If the saccade target is no longer displaced, saccades de-adapt to their initial amplitude size. In monkeys de-adaptation needs the same number of trials as the adaptation (Straube et al., 1997a). In humans de-adaptation seems to be different from adaptation (McLaughlin, 1967; Deubel et al., 1986).

The above mentioned evidence (describe in section 1.4.2) suggests that reactive and voluntary saccades are processed within different pathways in the oculomotor system. Therefore, the question arises whether adaptation of these saccade types also takes place independently within different pathways. If the adaptation of different saccade types is separate one would expect that it is possible to adapt one saccade type while leaving the other saccade type unadapted. Thus, if transfer of adaptation between saccade types is low, saccade adaptation may occur at multiple sites in the oculomotor system. Deubel (1995a) tested adaptation transfer between reactive, scanning, memory-guided and overlap saccades. The results suggested separate adaptation mechanisms at different neuronal loci. Adaptation of reactive saccades did not transfer to any other saccade type. The same holds true for adaptation of memory-guided saccades. No adaptation transfer to other saccade types was observed. However, when scanning saccades were adapted there was partial transfer to reactive saccades and strong transfer to memory-guided saccades. This asymmetric transfer profile has been confirmed by other studies (Collins, 2007; Cotti et al., 2007).

1.6 Goal of the thesis

Visual perception is an active process. From two retinal images which are distorted and upside-down the brain must provide a visual representation of the relevant information in the external world. The visual representation in turn must be precise and detailed enough to guide behavior in the external world. Sensorimotor coordination requires that visual perception is permanently adjusted to behavioral dispositions. A connection between visual and motor targeting would not only save computational resources it also would guarantee that vision and action are aligned. If action and perception share a common representation visual plasticity should covariate with motor plasticity. The general hypothesis which I investigate in my thesis is that perception and action receive their spatial metrics from the same representation. In my thesis I will present psychophysical experiments which tested the predicted link between the action and perception representation. The main approach was to observe whether modifications in motor coordinates were followed by homogeneous changes in visual localization. Utilizing oculomotor plasticity we modified saccade motor coordinates by inducing adaptive changes in saccade amplitudes.

In the first series of experiments I wanted to find out whether the adaptation of different saccade types induces changes in visual localization. Since adaptation of reactive and scanning saccades is independent different brain structures have to be involved in the generation of reactive saccade adaptation and scanning saccade adaptation. If the modifications of saccade targeting induced by adaptation also modify localization targeting differential mislocalization effects should be observable after the adaptation of reactive and of scanning saccades.

The second series of experiments should reveal whether adaptation-induced changes in visual localization also occurs when tested during continuous fixation. Using a novel adaptation method I investigated the influence of the post-saccadic mismatch between the intended and the actual landing position of the saccade.

Different coordinate systems might be responsible for the selectivity of reactive and scanning saccade adaptation. In the third series of experiments I tested the dependency of reactive and scanning saccade adaptation on eye position since different coordinate system make different predictions of eye position effects on saccade adaptation. With the same method I also tested eye position effects on adaptation-induced changes in visual localization.

2 General Methods

2.1 Eye movement recording

For eye movement recording we used the EyeLink 1000 (SR Research, Ltd., Canada), which is a video based eye tracking device. The system is remote desktop mounted and was placed just below the computer monitor.

Figure 2: Desktop mounted EyeLink 1000 system used for gaze recording. The EyeLink 1000 camera and the infrared illuminator was placed just below the computer monitor where the experimental stimuli were presented.

Eyelink 1000 has a monocular gaze sampling frequency of 1000 Hz. The average spatial accuracy ranges between 0.25 deg and 0.5 deg. The system tolerates head movements +- 25 mm horizontally or vertically. In the experiments viewing was binocular but only the dominant eye was recorded. Every experimental session began with the calibration of the eye tracker. Subjects had to fixate nine targets successively. The accuracy was checked afterwards in a validation procedure, in which the same targets were displayed and the subject had to fixate them again. Gaze position data were recorded every millisecond and stored in a separate data file. From the gaze position data the system identifies saccades, fixations and blinks. These are then marked in the data file. The system detected start and end of a saccade when eye velocity exceeds or falls below 22 deg/sec and acceleration was above or below 4000 deg/sec^2.

2.2 Computer monitor

Visual stimuli were presented on a cathode-ray tube (CRT) monitor. The 22" computer monitor (Eizo FlexScan F930) has a visible screen diagonal was 20", resulting in a visual field of 40 deg x 30 deg. Stimuli were presented on the monitor with a vertical frequency of 120 Hz at a resolution of 800 x 600 pixels. To avoid visibility of the screen borders the display monitor was covered with a transparent foil that reduced the luminance by about 2 log units.

2.3 Presentation of experimental stimuli

An inhouse software (iStimulator by Kim Boström), which was written in objective-C and run on Mac OS X provided the experimental control and design of the visual stimuli. For visual presentation graphic primitives from the Open Graphics Library (Open GL) were used, which is a open-source and cross-language application programming interface (API).

2.4 Data Analysis

Analysis of experimental data (gaze position, responses of the subject, etc.) was carried out in Mathematica Versions 6.0 and 7.0 (Wolfram Research, Inc.).

2.5 Subjects

A total of 25 subjects participated in the experiments. All subjects had normal or corrected-to-normal vision. Their mean age was 25 years. The subjects were psychology students of the University Münster or members of the working group in the Psychology Department. All subjects gave informed consent and the experiments were conducted along the principles laid down in the declaration of Helsinki.

3 Mislocalization of flashed and stationary bars

3.1 Abstract

When we look around and register the location of visual objects our oculomotor system continuously prepares targets for saccadic eye movements. The preparation of saccade targets may be directly involved in the perception of object location because modification of saccade amplitude by saccade adaptation leads to a distortion of the visual localization of briefly flashed spatial probes. Here we investigated effects of adaptation on the localization of continuously visible objects. We compared adaptation-induced mislocalization of probes that were present for 20 ms during the saccade preparation period and of probes that were present for over 1s before saccade initiation. We studied the mislocalization of these probes for two different saccade types, reactive saccades to a suddenly appearing target, and scanning saccades in the self-paced viewing of a stationary scene. Adaptation of reactive saccades induced mislocalization of flashed probes. Adaptation of scanning saccades induced in addition also mislocalization of stationary objects. The mislocalization occurred in the absence of visual landmarks and must therefore originate from the change in saccade motor parameters. After adaptation of one type of saccade the saccade amplitude change and the mislocalization transferred only weakly to the other saccade type. Mislocalization of flashed and stationary probes thus followed the selectivity of saccade adaptation. Since the generation and adaptation of reactive and scanning saccades are known to involve partially different brain mechanisms our results suggest that visual localization of objects in space is linked to saccade targeting at multiple sites in the brain.

3.2 Introduction

Saccadic adaptation occurs when the saccade target is systematically displaced during execution of the saccade (McLaughlin, 1967). This displacement induces a visual error after the saccade which is corrected by a short subsequent saccade. Over the course of successive trials the amplitude of the primary saccade is gradually changed to immediately reach the displaced target location.

Saccadic adaptation influences the localization of visual stimuli. Awater et al. (2005) asked subjects to report the location of a peri- saccadic flash after execution of an adapted saccade. Flashes that occurred before the saccade were systematically shifted in the direction of adaptation. This mislocalization can be observed several hundred milliseconds before the saccade and is distinct from other peri-saccadic mislocalizations such as peri-saccadic compression (Georg and Lappe, 2009). It occurs for verbal as well as for pointing responses (Bruno and Morrone, 2007). The mislocalization is confined to the area near the saccade target (Awater et al., 2005) and matches the spread of adaptation around the saccade target, the so-called saccade adaptation field (Collins et al., 2007). Investigations of the spatial (Collins et al., 2007) and temporal (Georg and Lappe, 2009) properties of the mislocalization have shown that both visual reference information from the post-saccadic target image and control parameters of the saccade contribute to the magnitude and direction of the mislocalization. Furthermore, a mismatch between the efference copy signal and the adapted saccade (Bahcall and Kowler, 1999) or an adaptation of eye position signals (Hernandez et al., 2008) may be involved.

While saccadic adaptation is known to rely strongly on cerebellar and other subcortical structures (Desmurget et al., 1998; Robinson and Fuchs, 2001;

Catz et al., 2008; Golla et al., 2008), the adaptation-induced mislocalization suggests effects of adaptation on the cortical level, or at least feedback from cerebellar or subcortical structures onto cortical localization mechanisms (Awater et al., 2005; Gaymard et al., 2001).

Influences of saccadic adaptation on space perception have so far been studied mostly with flashed visual localization probes. Flashed probes are special because they attract transient attention. Saccades that are induced by flashed or by suddenly appearing targets are called reactive saccades, and are believed to receive target localization signals from parietal pathways to the superior colliculus and the brainstem saccade generator (Pierrot-Deseilligny et al., 1991b; Gaymard et al., 2003; Müri and Nyffeler, 2008).

Such reactive saccades are often used in laboratory settings, but they occur rarely in normal viewing of a natural scene because few objects suddenly appear in a normal visual scene. Instead, during normal scanning of a stationary visual scene target selection is driven by task demands and by the voluntary selection between multiple targets. Such saccades have been called scanning (Deubel, 1995b; Cotti et al., 2007), internally triggered (Erkelens and Hulleman, 1993; Fujita et al., 2002), or voluntary (Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Walker and McSorley, 2006) saccades. Targeting of these saccades is believed to involve pathways from frontal cortex to SC and brainstem (Rivaud et al., 1994; Müri and Nyffeler, 2008).

In the present study we asked whether adaptation of scanning saccade induces mislocalization, and in particular whether it can induce mislocalization of stationary targets that are visible throughout the scanning period and attract continuous attention. We expect that scanning saccades differ from reactive saccades in their ability to induce perceptual effects because of the specificity of their adaptation: whereas selective adaptation of reactive sac-

cades induces little adaptation of voluntary saccades, selective adaptation of scanning saccades transfers substantially to reactive saccades (Erkelens and Hulleman, 1993; Deubel, 1995b; Fujita et al., 2002; Hopp and Fuchs, 2004; Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2007). Therefore, reactive saccade adaptation must occur mostly in the reactive pathway whereas scanning saccade adaptation may involve both the scanning and the reactive pathways. If visual localization and saccade targeting rely on common pathways in the brain we expect that adaptation of scanning saccades induces mislocalization of flashed and of stationary targets.
To investigate this question we varied the temporal properties of the localization stimuli. Flashed probe bars should mimic the suddenly appearing reactive saccade targets. Stationary probe bars, which were visible with trial onset should mimic scanning saccade targets. The hypothesis of Experiment 1 was that after reactive saccade adaptation mislocalization only for flashed bars will be observed. The rationale behind this hypothesis was that reactive saccade adaptation selectively adapts reactive saccades and does not transfer to scanning saccades. Therefore, only mislocalization for flashed and not for stationary probe bars was expected. After scanning saccade adaptation however mislocalization for flashed and stationary probe bars was expected since scanning saccade adaptation does transfer to reactive saccades.

3.3 Methods

3.3.1 Adaptation of reactive saccades

Adaptation of reactive saccades follows the procedure of McLaughlin (1967). In this procedure, a saccade target suddenly appears while the subject is looking at a fixation point. The subject makes a saccade to the target. While the

saccade is in flight the saccade target is displaced by a small amount. This displacement induces a visual error after the saccade which is corrected by a short subsequent saccade. Over the course of successive trials with consistent displacement the amplitude of the primary saccade is gradually changed to immediately reach the displaced target location. The adaptation involves gain changes in cerebellar and other subcortical structures (Desmurget et al., 1998; Robinson and Fuchs, 2001; Catz et al., 2008; Golla et al., 2008). The adaptation- induced mislocalization suggests effects of adaptation on the cortical level, or at least feedback from cerebellar or subcortical structures onto cortical localization mechanisms (Awater et al., 2005; Gaymard et al., 2001).
In the experiment, the subject was seated 57 cm in front of a 22” computer monitor (Eizo FlexScan F930) with the head stabilized by a chin rest. The visible screen diagonal was 20”, resulting in a visual field of 40 deg x 30 deg. Stimuli were presented on the monitor with a vertical frequency of 120 Hz at a resolution of 800 x 600 pixels. The room was completely dark. To avoid visibility of the screen borders the display monitor was covered with a transparent foil that reduced the luminance by about 2 log units. Eye movements were monitored by the Eyelink 1000 system (SR Research, Ltd., Canada), which samples gaze positions with a frequency of 1000 Hz. Viewing was binocular but only the dominant eye was recorded. The system detected start and end of a saccade when eye velocity exceeded or fell below 22 deg/sec and acceleration was above or below 4000 deg/sec^2.
Figure 3A and B depict the procedure for adaptation of reactive saccades. A fixation point (1 deg x 1 deg, luminance 0.06 cd/m^2, red color), illustrated by the square in Figure 3A, was first placed 5 deg to the right of the left screen border. The subject had to establish and maintain fixation at this point. The circle in Figure 3A indicates the gaze of the subject. After 1 s

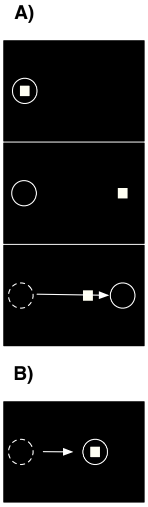

Figure 3: A: experimental procedure for reactive saccade adaptation. At the beginning of the trial (top panel) a fixation point (square) is presented near the left screen border. The subjects gaze (circle) is directed to the fixation point. After 1000 ms (middle panel) the fixation point disappears and a saccade target appears 30 deg to the right of the fixation point. The subject initiates the saccade to the target. When the saccade onset is detected (bottom panel) the saccade target is displaced, inducing a visual error after the saccade. B: after several such adaptation trials the saccade amplitude becomes shorter. The saccade ends on the displaced target and the visual error after the saccade is reduced.

the fixation point was extinguished and a saccade target (red, 1 deg x 1 deg, luminance 0.06 cd/m^2) suddenly appeared 30 deg to the right of the fixation point. The subject was instructed to make a saccade to the target as quickly as possible. Eye position was monitored online. As soon as the eye crossed an invisible border at 2.5 deg to the right of the fixation point the saccade target was stepped back by 6 deg. In the initial trials, this back step caused a visual error at the end of the saccade. With increased number of trials this error is reduced such that the eye lands closer to the back-stepped target location (Figure 3B). After 70 adaptation trials, when the subject already had begun to adapt, the back-step was increased to 9 deg to increase the final amount of adaptation.

In order to ensure that the subject really reacted to the sudden appearance of the target, and did not pre-plan the saccade, some trials were randomly interspersed (probability 0.33) in which the saccade target appeared 10 deg above or below the fixation point. These trials were checked for compliance with the instruction, but were not used for adaptation, and did not enter into the data analysis. They did not interfere with adaptation because adaptation is direction specific (Frens and Van Opstal, 1994; Albano, 1996). Moreover, in order to counteract dark-adaptation of the subject these trials were followed by a 1 s period in which the screen turned white (luminance 0.6 cd/m^2) while the subjects had to maintain fixation at the target location.

3.3.2 Adaptation of scanning saccades

The procedure for scanning saccades followed the paradigm introduced by Deubel (1995b). In this procedure, saccade targets are continuously visible and the subjects looks at each with a self-paced sequence of voluntary saccades. Four saccade targets (1 deg x 1 deg, luminance 0.06 cd/m^2, red color) were presented at trial onset (Figure 4). The saccade targets were arranged in a rectangle with a horizontal distance of 30 deg and a vertical distance of 20 deg. The left edge of the rectangle was 5 deg to the right of the left screen border. Subjects began by fixating their gaze (circle) at the bottom right target. They then had to scan the other saccade targets in a counterclockwise manner at a voluntary pace. In order to ensure that subjects truly scrutinized each target, the saccade targets contained small discrimination dots, either one or two, that could be seen only by foveal inspection of the target. The subject had to count how often a pair of two discrimination dots was present in a trial.

While the subject made saccades from one target to the next the previously inspected targets were extinguished. The top right target was turned off during the saccade from the top right target to the top left target. The top left target was turned off during the saccade to the bottom left target. The bottom left target was turned off during the final saccade from the bottom left to the bottom right target. Each target was extinguished when the eye had travelled a distance of 2.5 deg along the path of the respective saccade.

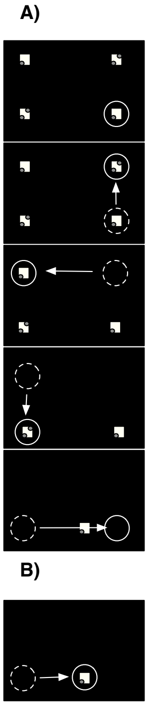

Figure 4: A: experimental procedure for scanning saccade adaptation. At trial onset (top panel) four saccade targets (squares) are presented. The subject fixates the bottom right target (circle). At a voluntary pace, the subject scans the targets in a counterclockwise manner. As the subject executes each saccade the previously inspected target is extinguished. Adaptation takes place during the saccade from the bottom left to the bottom right target (bottom panel). When the onset of the saccade is detected the bottom right target is displaced to the left, inducing a visual error after the saccade. B: after several adaptation trials the saccade amplitude is adapted to the displaced target location.

When the subject performed the final saccade, i.e. the 30 deg rightward saccade from the bottom left target to the bottom right target, only the final target (bottom right) remained on the screen. This saccade was adapted. The bottom right target was shifted 6 deg to the left as soon as the eye crossed the invisible border at 2.5 deg to the right of the bottom left target. After 70 consecutive adaptation trials the displacement was increased to 9 deg. The scanning adaptation procedure therefore differed from the reactive adaptation procedure in the way in which the saccades were initiated, but it was similar in terms of the metric of the adapted saccade, the stimuli visible at the time of adaptation, and the timing and size of the target backstep. Reactive and scanning saccades are known to differ strongly in latency (Deubel, 1995b; Cotti et al., 2007). We therefore used latency differences in the two conditions as a first test of whether we were successful in eliciting different saccade types. Latency in the reactive case was measured from the onset of the target. Since for scanning saccades there is no target onset, latency for scanning saccades was calculated from the onset of the preceding fixation. This measure includes the fixation duration during which the data for the discrimination task must be gathered. It is thus not directly equivalent to the latency in the reactive case, but it is commonly used as a check for differences between saccade types (Deubel, 1995b; Cotti et al., 2007), and will serve for this purpose here as well. Saccade latencies differed between the reactive and the voluntary saccade trials as expected. The mean reactive saccade latency over all reactive saccade adaptation sessions and all subjects was 210 ± 56 ms. The mean scanning saccade latency was 515 ± 113 ms. We also checked latencies in transfer trials (described later in detail) in which reactive saccades were performed after scanning saccade adaptation, and vice versa. The mean latency of reactive saccades performed in these transfer trials was 224 ± 44 ms. The mean latency of scanning saccades performed in the transfer trials was 484 ± 123 ms. A two-way repeated measures ANOVA revealed a significant difference between saccades types in both regular and transfer trials ($F = 75.41$, $p < 0.01$). The difference latency suggests that we were successful in eliciting different saccades types in the different conditions.

3.3.3 Localization

Localization was tested before and after adaptation, while subjects performed normal or adapted saccades, respectively. Two types of localization trials were run. One used a flashed localization probe, like the targets used for reactive saccades. The other used a stationary localization probe like the targets used for scanning saccades. These stimuli were designed to imitate the temporal properties of the saccade targets that trigger reactive and scanning saccades.

In other respects the probe stimuli were visibly distinct from the saccade target to avoid confusion in the localization task. The flashed localization probe was a small bar (0.3 deg x 4 deg, luminance 0.2 cd/m^2). The probe was presented for 20 ms at a randomly chosen horizontal position in a range of 2 deg around the saccade target (i.e., between 28 and 32 deg).

The vertical position of the bar was the same as that of the saccade target. In reactive saccade trials, the bar was flashed 50 ms after the appearance of the saccade target, i.e. about 150 ms (depending on saccade latency) before the reactive saccade. In scanning saccade trials, the bar was flashed when the eye tracker detected that the eye position was on the bottom left saccade target, i.e., before the saccade that was adapted. In both cases, trials in which the bar was flashed less than 100 ms before saccade onset were omitted from analysis because we did not want any interference from peri-saccadic mislocalizations (Georg and Lappe, 2009). Furthermore, occasional trials in which subjects failed to notice the bar were also omitted from analysis. Subjects indicated when they did not see the bar by clicking with the mouse pointer in the lower right corner of the screen. Based on these two criteria, 6% of the data had to be omitted from analysis. If for any subject this resulted in less that ten trials in either the target–off, the target–on, or the transfer trials that subject repeated the recording session and we collapsed the data from both sessions.

The stationary localization probe was identical to the flashed probe but was presented from trial start until the occurrence of the saccade, i.e. when the eye tracker detected that the eye had travelled 2.5 deg along the path of the saccade. Thus, in the reactive saccade trials the bar was continuously visible throughout the 1 s fixation period and during the latency of the saccade. In the scanning saccade trials, the bar was continuously visible throughout the time that the subject took to look at all but the final target.

The task of the subject in the localization trials was to indicate the location of the bar with a mouse pointer. The pointer appeared 1000 ms after the saccade near the bottom of the screen at a randomly assigned horizontal position between 35 deg and 40 deg. The localization error was calculated as the deviation of the mouse click position from the position where the bar was presented.

Normally, because the localization was performed in conjunction with the execution of normal or adapted saccades, the saccade target either remained stationary or jumped back in the respective cases. Thus, it was visible after the saccade and during the reporting with the mouse. Therefore, the saccade target might serve as a visual reference for the localization task. To test for the influence of the post-saccadic target reference we included also trials in which the target was turned off during the saccade. In these target-off trials no visual references were available after the eye landed.

3.3.4 Sequence of events during a single adaptation and localization session

A single session consisted of one type of saccade adaptation (reactive or scanning) with one type of localization task (flashed or stationary). Therefore, each subject had to complete four sessions: reactive saccade adaptation with flashed localization probes, reactive saccade adaptation with stationary localization probes, scanning saccade adaptation with flashed localization probes, and scanning saccade adaptation with stationary localization probes. These four sessions were run on different days and in counterbalanced order across subjects.

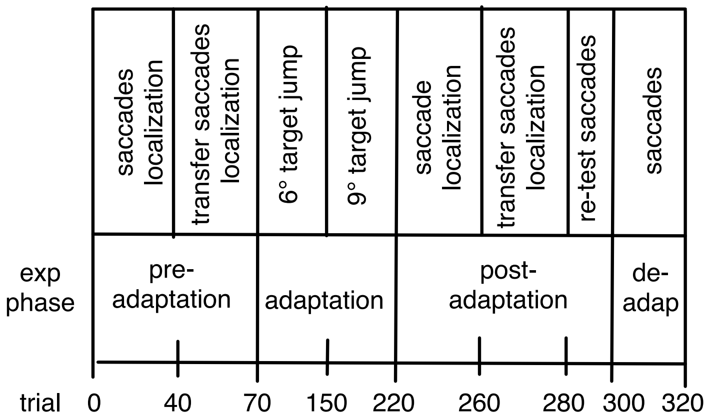

Figure 5: Trial structure for a single saccade adaptation sessions. In the pre-adaptation phase, saccades of the to-be-adapated type and of the transfer type are performed, together with the localization task. In the adaptation phase, only adaptation saccades are performed without localization. About halfway during the adaptation phase the target backstep is increased from 6 deg to 9 deg to increase the final amount of adaptation. In the post adaptation phase, adapted saccades and transfer saccades are performed together with the localization task. A small number of deadaptation saccades end the session.

The basic structure of trial blocks was the same for each session (Figure 5). The session started with a block of 40 pre-adaptation trials of the respective saccade type. These trials allowed to calculate saccade amplitudes as a baseline before adaptation. Moreover, all pre-adaptation trials included the localization task to record a baseline for localization error. Trials in which the saccade target was turned off during execution of the saccade (target-off trials) were randomly interspersed (probability 0.33) with trials in which the saccade target remained illuminated (target-on trials).

Next came a block of 30 pre-adaptation trials of the opposite saccade type (i.e. scanning saccades for reactive saccade adaptation sessions, and reactive saccades for scanning saccade adaptation sessions). These trials served as a baseline for the transfer test between saccade types. The localization task was included in all of these trials. Target-off trials in which the saccade target was turned off during execution of the saccade were randomly interspersed (probability 0.33) with target-on trials in which the saccade target remained illuminated.

The third block consisted of 150 adaptation trials. Saccade adaptation was induced stepwise in order to avoid that subjects notice the saccade target backstep. In the first 80 of the adaptation trials the target stepped back 6 deg to the left of the initial saccade target position. In the remaining 70 trials the back step was increased to 9 deg. These trials did not contain a localization task. They only served to establish adaptation.

The fourth block (post-adapatation, 40 trials) continued with further adaptation trials but also included the localization task. Target-on and target-off conditions were randomly intermixed. The saccade amplitude data from the target-off trials was used to measure the amount of adaptation.

Then, a block of 20 transfer-test trials was performed, in which saccades of the opposite type had to be performed, i.e. scanning saccades after reactive saccade adaptation and reactive saccades after scanning saccade adaptation. These trials served to measure the amount of adaptation transfer from the adapted saccade type to the other saccade type. The localization task was also included to measure the amount of mislocalization transfer. In all trials, the saccade target was turned off during execution of the saccade to avoid deadaptation.

Thereafter, the opposite saccade type was tested again in 20 retest trials. The aim of the retest trials was to check for any deadaptation of saccade amplitude size after the transfer-test trials. Again, to prevent deadaptation the saccade target was turned off during execution of the saccade.

Finally, in 20 deadaptation trials the saccade target remained in its initial position in order to help the subject to deadapt before leaving the experiment.

Participants

Nine subjects, 5 male, 4 female (1 author, 8 naive subjects, mean age = 23 years) participated in all of the experiments. All subjects were students from the Psychology Department and had normal or corrected-to-normal vision. Subjects gave informed consent. All subjects underwent all experimental conditions. The experiments were carried out along the principles laid down in the declaration of Helsinki.

3.4 Results

We performed adaptation experiments with reactive and voluntary saccades. After adaptation we measured the adaptation-induced mislocalization of probe stimuli. We used two different sets of probes, one flashed and one stationary, to study whether the mislocalization is specific to the visual properties of the associated saccade targeting pathway. We will first report measurements of the saccade amplitude adaptation and thereafter the results of the localization task.

3.4.1 Saccade adaptation and transfer

Figure 6A shows saccade amplitudes over a single session of reactive saccade adaptation. Trials in which reactive saccades were performed are shown in red. Pretest and transfer-test trials in which scanning saccades were performed are shown in blue. The first 40 trials were pre-adapation reactive saccade trials in which the subject performed normal reactive saccades to a suddenly appearing target at 30 deg. The target remained at its position and did not jump during the saccade. These saccades were hypometric with a median at 26.43 ± 1.15 deg (black horizontal line), which is normal for

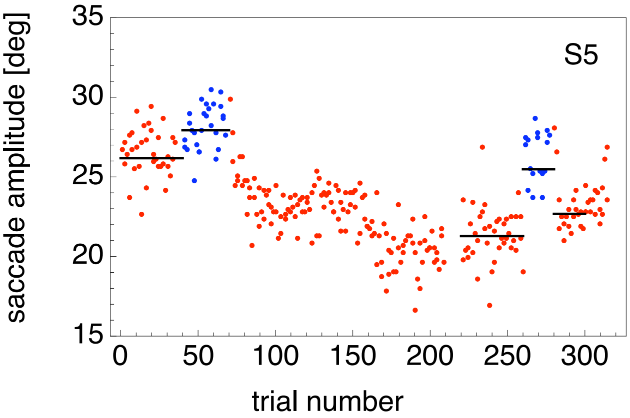

Figure 6: Example adaptation curve for reactive saccades. Reactive saccades are plotted in red, intermixed scanning saccades in blue.

saccades of this size.

The next 30 saccades (from trial 41 to trial 70) were pre-adapation scanning saccades, which were performed as part of a scanning sequence across four targets as described in Methods. The saccade shown is the last of those four saccades. It is directed from a target on the left to a stationary target 30 deg to the right, and matches the reactive saccade in terms of target direction and amplitude. The only difference to the reactive saccade is that this saccade is conducted to a target that was present on the screen during the entire scanning series whereas the reactive target suddenly appeared and triggered saccade execution. Like the reactive pre-adaptation saccades (first 40 trials) the scanning pre-adaptation saccades (trials 41 to 70) were somewhat hypometric in this subject. The median saccade amplitude (black line) was 28.25 ± 1.13 deg.

Trials 71 to 220 were reactive saccade adaptation trials in which the target was displaced to the left during the saccade. The displacement was initially 6 deg and was increased to 9 deg from trial 150 onward. The saccade amplitude decreases gradually over the adaptation period towards a value close to the displaced target location at 21 deg.

The amount of adaptation was measured in the post-adaptation trials (221 to 260). The median saccade amplitude in the post-adaptation trials in this session was 21.39 ± 1.24 deg (black line in trials 221 to 260 in Figure6A).

The post-adaptation trials were followed by transfer-test trials (trials 261 to 280). In these trials, scanning saccades were performed in the identical procedure to that in the pre-adaptation scanning trials (41 to 70). The amplitude of these scanning saccades showed little indication of adaptation. The median saccade amplitude (black line) was 26.31 ± 1.43 deg.

After the transfer-test trials, which often showed less adaptation for the scanning than for the reactive saccades, we checked that reactive saccades were still adapted. This was done in retest trials (numbers 281 to 300) that were identical to the target-off trials of the post-adaptation reactive block (trials 261 to 280). The median saccade amplitude in these retest trials was 22.61 ± 0.85 deg. Thus, a large amount of adaptation for reactive saccades was retained across the block of scanning saccades that had shown little adaptation. Lastly, a few deadapation saccades (301 to 320) were performed to start extinguishing the adaptation. In these trials, the target did not jump during the saccade but stayed at the initial position. These trials were not used for data analysis.

Comparison of the saccade amplitude data from the different phases of the session clearly shows that adaptation occurs during the reactive adaptation trials and is retained through the post- and retest phases, while scanning saccades in the transfer trials showed little modification of saccade amplitude. To quantify the amount of adaptation of the reactive saccades we subtracted the average of the median saccade amplitudes in the post-adaptation (21.39 ± 1.24 deg) and the retest (22.61 ±1.06 deg) trials from the median saccade amplitude in the reactive pre-adaptation trials (26.43 ± 1.15 deg). For the data of Figure 6A this gave an adaptation of 4.4 deg. The amount of adaptation to scanning saccades in the transfer condition was calculated from the difference between the median saccade amplitude in the scanning pre-adaptation trials (28.25 ± 1.13 deg) and the transfer-test trials (26.31 ± 1.43 deg). This gave a transfer adaptation of 2 deg.

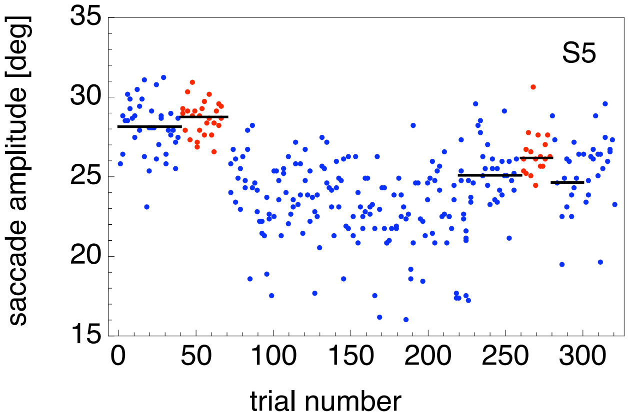

Figure 7: Example adaptation curve for scanning saccades. Scanning saccades are plotted in blue, intermixed reactive saccades in red. The example for reactive adaptation contained flashed localization trials. The example for scanning adaptation contained stationary localization trials.

Saccade amplitudes over a single session of scanning saccade adaptation are shown in Figure 7. Scanning saccade trials are shown in blue. Pretest and transfer-test trials in which reactive saccades were performed are shown in red. The first 40 trials were pre-adaptation scanning saccade trials. As in the scanning pre-adaptation trials of the reactive saccade adaptation session (blue dots in Figure 6) the saccades prior to adaptation are slightly hypometric with a median saccade amplitude of 28.51 ± 1.36 deg. The following 30 trials (41 to 70) were pre-adaptation reactive saccades. They were elicited in the same way as in the reactive saccade adaptation sessions and differed from the scanning saccade trials only in that the saccade target was suddenly appearing. The median saccade amplitude was 28.7 ± 0.83 deg.

Adaptation of scanning saccades began with trial 71. An initial 6 deg jump displaced the saccade target from 30 deg to 24 deg for the next 80 trials (71 to 150). From trial 151 to 220, the size of the saccade target jump was increased to 9 deg displacing the target to 21 deg. After adaptation the median scanning saccade amplitude in the post-adaptation trials (trials 221 to 260) was 24.91 ± 1.91 deg, indicating an adaptation of 3.6 deg.

Reactive saccade amplitudes in the transfer-test trials (red dots, trials 261 to 280) were partially affected by the adaptation of scanning saccades. The median saccade amplitude in the transfer-test trials was 26.21 ± 0.93 deg, indicating an adaptation of 2.49 deg. Scanning saccades performed afterwards in the retest trials (trials 281 to 300) remained largely adapted. The median saccade amplitude was 24.48 ± 2.81 deg, close to the median saccade amplitude of the post-test trials (24.91 ± 1.91 deg). Finally, trials 301 to 320 were deadaptation trials in which the saccade target remained in its initial position at 30 deg.

The median saccade amplitudes in the reactive and the voluntary pre-adaptation trials in this subject differed slightly across sessions. In Figure 6 reactive saccades are more hypometric than scanning saccades, whereas this is not the case in Figure 7. Such differences occurred in some subjects but were not consistent. We calculated the median saccade amplitudes of the reactive and voluntary saccade amplitudes over all pre-adaptation trials for each subject. A paired t-test revealed no significant difference between the reactive and the voluntary saccade pre-adaptation amplitudes.

The example results from Figures 6 and 7 show that adaptation occurred for both saccade types, and that transfer between the saccade types was limited. Figure 8 shows adaptation and transfer amounts for reactive and scanning

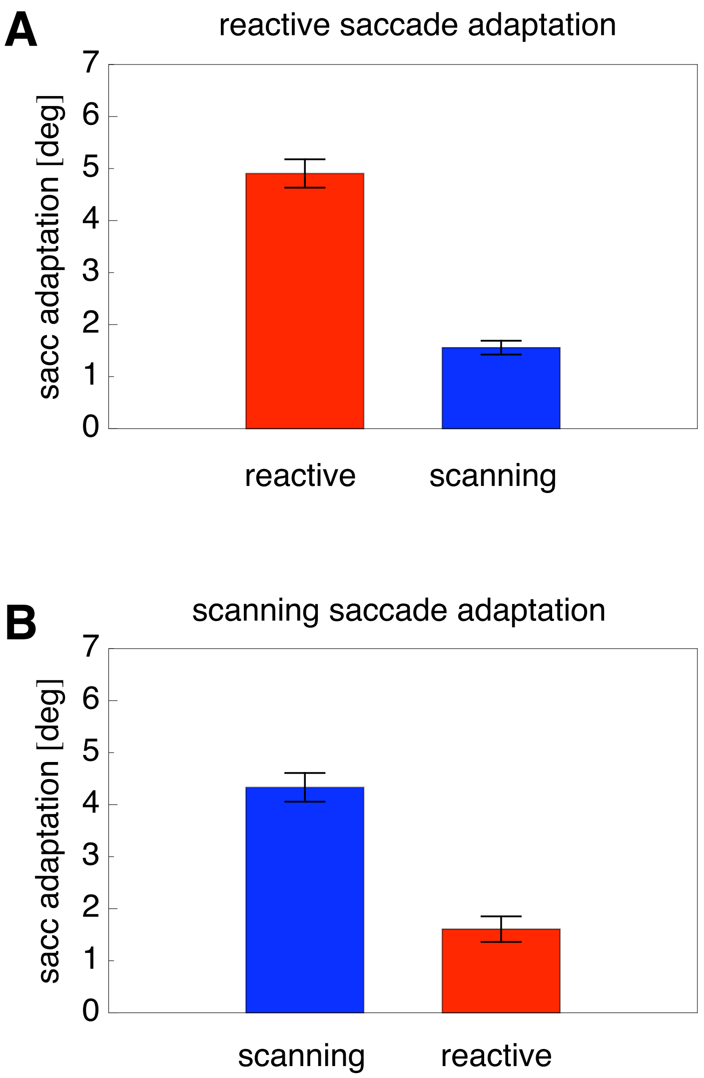

Figure 8: A: average amplitude reduction after reactive saccade adaptation for reactive saccades (red) and for scanning saccades (blue). B: average amplitude reduction after scanning saccade adaptation for reactive saccades (red) and for scanning saccades. In both cases there is strong adaptation and small transfer to the other saccade type. Error bars are standard errors.

sessions averaged across all subjects. After reactive saccade adaptation (Figure 8A), saccadic amplitudes to reactive targets were decreased on average by 4.9 ± 0.27 deg. Amplitudes of scanning saccades in that situation (transfer-test) were decreased by only 1.6 ± 0.13 deg. After scanning saccade adaptation (Figure 8B), saccadic amplitudes to scanning targets were decreased on average by 4.4 ± 0.27 deg, and transfer saccades to reactive targets were decreased on average by 1.6 ± 0.24 deg. A two-way repeated measures ANOVA confirmed a significant reduction in the transfer condition but no difference between saccade types, (F = 100.12,$p < 0.01$).

We also tested whether the amount of transfer of adaptation from one saccade type to the other was different between reactive and scanning saccade adaptation sessions. We therefore calculated the percentage of transfer for each subject (amplitude decrease in transfer trials / amplitude decrease in adaptation trials *100). Average transfer across all subjects was 36% from the adaptation of reactive saccades to the amplitude of scanning saccades and 43% from the adaptation of scanning saccades to the amplitude of reactive saccades. The transfer from scanning to reactive was, therefore, somewhat higher then from reactive to scanning, but the difference failed to reach significance, ($p = 0.06$, paired t-test).

The above analysis of saccade amplitude reduction shows that we adapted reactive and scanning saccades individually, and that adaptation of one saccade type led to only partial adaptation of the other. This is consistent with earlier reports of limited transfer between reactive and voluntary saccades. Reactive saccade adaptation has been found to transfer little (between 6 % and 56 %) to scanning (Deubel, 1995b; Alahyane et al., 2007; Cotti et al., 2007) and other types of voluntary saccades (Erkelens and Hulleman, 1993; Deubel, 1995b; Fujita et al., 2002; Collins and Dore-Mazars, 2006). Our findings are fully consistent with this. Adaptation of scanning saccades, on the other hand, also transfers only partially to reactive saccades, but the reported transfer rates are usually higher (between 24 % and 74 %) (Deubel, 1995b; Alahyane et al., 2007; Cotti et al., 2007). Therefore, the transfer between reactive and scanning saccades has been called asymmetric: small from reactive to scanning and larger from scanning to reactive. The transfer from scanning to reactive saccades in our data is near the lower end of the range reported in the literature. However, it is still larger than the transfer from reactive to scanning saccades, and, thus, consistent with an asymmetric transfer. Most importantly, however, the limited transfer in either direction is indicative of adaption of different saccade targeting pathways, which is a prerequisite for the study of differences in mislocalization that we report next.

3.4.2 Localization results

In order to test influences of saccade adaptation on visual localization, a localization task was included in the trials before and after adaptation of each saccade type. In every adaptation session, localization was tested both in trials in which the adapted saccade type was performed, and in trials in which the opposite saccade type was performed. The subject had to indicate the perceived bar position with the mouse pointer after execution of the saccade. Localization error was calculated as the difference between the horizontal position of the mouse click and the position where the bar was presented on the screen. Negative values indicate that the subject reported the perceived bar position to the left of the veridical bar position. This corresponds to a shift in the direction of adaptation.

The left panel of Figure 9A shows localization errors for flashed bars in a reactive saccade adaptation session of the subject of Figure 6. Each dot is the measurement from a single trial. The dots on the left present pre-adaptation measurements from the pre-adaptation target-off trials. The localization er-

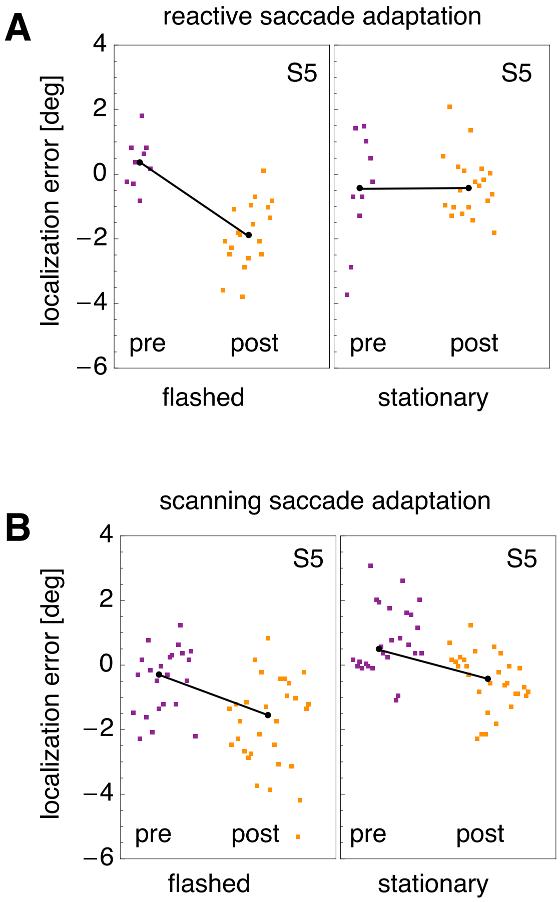

Figure 9: Examples of localization results from the subject of Figures 6 and 7. The localization error plotted on the abscissa is the difference between true and perceived location of a probe stimulus. Each point is data from a single trial. Trials are arranged in the order in which they were conducted. In each sub-figure, pre-adaptation data are plotted on the left, post-adaptation data on the right. The black line connects the medians of both data sets. A: localization results for reactive saccade adaptation with flashed (left) and stationary (right) probes. B: results for scanning saccade adaptation. Note that the data from this subjects was recorded in two adaptation sessions and that the combined data from both sessions is shown.

rors are small with a median at 0.4 ± 0.58 deg, illustrating that localization was nearly correct before adaptation. The dots on the right are localization errors measured after adaptation in the post-adaptation target-off trials. These localization errors are shifted into the direction of adaptation with a median at -1.9 ± 0.8 deg. A paired t-test revealed a significant difference between pre-adaptation and post-adaptation localization, (t-test, $p < 0.01$). The right panel of Figure 9A shows localization errors of the same subject in the reactive saccade adaptation session with stationary bars. These bars were continuously visible from trial start onwards and were turned off only when the eye tracker detected the onset of the saccade. Evidently, the localization of stationary bars was little affected by the adaptation of reactive saccades in this subject. The median localization error before adaptation was -0.5 ± 1.36 deg, and the a median localization error of 0.43 ± 0.72 deg was found after adaptation. Reactive saccade adaptation in this subject, therefore, only influenced the localization of flashed bars (Figure 9A, left panel), which were mislocalized in direction of adaptation, but not of stationary bars (Figure 9A, right panel).

Figure 9B presents localization data from the scanning saccade adaptation sessions. In these sessions the subject had to scan across four continuously visible targets at a voluntary pace, and the last saccade of that scanpath was adapted. The left panel of Figures 9B presents data obtained with flashed targets. In the pre-adaptation trials, localization errors were near 0 deg, with a median at -0.3 ± 0.82 deg. In the post-adaptation trials, localization errors for flashed bars shifted significantly in the direction of adaptation (t-test, $p < 0.01$). Median localization error was at -1.6 ± 1.34 deg. The right panel of Figure 9B shows localization errors for stationary bars. Median localization error before adaptation was 0.5 ± 0.81 deg. In the post-adaptation trials, localization error for stationary bars were significantly (t-test, $p < 0.01$) shifted into the direction of adaptation with a median at -0.4 ± 0.71 deg. Thus, scanning saccade adaptation influenced both the localization of flashed and the localization of stationary bars.

To quantify the adaptation-induced mislocalization in each condition, we took the difference between the median localization errors before and after adaptation in the direction of the adaptation. For the data of Figure 9 the mislocalization values were 2.3 deg. for reactive saccade adaptation and flashed bars, 0 deg for reactive saccade adaptation and stationary bars, 2.5 deg. for scanning saccade adaptation and flashed bars, and 1.6 deg for scanning saccade adaptation and stationary bars.

Figure 10 shows the adaptation-induced mislocalization averaged across all subjects. After adaptation of reactive saccades (Figure 10A), flashed bars were mislocalized with a mean across subjects of 1.8 ± 0.45 deg. in the direction of saccade adaptation. There was no mislocalization for stationary bars (mean across subjects of: 0.08 ± 0.23 deg).

After scanning saccades were adapted (Figure 10B), flashed bars were mislocalized on average by 1.8 ± 0.49 deg. in the direction of adaptation. Stationary bars were mislocalized on average by 1.4 ± 0.36 deg. in the direction of adaptation. A two-way repeated measures ANOVA revealed a significant effect of the probe type (flashed or stationary, F = 11.13, $p < 0.05$), and a significant interaction between probe type and saccade type (F = 7, $p < 0.05$). We conclude that reactive saccade adaptation induces mislocalization for flashed but not for stationary probes, whereas scanning saccade adaptation induces mislocalization for both flashed and stationary probes.

It seems possible that saccade amplitudes are also influenced by the probes, and flashed and stationary probes could have differential influences on amplitudes which then might have differential effects on mislocalization. We have therefore analyzed how the appearance of the bar influenced the saccade amplitudes: For every subject we calculated the difference between the median amplitudes of the last 10 adaptation trials before a locatization phase and the median amplitudes in the localization phase. This quantifies how

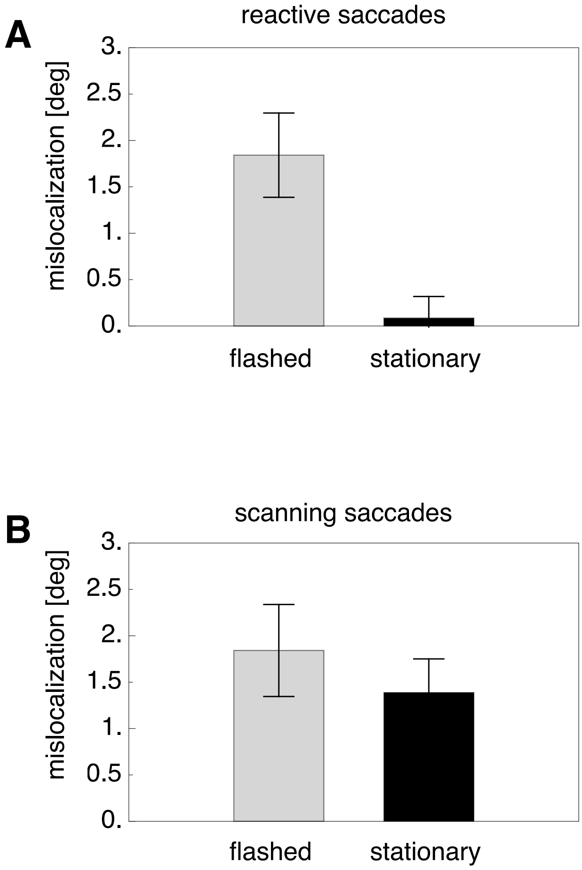

Figure 10: Average mislocalization after saccade adaptation. Plotted on the abscissa is the difference between the localization before and after adaptation. A: mislocalization of flashed (left) and stationary (right) probes after reactive saccade adaptation. B: mislocalization of flashed (left) and stationary (right) probes after scanning saccade adaptation. All data is from trials in which the saccade target was turned off during execution of the saccade (target-off trials). Error bars are standard errors.

much the appearance of the probes changed the amplitude of the saccades. Averaged over all subjects the appearance of the bars increased saccade amplitudes by about 1 ± 0.56 deg. However, this influence of bar appearance on saccade amplitudes was equal across conditions and there were no significant differences between session types. An influence of the probes on the saccade amplitude can therefore not explain the different mislocalization effects.

The adaptation-induced mislocalization for flashed targets after reactive saccade adaptation is consistent with several earlier studies that found similar effects (Awater et al., 2005; Bruno and Morrone, 2007; Georg and Lappe, 2009). Mislocalization of flashed probes after scanning saccades has not been tested previously, but adaptation of saccades in an overlap paradigm, which is usually considered to induce voluntary saccades, also induced mislocalization of flashed targets (Collins et al., 2007). The adaptation-induced mislocalization of stationary targets is a novel finding. Our observation that mislocalization of stationary targets occurs only after adaptation of scanning saccades, and not after adaptation of reactive saccades, suggests that the origin of this mislocalization is confined to the scanning saccade pathway. Because mislocalization of flashed targets occurs for both saccade types, it may originate from mechanism that are shared between both pathways.

The flashed targets that we used as probe stimuli were intended to mimic the temporal properties of the typical targets of reactive saccades. In a reactive saccade trial, the saccade target suddenly appeared, like the flashed probes, but unlike the flashed probes the saccade target thereafter stayed on for the entire saccadic reaction time. To check whether the results obtained with flashed probes are also pertinent to appearing probes, we ran a control condition with reactive saccade adaptation and probes which suddenly appeared and, like the reactive saccade targets, stayed on thereafter. In this condition, the bars appeared 50 ms before saccade target onset. They disappeared when the saccade onset was detected. Hence they stayed visible through the saccadic reaction time, like the saccade target. The average duration of bar presentation over all trials from both subjects was 328 ms. All other procedures were the same as in the flashed bar condition. We performed this control condition with two subjects, one of them the subject of Figure 9. The mislocalization results of the two subjects are shown in Figure 11. Both subjects show a consistent adaptation-induced mislocalization. The difference between the median localization in the pre-adaptation trials and the post-adaptation trials was 4.24 deg for subject S5 and 4.75 deg for subjects S8, and thus at least as large as their localization differences for flashed probes in the regular reactive adaptation sessions (2.25 deg for S5 and 4.35 deg. for S8). We are therefore confident that our flashed target condition captures the essential properties of saccade targets that trigger reactive saccades.

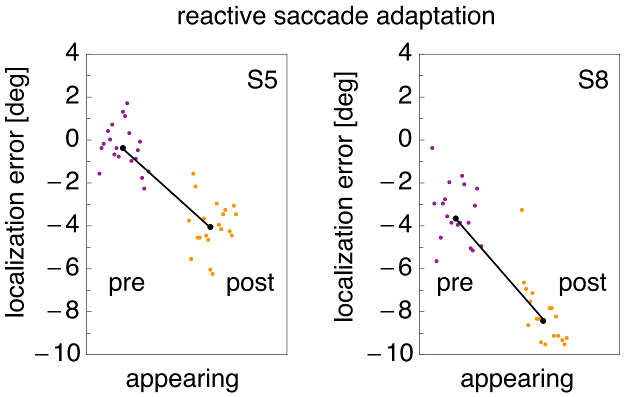

Figure 11: Localization results from reactive saccade adaptation with appearing probes. Two subjects were tested, one of them the subject of Figure 9. The localization error plotted on the ordinate is the difference between true and perceived location of a probe stimulus. Each point is data from a single trial. In each sub-figure, trials are arranged in the order in which they were conducted. Pre-adaptation data are plotted on the left, post-adaptation data on the right. The black line connects the medians of both data sets. Same conventions as in Figure 9

The selectivity of the mislocalization for target types (flashed vs stationary) is reminiscent of the asymmetry often observed in the transfer of adaptation between saccade types. Adaptation transfers little from reactive saccades elicited by flashed targets to scanning saccades directed to stationary targets (Deubel, 1995b; Fujita et al., 2002; Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2007). Similarly, mislocalization after reactive saccade adaptation occurs for flashed targets but not for stationary targets. Adaptation of voluntary saccades to stationary targets has been reported to transfer well to reactive saccades elicited by flashed targets (Deubel, 1995b; Fujita et al., 2002; Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Cotti et al., 2007). Similarly, mislocalization after scanning saccade adaptation occurs for stationary targets and also for flashed targets. Reactive saccade adaptation thus influences saccades to and localization of flashed targets. Scanning saccade adaptation influences saccades to and localization of flashed and stationary targets.

3.4.3 Localization results in the target-on and transfer conditions

For the above analysis, we have used only data from target-off trials in order to avoid any interference of visual reference information from the view of the post-saccadic target. A similar analysis of the target-on trials gave localization results very similar to those of the target-off trials (Figure 12). After reactive saccade adaptation, flashed bars were mislocalized by on average 2.3 ± 0.37 deg, and stationary bars were mislocalized by on average 0.7 ± 0.24 deg. After scanning saccade adaptation, flashed bars were mislocalized by 1.9 ± 0.33 deg, and stationary bars were mislocalized by 1.6 ± 0.32 deg. A two-way repeated measures ANOVA revealed a significant main effect of probe type, (F = 10.24, $p < 0.05$) and a significant interaction between the probe type and saccade type, (F = 16.55, $p < 0.01$).

Overall, mislocalization in the target-on condition was slightly higher than in the target-off condition. The differences were small (about 0.3 deg), and did not reach significance (t-test, $p = 0.06$). We conclude that post-saccadic visual references from the target location contribute only little to the mislocalization effect. This is consistent with earlier observations with reactive saccades and flashed probes in which target-on and target-off trials gave similar mislocalization (Awater et al., 2005). Collins et al. (2007), on the other hand,

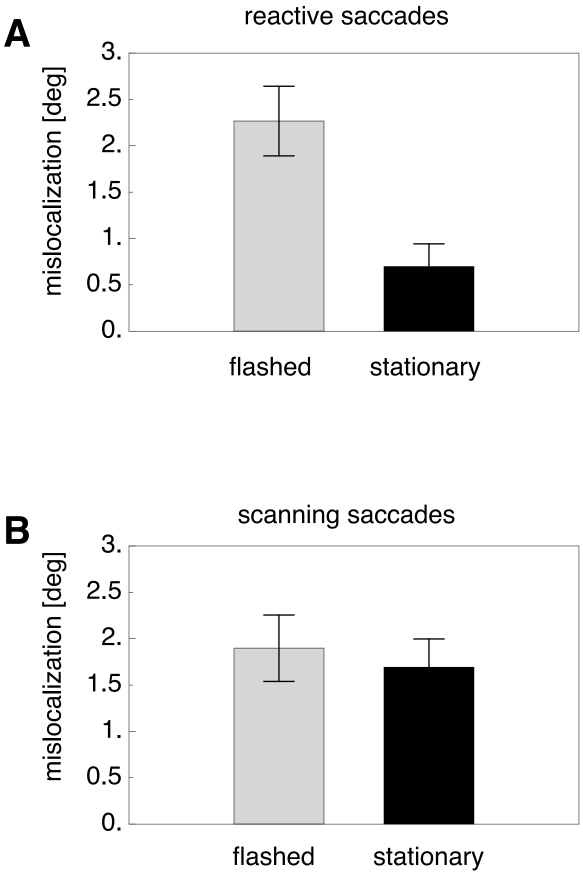

Figure 12: Average mislocalization after saccade adaptation in trials in which the saccade target was visible after saccade offset (target-on trials). Same conventions as in Figure 10.

observed differences in mislocalization of flashed targets between target-on and target-off conditions with overlap saccades. However, these differences were most pronounced for probe locations further away from the saccade target, and were only small in the vicinity of the saccade target where the measurements in our study were taken.

We also measured mislocalization in the transfer trials. In these trials, one type of saccade was adapted, but the other type of saccade was performed. Because adaptation transfer was only partial (Figure 8) the amplitudes of saccades in the transfer trials were typically less adapted than when the same

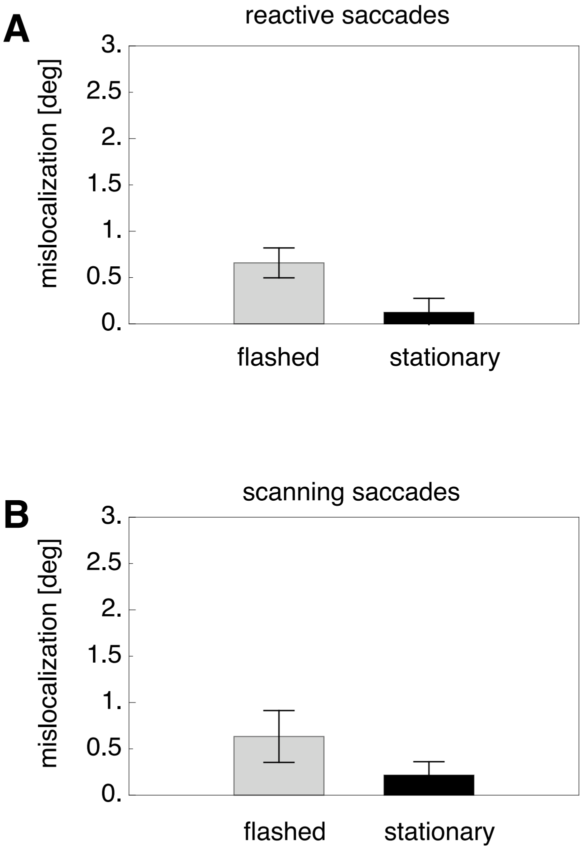

Figure 13: Average mislocalization in the transfer-test trials. A: mislocalization when reactive saccades were performed after adaptation of scanning saccades. B: mislocalization when scanning saccades were performed after adaptation of reactive saccades. In all cases the saccade target was turned off during execution of the saccade. Error bars are standard errors.

saccades were performed after genuine adaptation. Figure 13A shows mislocalization when reactive saccades were performed after scanning saccades had been adapted. Mean mislocalization across subjects was 0.7 ± 0.24 deg for flashed bars and 0.2 ± 0.16 deg for stationary bars. Mean mislocalization across subjects when scanning saccades were performed after reactive saccades had been adapted was 0.6 ± 0.28 deg for flashed bars and 0.2 ± 0.14 deg for stationary bars (Figure 13B). There was no significant difference between the conditions, but the average mislocalization in the transfer trials was significantly different from zero (t-test, $p < 0.01$).

The comparison with Figure 10 reveals that the amount of mislocalization is overall lower in the transfer trials. To compare results from the transfer trials with results from the adaptation trials we ran a three-way ANOVA with the factors experimental condition (target-off / transfer), saccade type that was adapted (reactive / scanning), and probe type (flashed / stationary). A significant main effect in the factor experimental condition (F = 9.263, $p < 0.016$) confirmed that mislocalization in the transfer trials was lower than in the target-off trials. A significant main effect in the factor probe type (F = 8.425, $p < 0.02$) showed that mislocalization for flashed and stationary probes differed. Saccade type had no main effect but a significant interaction occurred between saccade type and probe type (F = 7.758, $p < 0.02$), confirming that mislocalization depends on the properties of the probe and the saccade that is adapted. No other interaction was significant.

The smaller mislocalization in the transfer condition than in the target-off condition is consistent with the amplitudes of the transfer saccades being only weakly adapted. It shows that not only the type of saccade that is adapted influences the mislocalization but also the type of saccade that is prepared.

In summary, we conclude that adaptation both of reactive and of scanning saccades influences the localization of visual stimuli, and that this influence depends on whether the stimulus is flashed or stationary. After adaptation of reactive saccades localization of flashed bars was shifted into the direction of adaptation as observed in earlier studies (Georg and Lappe, 2009; Awater et al., 2005). The localization of stationary bars however was unaffected by reactive saccade adaptation. After adaptation of scanning saccades, in contrast, both flashed and stationary bars were mislocalized into the direction of saccade adaptation. The magnitude of mislocalization depends on the amount of adaptation, since in the transfer trials, in which the amount of adaptation was reduced, mislocalization was also smaller.

3.5 Discussion

To explain the different influences of reactive and scanning saccade adaptation on the localization of flashed and stationary targets, we must discuss the possibilities by which the visual system may estimate the location of the targets. The bars in our study were presented before the execution of the saccade. Thus, the position of the bar had to be encoded before the saccade, then retained in transsaccadic memory, and later retrieved after the saccade ended. For such trans-saccadic localization, the visual system might encode objects with respect to visual landmarks, such as the saccade target, and retrieve them after the saccade from visual information about the post-saccadic location of the saccade target (McConkie and Currie, 1996; Deubel et al., 1996, 2002; Awater and Lappe, 2006). However, in the target-off trials, on which we based our main analysis, the target was not visible after the saccade, and could not have served as a landmark for retrieval. Thus, visual reference information cannot explain the mislocalization.

In the absence of the saccade target, the visual system may instead use the current gaze direction as reference for the retrieval from trans-saccadic memory. In this scenario, the stimulus is again encoded relative to the saccade target position. After the saccade, the position of the bar is retrieved relative to the post-saccadic gaze direction. Because the post-saccadic gaze direction after an adapted saccade is different from that after a normal saccade, the reported location should be shifted in the direction of adaptation. However, in this scenario the amount of mislocalization should be the same as the amount of adaptation. Since in our study (and in several others (Georg and Lappe, 2009; Collins et al., 2007; Awater et al., 2005)), the amount of mislocalization was much smaller than the amount of adaptation this scenario is unlikely.

A further possibility for trans-saccadic localization is the remapping of spatial location based on an efference copy signal. An efference copy of the saccade motor command may be used to predict the post-saccadic location of the object based on its pre-saccadic location and the amplitude of the saccade. Mislocalization may then arise if the efference copy signal does not match the amplitude of the saccade. This might occur if the efference copy reflects the size of the unadapted saccade, e.g. if adaptation takes place in a neural structure that is downstream from the structure that generates the efference copy. If this were the case, then the pre-saccadic location would be remapped to a post-saccadic location as if the saccade were unadapted. Since the saccade is actually shorter, a mislocation in the direction of the saccade would be the consequence (Bahcall and Kowler, 1999; Hernandez et al., 2008). However, the unadapted efference copy explanation would predict the same amount of mislocalization for all saccade and stimulus types. Our results show that this is not the case: first, the amount of mislocalization for flashed and stationary bars is clearly different after reactive saccade adaptation. Second, the mislocalization of stationary bars is different after reactive and after scanning adaptation. One may salvage the efference copy explanation by postulating different efference copy signals for different saccade types. The efference copy of reactive saccades would remap flashed objects, while the efference copy for scanning saccades would remap both flashed and stationary objects. Such a concept of multiple efference copies is not unrealistic since many brain structures take part in saccade generation, and the difference between reactive and voluntary saccade adaptation already indicates partially separate pathways. However, if the efference copy for reactive saccades remaps only flashed, but not stationary targets then, during normal reactive saccades, stationary objects should appear perceptually unstable, which is clearly not the case. The efference copy explanation is also inconsistent with the spatial pattern of mislocalization reported by Collins et al. (2007). Their data indicated that mislocalization for objects further away from the saccade target is not correlated with the performed saccade, i.e., the saccade for which the efference copy signal is generated, but with the adaptation state for the saccade that would be required to reach the object, even when this saccade is not performed.

According to the above considerations neither post-saccadic reference signals nor efference copy or eye position signals can explain the dependence of the mislocalization on the target properties. We must therefore consider differences between the processing of the flashed and the stationary targets in the pre-saccadic encoding or memory stages. One possibility is that the mechanism of adaptation includes a modification of target location at an early stage of the sensorimotor transformation, and that this modified target location is used for the trans-saccadic memory. If this were the case, visual localization and saccade targeting would be equivalent in the sense that the perceived location of an object is derived from the target metrics of the saccade that would be needed to acquire the object (Collins et al., 2007). In this view, visual localization and saccade targeting are equivalent in the sense that the perceived location of an object is derived from the target metrics of the saccade that would be needed to acquire the object. Thus, saccade metrics would be used for saccade targeting and visual localization alike. If saccade adaptation involves a change to the saccade target metrics then the perceived location of the object at the target location must change in a similar fashion. In this view, if the pathways that generate the saccade differ for different target conditions (flashed vs. stationary) then the localization should also differ and depend on the target properties.

This proposal predicts that part of the adaptation of the saccade amplitude stems from the remapping of target location rather than from the adjustment of motor execution. Some evidence for an involvement of target remapping in saccade adaptation is reported in a few recent studies. Ethier et al. (2008a) have analyzed the temporal velocity profile of adapted saccades and compared it to predictions of a model that can adjust saccade amplitude either by adjusting the parameters of the forward model of the saccade generator or by adjusting the target signal (Chen-Harris et al., 2008). The comparison showed evidence for adjustment of both motor and target parameters, although the target parameter adjustment was necessary only for gain increasing saccades. Other evidence that saccade adaptation may, in some conditions, include changes in target localization stages in addition to changes in motor execution comes from recent studies of transfer of adaptation between saccades and anti-saccades (Cotti et al., 2009; Collins et al., 2008; Panouilleres et al., 2008). Adaptation in target localization stages is also supported by the finding that hand pointing movements to a continuously presented target were misdirected after voluntary saccade adaptation but not after reactive saccade adaptation (Cotti et al., 2007). This is consistent with our data since we also found mislocalization for stationary bars only after adaptation of voluntary saccades. However, we also found that reactive saccade adaptation affects the localization of flashed bars. Evidence that reactive saccade adaptation affects localization via hand pointing movements for flashed bars comes from Bruno and Morrone (2007).

However, if mislocalizations were the result of a simple modification of early stage of the sensorimotor transformation then this modification should be revealed whatever the type of saccade being prepared. In the transfer-test trials, however, localization is also a function of the type of saccade that is prepared, not only the type of saccade that is adapted. In addition, one might expect that a modification of early stage of the sensorimotor transformation should also lead to a mislocalization when the saccade is not performed. Such a mislocalization has been reported by Moidell and Bedell (1988) but it seems small and difficult to measure reliably (Awater et al., 2005; Collins et al., 2007). However, if the mislocalization results from modifications in the pre-saccadic encoding or memory stages of trans-saccadic memory, then it must not necessarily appear also during fixation, since in this situation trans-saccadic memory is not involved. To reconcile such a trans-saccadic memory explanation with the results from the transfer-test trials, one would have to assume that trans-saccadic memory draws on sensorimotor representations which are specific to the saccade that is currently prepared, mainly process particular types of stimuli, i.e. flashed or stationary, and may be modified by saccade adaptation. This explanation is quite speculative and should be treated cautiously, but in essence it predicts that trans-saccadic memory is formed not as a visual buffer but as a buffer constructed from the activities in brain areas that are already involved in saccade planning and preparation. The difference between the mislocalization of flashed and stationary targets may also relate to different coordinate frames in which saccades are planned. Niemeier and Karnath (2003) proposed that reactive saccade are coded in eye-centered coordinates whereas voluntary saccades are coded in head-centered coordinates. In a computational model by Gancarz and Grossberg (1999) adaptation of scanning saccades occurs via target remapping in head centric coordinates whereas adaptation of reactive saccades takes places via cerebellar gain learning. Thus, our data might be explained by assuming that stationary targets are coded in head-centered coordinates and thus mislocalized for adapted scanning saccades only whereas flashed targets might be coded in different coordinates and are adapted by a different mechanism. If we assume that head-centric encoding takes some time to complete then flashed targets might not be present long enough to enter the head-centric stage. Likewise, reactive saccades which have a much shorter latency than scanning saccades may be prepared in response to suddenly appearing targets before these can be transformed to a head centric representation.

In conclusion, object localization in space is strongly connected to object targeting for motor events instead of being just a readout of sensory input. Object localization is not the result of a static internal representation in the visual system but is tightly linked to the ability to move. Changes in motor targeting parameters thus result in parallel changes in visual object localization. This finding reflects the aim of object localization, which is mostly to guide further movements.

4 Motor signals in visual localization

4.1 Abstract

Oculomotor plasticity adapts the amplitude of saccades, which systematically fail to reach their target. In standard saccade adaptation tasks a saccade target is displaced during the execution of a saccade. After 20-50 trials the saccade is adapted to the new target position. Saccade adaptation although motor affects the spatial perception of objects. We measured how saccade adaptation modifies the perception of visual space. In each block fixation trials were intermixed in the course of adaptation. While the subject kept fixation a bar was flashed for 20 ms. The subject should localize the position of the bar with a mouse pointer without doing a saccade. We found strong mislocalization after outward and little after inward adaptation. An analysis of saccadic velocity profiles indicated that outward, but not inward, adaptation was consistent with a change of the saccade target representation. We investigated the influence of constant visual error size on the localization of briefly flashed bars. To induce saccade adaptation we used a method originally invented by Robinson et al. (2003). This method predicts the saccade landing position and presents the saccade target relative to this position. The visual error after each saccade thus can be kept at a fixed value. In different blocks we adapted saccades with a 1 deg, 2 deg and a 3 deg saccade target displacement. Analysis of velocity profiles suggested that this method evoked target remapping for both inward and outward adaptation. With this method, we found mislocalization after both inward and outward adaptation depending on visual error size. We conclude that changes in saccade metrics are paralleled by changes in visual localization, thus emphasizing the importance of saccade vectors for the representation of space.

4.2 Introduction

Vision informs us about the location of the objects around us. Most visual areas of the brain show some form of spatial selectivity. This multitude of capabilities, however, makes the basic question of where in the brain the locations of visual objects are determined difficult to answer. From an ecological perspective, localization is plainly needed for behavior control. Eye movements are the most ubiquitous behavior, and if we want to know anything about an object somewhere in the scene we first look at it. Thus, the most pressing need of visual localization of any object is to guide eye movements to that object. Indeed, it has been proposed that our perceptual experience of the world is composed of the sensorimotor transformation laws that govern how we interact with the world (O'Regan and Noe, 2001; Varela et al., 1992). This proposal predicts that our spatial perception of objects draws on the knowledge of the motor system about how to target this object with an eye movement. Here we report that an experimental modification of the motor control of saccadic eye movements leads to an associated change in the perceived location of objects. Amplitudes of saccades to a peripheral target were altered by saccadic adaptation, induced by an artificial step of the saccade target during the eye movement. Perceptual localization of visual stimuli in the peripheral field during continuous fixation was tested before and after adaptation. Increasing saccade amplitudes induced concurrent shifts in perceived location of visual objects. The magnitude of perceptual shift depended on the size and persistence of errors between intended and actual saccade amplitude. This tight agreement between the change of eye movement control and the change of localization shows that perceptual space is shaped by motor knowledge rather than simply constructed from visual input.

We have used saccadic adaptation to modify the motor response to a target object. Normally, when a saccadic eye movement is initiated to an eccentric target the oculomotor system calculates the correct speed and duration of the movement in advance since, because of latencies in the visual system, visual feedback about the accuracy of the eye movement arrives in the brain only after the saccade is finished. Thus, saccades are 'ballistic' and oftentimes not very accurate. If a saccade happens to be inaccurate the error between the final gaze direction and the target can only be registered after the saccade. This post-saccadic visual error is used by the oculomotor system to check saccadic accuracy and, if needed, re-calibrate motor control for subsequent saccades to be more accurate (Kommerell et al., 1976). In the experimental paradigm of saccadic adaptation, a post-saccadic visual error is introduced artificially by stepping the target while the saccade is in flight (Figure 13A) (McLaughlin, 1967). Because vision is suppressed during saccades (Bridgeman et al., 1975; Ross et al., 2001) the step itself is not seen by the subject, but the oculomotor system registers the post-saccadic error and adapts saccade behavior accordingly: over the course of several such trials, the amplitude of the saccade to the target eventually matches the stepped location of the target, rather than the initial location (Figure 13B).

The saccadic adaptation procedure, therefore, introduces a dissociation between the physical location of the target as registered by the retina and the motor program that is executed to shift gaze onto that target. This dissociation allows us to investigate whether the perceptual localization of a stimulus at the target location follows the physical location of the stimulus or the motor program set-up by the saccadic system.

4.3 Methods

To decide this question we combined a series of adaptation trials with an interspersed localization task. The subject sat in a completely dark room in front of a computer monitor which displayed target and localization stimuli. Care was taken to avoid any visual stimulation other than that displayed on the monitor. This was done to prevent the use of landmarks or references for localization (Deubel et al., 2002; Awater and Lappe, 2006). Saccades were elicited by a small target stimulus (0.75 x 0.75 deg, 0.06 cd/m^2, red) that appeared 10 deg to the left of the screen center, stayed there for between 800 and 1100 ms, and then jumped 13 deg to the right. The subject had to fixate the stimulus and initiate a saccade as soon it moved to the right. Eye position was monitored by the Eyelink 1000 system (SR Research, Ltd., Canada), with a sample rate of 1000 Hz. To induce saccadic adaption, the target stimulus was stepped a further 3 deg to the right when the eye tracker detected the onset of the saccade. This procedure was repeated for 1000 trials to achieve stable adaptation and allow the investigation of localization effects over the course of the modification of the saccade parameters.

After every 200 adaptation trials localization was tested in a block of 20 trials (Figure 14C). Subjects were instructed to direct gaze to the center of the screen and avoid any eye movement during the entire block of localization trials. Eye position was monitored to check for compliance and to record the current gaze direction of the subject. When ready, the subject pressed the space button on the keyboard to start a trial. A small localization probe (0.2 x 3 deg 0.02 cd/m^2, white) was presented for 30 ms 13 deg to the right of the subject's current gaze position. One second later a mouse pointer appeared near the right border of the screen at a random position. The subject indicated the apparent location of the probe with the mouse pointer.

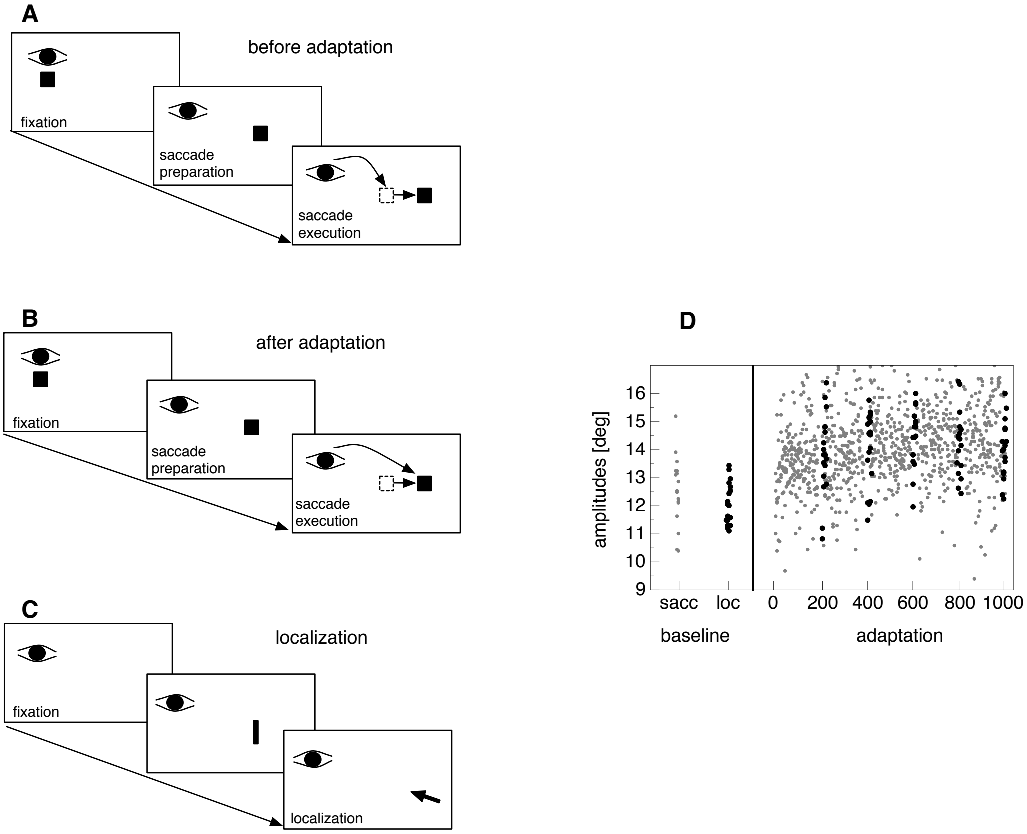

Figure 14: Saccadic adaptation and visual localization. A, at the beginning of an adaptation session the eye of the subject fixates a target on a black screen. When the target jumps 13 deg to the left the subject prepares a saccade. Then, while the saccade is underway, the target is stepped further 3 deg to the right. At the time of arrival the saccade has not reached the target, and a post-saccadic error is registered that corresponds to the distance of the target from the fovea after the saccade. B, after several adaptation trials the saccade amplitude increases, such that the eye now lands closer to the final target location. C, intermixed within the course of adaptation trials were localization trials. In these, the subject had to keep a constant eye position in darkness while a localization probe was briefly presented 13 deg in the visual periphery. The subject had to indicate the perceived location of the probe with a mouse pointer. D, development of saccadic adaptation and localization changes over the course of a single adaptation session. In baseline trials without adaptation steps of the target, saccade amplitudes (grey points) and probe localizations (black points) lie around 12.5 deg and 12 deg, respectively. During the course of adaptation saccade amplitudes increased to 13.8 deg. Location judgments changed along with the adaption resulting in an average mislocalization of 2 deg for this subject.

A similar block of 20 localization trials at the beginning of the experiment served as a baseline of localization performance before saccadic adaptation. Likewise, an initial block of 20 saccade trials without the adaptation step of the target served as a baseline for saccade performance.

4.3.1 Saccade Trials

At trial onset a fixation point (0.75 x 0.75 deg) appeared at a horizontal position 10 deg to the left of the central position. The vertical position varied from trial to trial and was a randomly assigned value between 10 deg above and 10 deg below the screen center. This method is preventing fatigue effects due to a monotonous setup. The subject was instructed to direct gaze on the fixation point. The fixation point was presented for 800 ms plus a randomly chosen period between 0 and 300 ms. Simultaneously with offset of the fixation point a saccade target (0.75 x 0.75 deg) appeared 13 deg to the right of the fixation point. The subject is supposed to perform a saccade to the target as soon as possible. The trial ended 830 ms after saccade target onset and the next trial started automatically.

4.3.2 Saccade Adaptation

Saccade adaptation was induced with two different methods. In the normal saccade adaptation method the saccade target was displaced when the eye-tracker detected the gaze position to be more than 2.5 deg rightward of the fixation point. With this method we induced inward and outward adaptation with a 3 deg target displacement.

In the constant visual error adaptation a method was used which first used by Robinson et al. (2003). In this method the saccade landing position is predicted online. The saccade target is displaced with a constant degree

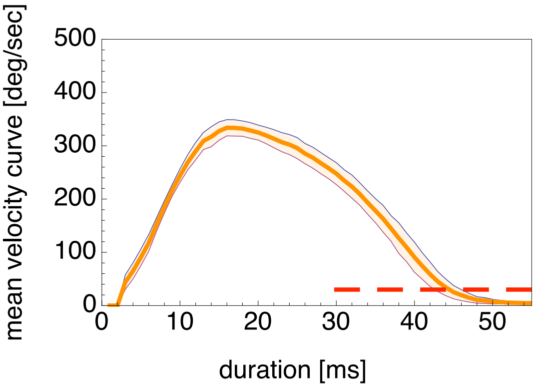

Figure 15: Example mean velocity curve of saccades from an adaptation session. The dashed line (red) indicates the velocity threshold. When eye velocity fell below 30 deg/sec^2 gaze position was sampled and used for the prediction of saccade landing position.

relative to the predicted landing position of the saccade. To predict the saccade landing position a velocity criterion was used (Figure 15). Gaze position was sampled with 1000 Hz.

On the basis of the gaze position data saccade velocity was calculated online. When the velocity came under a predetermined threshold of 30 deg/sec, gaze position was taken as the prediction of the saccade landing point. This method displaces the saccade target at the end of the saccade, which however is not critical since adaptation can be induced with a target movement maximally 80 ms after saccade end (Fujita et al., 2002). The mean error of the landing point prediction was 0.1 deg. With this method six different constant visual errors were applied in separate sessions, (-1, -2 and -3 deg) for inward adaptation and (1, 2 and 3 deg) for outward adaptation.

4.3.3 Localization Trials

Localization was tested in a block of trials before adaptation and in 5 blocks of trials interleaved in the course of adaptation. Each block contained 20 localization trials. During the fixation trials no fixation point or any other visual cue were present. Subjects were instructed to direct gaze at the center of the screen and avoid any eye movement during the entire block of localization trials. When ready, the subject had to press the space button on the keyboard to start a trial. The eyetracker sampled gaze position online. 30 ms after the subject pressed the space button a small bar (0.2 x 3 deg) appeared 13 deg to the right of the subjects current gaze position. The bar was flashed for 30 ms. 1000 ms after bar offset a mouse pointer appeared on the right border of the screen. The mouse pointer appeared at the bottom border of the screen and a randomly chosen horizontal position between 35 deg and 40 deg. The subject was instructed to indicate the perceived position of the bar by pressing the mouse button. After the mouse button was pressed the mouse pointer disappeared and the subject could start the next trial with the space button. The localization error was calculated as the deviation of the mouse click position from the position where the bar was presented. Subjects were instructed to click in the right corner of the screen in case they did not perceive the bar. Localization trials were discarded from analysis when subjects clicked in the right corner or a saccade was detected. In total, 12 % of all localization trials were discarded.

4.3.4 Mimic adaptation

To analyze, whether saccade adaptation induced changes in peak velocities, sessions were run, which allowed to compare peak velocities of adapted saccades with peak velocities of unadapted saccades with the same amplitude size. Since saccade velocities depend on saccade amplitudes we chose saccade amplitudes from the adaptation sessions and used them to determine saccade target position in the mimic trials. For each adaptation session a mimic saccade session was run which included the same number of trials and was intended to elicit the same saccade amplitudes. In each trial of the mimic saccade session, the saccade target was placed at the saccade endpoint of the corresponding trial of the adaptation session, and stayed there throughout the saccade. We then compared saccade characteristics from the adaptation trials with the mimic trials. In the analysis we compared saccade amplitudes of trial n from the adaptation session with saccade amplitude of trial n from the mimic adaptation session. We analyzed all trials in which saccade amplitudes in the adaptation condition did not differ more than 0.5 deg from the mimic condition. The comparison was accomplished for standard adaptation data and constant error adaptation data.

4.3.5 Trial Sequence

The trial sequence was the same in all experiments. An experiment started with 20 localization trials. These were followed by 20 pre-adaptation trials. During the pre-adaptation trials the saccade target remained in its initial position. Every 40 trials a white screen was presented for 4 sec. The white screen served as a rest and prevented dark adaptation. After trial 39 saccade adaptation trials started. Here, the saccade target was displaced with one of the methods described above. In the course of adaptation, blocks of localization trials (each 20 trials) were interleaved every 200 adaptation trials (trials: 240-260, 460-480, 680-700, 900-920, 1120-1140).

4.3.6 Experimental Setup

All experiments were conducted in complete darkness to avoid the influence of any visual landmarks. The subject was seated 57 cm in front of a 22" computer monitor (Eizo FlexScan F930) with the head stabilized by a chin rest. The visible screen diagonal was 20", resulting in a visual field of 40 deg x 30 deg. Stimuli were presented on the monitor with a vertical frequency of 120 Hz at a resolution of 800 x 600 pixels. The room was completely dark. To avoid visibility of the screen borders the display monitor was covered with a transparent foil that reduced the luminance by about 2 log units. Eye movements were monitored by the Eyelink 1000 system (SR Research, Ltd., Canada), which samples gaze positions with a frequency of 1000 Hz. Viewing was binocular but only the dominant eye was recorded. 5 subjects (4 female, 1 male, mean age: 25) participated in the inward adaptation experiments. 5 different subjects (4 female, 1 male, mean age: 28) participated in the outward adaptation experiments. The order of conditions was counterbalanced across subjects. For every subject a break of at least 48 h was interposed between successive sessions.

4.4 Results

The adaptation of saccadic amplitude had a clear effect on visual localization (Figure 13D). While saccade amplitude (grey dots) changed from 12.5 deg ± 2.14 deg in the pre-adaption baseline trials to 13.8 deg ± 1.01 at the end of the adaptation period perceived location (black dots) changed from 12.0 deg ± 0.59 to 14.0 deg ± 0.84.

To compare saccade amplitude changes and localization changes over the course of adaptation we calculated the deviation of each from the pre-adapation baseline trials. The localization change was calculated as the difference between median localization in the baseline trials and median localization in each of the 5 localization blocks during adaptation. The amplitude change was calculated as the difference between median saccade amplitudes in the baseline trials and median saccade amplitudes around the time when localization was tested, i.e., the last ten trials before a localization phase and the following ten trials after that localization phase.

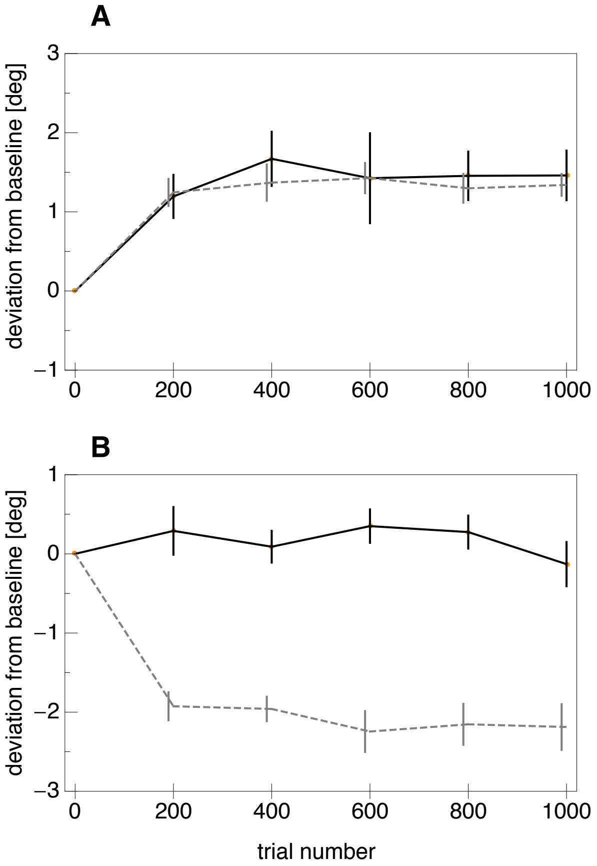

Figure 16: Mean mislocalization (dashed line) and mean adaptation (solid line) averaged over all subjects. The upper panel shows results from outward adaptation sessions and the lower panel shows results from inward adaptation sessions. Error bars are standard errors.

Figure 16a shows the amount of adaptation (dashed line) and the amount of mislocalization (solid line) averaged over 5 subjects. Adaptation reached a maximal amplitude increase of 1.4 deg ± 0.23 deg, or 46 % of the 3 deg outward target displacement. Localization developed very similarly to the adaptation and also changed over the course of trials (ANOVA, $F = 7.425$, $p = 0.016$). After 1000 trials of adaptation localization probes were mislocalized by 1.5 deg ± 0.31 in the direction of adaptation.

These results clearly show that modifications of saccadic amplitude by saccadic adaptation can induce associated changes in visual localization. This is consistent with our hypothesis that oculomotor knowledge is used for perceptual space, and cannot be explained by mismatches between eye movement and efference copy signals (Bahcall and Kowler, 1999) because the localization task was performed during steady fixation. However, a different pattern of results appeared when the saccadic adaptation was induced in the opposite direction, i.e. by an intra-saccadic step of the target to the left, which induces a shortening of saccade amplitude (Fig. 16b). This experiment was done with the same methods as before with the only exception that the target stepped 3 deg to the left during the initial saccade. The inward step of the target induced a strong adaptation of saccade amplitude (-2.2 deg ± 0.26 deg), or 73 % of the target displacement) but no localization change.

This difference between inward and outward saccadic adaptation may be related to partially different mechanisms for the two directions of adaptation (Golla et al., 2008; Ethier et al., 2008a; Panouilleres et al., 2008). Inward adaptation is faster and and stronger than outward adaptation (Noto et al., 1999; Bahcall and Kowler, 1999; Robinson et al., 2003) and can be achieved by decreasing saccade velocity and taking advantage of the systems tendency to fatigue (Golla et al., 2008). Decreasing saccade velocity is an energetically efficient way to achieve smaller saccade amplitudes (Ethier et al., 2008a). Outward adaptation, on the other hand, inevitably requires more effort to sustain, and energy considerations suggest that it would best be achieved by changing the saccade target signal (i.e. remap the target location) rather than manipulate saccade dynamics (Ethier et al., 2008a). This difference may explain why inward adaptation is less tied to localization: it relies on a lower-level mechanism of adaptation.

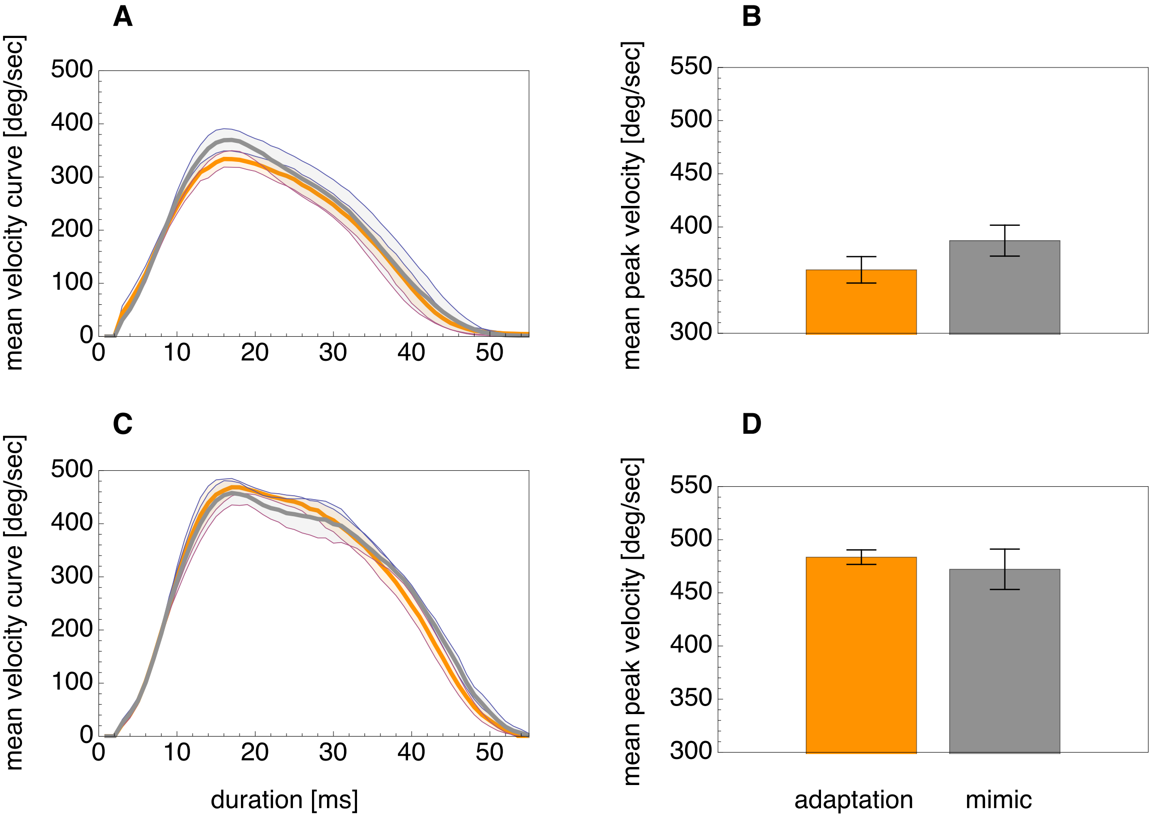

Figure 17: A: average velocity curves from inward adaptation (orange) and mimic (gray) sessions. Peak velocities were decreased after inward adaptation compared to the mimic sessions. B: average peak velocities from inward adaptation (orange) and mimic (gray) sessions. Error bars are standard errors. C: average velocity curves from outward adaptation (orange) and the mimic (gray) sessions. D: average peak velocities from outward adaptation (orange) and the mimic (gray) sessions. Error bars are standard errors.

In order to estimate whether adaptation was based on a remapping of the target signal or on a change in the dynamic control of the saccade we compared velocity profiles from the adapted saccades and from separate sessions of 1000 saccade trials without adaptation, but in which the saccade amplitude was the same as in the adaptation session (Ethier et al., 2008a). This mimic adaptation sessions were designed to evoke the same amplitude sizes in the same trial order as in the adaptation sessions and thus allow a direct comparison of the mean peak velocities. Figure 17 shows average velocity curves and average peak velocities for inward and outward adaptation. Mean peak velocity in inward adaptation sessions was 357 deg/s ± 10 deg/s, significantly lower that that of the mimic sessions 390.8 deg/s ± 16.61 deg/s, one-tailed paired t-test, $p = 0.014$). Mean peak velocity in outward adaptation sessions was 475 deg/s ± 5.83 deg/s, and not significantly different from that of the mimic sessions 477 deg/s ± 26.04 deg/s, one-tailed paired t-test, $p = 0.237$). This analysis confirmed different mechanisms for inward and outward adaptation, and further suggested that only the mechanism of target remapping during outward adaptation provides a link to visual localization. We next wondered whether it would be possible to induce target remapping also for inward adaptation. Since the modification of the saccade dynamics that underlies inward adaptation is a faster process than the modification of the target command (Chen-Harris et al., 2008), inward adaptation asymptotes rather quickly to a stable state in which the post-saccadic error is small. We reasoned that, if the post-saccadic error would remain high for a longer number of trials, then target remapping may become relevant also during inward adaptation.

We tested this prediction in a paradigm that creates a constant post-saccadic error (Robinson et al., 2003). In this paradigm, the saccade landing position is predicted from in-flight measurements of gaze position and the target is stepped to a location that is a constant, pre-determined distance from the predicted landing position of the saccade. Thus, the saccade can never reach the target, and, independent of how accurate or how adapted the saccade to the initial target is, there is always a post-saccadic error that continuously steers saccadic adaptation towards lower amplitudes. We used this procedure with three different error sizes (-1, -2 and -3 deg) for inward adaptation, and, for comparison, also with three sizes (1, 2 and 3 deg) for outward adaptation. Each constant visual error condition was tested in a separate session.

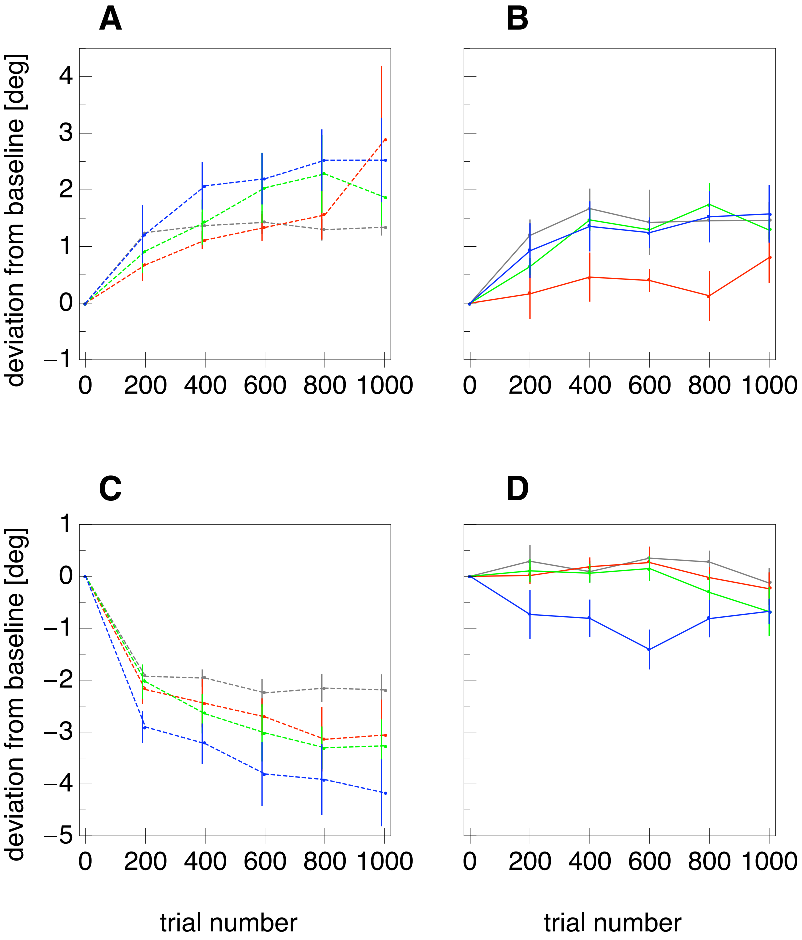

Figure 18: Mean curves from adaptation with the constant visual error method. Results are shown for adaptation with 1 deg visual error (red), 2 deg visual error (green) and 3 deg visual error (blue). Mean curves from adaptation with the normal adaptation method are shown in gray. The upper panel shows curves from outward adaptation sessions and the lower panel shows results from inward adaptation sessions.

The amount of adaptation that we obtained with this procedure increased with post-saccadic error size for both adaptation directions (Figure 18A,B).

After 1000 trials every constant post-saccadic error condition produced a stronger adaptation than the normal method (grey curves Figure 18A,B). Moreover, for large constant errors adaptation continues to increase over the entire duration of the experiment, showing that the adaptation mechanism asymptotes very slowly.

The constant post-saccadic error method succeeded in inducing localization changes for inward adaptation when the post-saccadic error was large (Figure 18C.D). For adaptation with a 3 deg constant error the maximal mislocalization of -1.41 deg ± 0.37 deg was reached after 600 trials (ANOVA, $F = 2.079$, $p = 0.019$). Mislocalization after inward adaptation with 1 deg and 2 deg was not different from zero but increasing amounts of mislocalization were observable after 1000 trials (-0.24 deg ± 0.3 deg) for 1 deg constant visual error and -0.68 deg ± 0.46 for 2 deg constant visual error). For outward adaptation, localization changes for 2 deg and 3 deg constant post-saccadic error were significant (ANOVA, $F = 13.203$, $p = 0.001$ at 2 deg; $F = 5.501$, $p = 0.023$ at 3 deg) and identical to those of the normal method. The constant post-saccadic error of 1 deg induced virtually no localization change. Peak velocities of adapted and mimic saccades were not significantly different in any of the conditions (one-tailed paired t-tests, $p > 0.05$). This suggests that the constant post-saccadic error condition induced a contribution of target remapping not only for outward but also for inward adaptation.

Figure 18 further shows that the occurrence of induced shifts of visual localization is related to the size and persistence of the post-saccadic visual error. For outward adaptation, constant post-saccadic errors of 2 or 3 deg induced changes of visual localization, whereas a constant post-saccadic error of 1 deg did not. For inward adaptation, a constant post-saccadic error of 3 deg induced localization changes, but smaller post-saccadic errors did not.

This dependence on post-saccadic error might explain why in the normal adaptation condition changes in localization were only observed in outward and not in inward adaptation. In inward adaptation, which is faster than outward adaptation, the reduction of saccade amplitude that is accomplished via modifications to the saccade dynamics within a few tens of trials is already strong enough to lower the post-saccadic error to below 1 deg. This remaining error is too small to drive further adaptation (i.e. the adaptation levels asymptotically) or any target remapping. For outward adaptation, which is slower and less efficient, the post-saccadic error remains high for a large number of trials – even after 1000 trials it is still 1.6 deg – and is large enough to require target remapping and induce localization changes.

4.5 Discussion

Why would the amount of localization change depend on the size of the post-saccadic error? When a saccade fails to reach its target, the oculomotor system is faced with the problem to decide whether the post-saccadic error is due to an inaccurate motor command or to inaccuracies in the sensory representation of the target (Kording et al., 2007). Depending on the outcome of this error assignment different stages of the oculomotor transformation are modified (Chen-Harris et al., 2008). Only the target representation stage would be expected to be associated with visual localization. Adaptation at other levels should take place without influences on localization. Our results show that only a large and enduring post-saccadic error leads to the development of localization changes. Consistent with this, earlier studies that used only inward adaptation or small target steps reported only small (Moidell and Bedell, 1988) or insignificant localization changes during fixation (Awater et al., 2005; Collins et al., 2007). A transfer of saccadic adaptation to pointing movements for outward but not for inward adaptation (Hernandez et al., 2008) is also consistent with the present findings.

We conclude that consistent visual indications of large oculomotor errors induce not only adaptations of the motor commands but also affect visual perception of location. Thus, visual localization is not simply based on retinal signals but takes into account the sensorimotor contingencies of reaching for a location with an eye movement. Such a coupling of localization and saccade targeting may occur if perceptual localization is based on activities in oculomotor maps. Alternatively, the brain may keep visual and oculomotor maps in register by updating visual representations when eye movements consistently fail to reach the target. Using the same spatial map for sensory and motor processes has the advantage that perception and action are instantaneously aligned onto each other. A perceptual map that is not updated of modifications of motor metrics would lead to discrepancies between perceptual and motor targeting which would be calamitous in everyday action.

5 Eye position effects on saccade adaptation and adaptation-induced mislocalization

5.1 Introduction

To bring visual objects on the part of the retina where acuity is highest we perform fast and ballistic eye movements called saccades. Saccades can be classified according to the way they are triggered: Reactive saccades are executed as a reaction to changes in the external environment triggered by suddenly appearing events. However, in most normal situations we intentionally decide to move our eyes to gather information of interesting parts in scenes. These saccades have been termed scanning saccades. The accuracy of saccades is constantly monitored by the oculomotor system. Systematic inaccuracies in saccadic targeting are adaptively compensated. A systematic intrasaccadic displacement of a saccade target leads to an adaptive adjustment of the saccade amplitude (McLaughlin, 1967). Depending on the direction of the target displacement saccade amplitudes can be lengthened or shortened. Adaptation of reactive and scanning saccades is assumed to occur at different sites in the oculomotor system since the results described in section 3 as well as from several other studies showed that reactive and scanning saccades can be selectively adapted (Erkelens and Hulleman, 1993; Fujita et al., 2002; Collins and Dore-Mazars, 2006; Alahyane et al., 2007; Deubel, 1995b; Cotti et al., 2007). The adaptation of reactive saccades does not transfer to scanning saccades. After adaptation of scanning saccades, however, some amount of reactive saccade adaptation can be observed. A close link between saccade targeting and localizational targeting was suggested by the different mislocalization effects after reactive and scanning saccade adaptation: The adaptation of scanning saccades induced mislocalization for flashed as well as for stationary objects. Reactive saccade adaptation, however, selectively affected flashed objects. A reason for these different mislocalization and adaptation effects might be that they are coded in different coordinate systems. It has indeed been proposed that reactive and scanning saccades are coded in different coordinate systems (Niemeier and Karnath, 2003). Since reactive and scanning saccades are adapted in different parts of the oculomotor system, also the adaptation of these saccades might be coded in different coordinate systems. However, the coordinate systems of reactive and scanning adaptation are not unambiguously determined. A purely retino-centered coding of saccade adaptation would predict that the amount of adaptation only depends on the displacement vector of the eye, irrespective of eye position. Thus, if the amplitude size of the saccade is kept constant adaptation magnitude should not vary when tested at different positions on the screen with different position of the eye in the orbita. In a purely head-centered coding of saccade adaptation, however, the amount of adaptation should decline as a function of distance from the training location. Earlier studies have tried to answer this question for reactive saccades (Semmlow et al., 1989; Frens and Van Opstal, 1994; Deubel and Bridgeman, 1995; Albano, 1996; Noto et al., 1999). They investigated how far the amount of saccade adaptation depends on the position of the eye in the orbita. In humans a strong dependency on eye position was found for reactive saccade adaptation in outward but not in inward direction. Other studies found that adaptation magnitude of reactive saccade was unaffected by changes in eye position (Frens and Van Opstal, 1994; Deubel and Bridgeman, 1995; Albano, 1996). These results suggest that reactive saccade adaptation is coded in a retino-centered coordinate system. However, inconsistent with this interpretation it is possible to simultaneously adapt reactive saccades at a specific eye position in inward direction and at another eye position in outward direction (Shelhamer and Clendaniel, 2002; Alahyane et al., 2004). If reactive saccade adaptation would be truly retino-centered simultaneous inward and outward adaptation should cancel each other out. We tested eye position effects on reactive and scanning saccades. Both saccade types were adapted in inward and in outward direction.

5.2 Methods

To test the influence of eye position on saccade adaptation saccades with a fixed required amplitude size were measured at different positions on the screen. Before adaptation the combination of fixation point and saccade target was presented in every corner of the screen. In saccade adaptation trials the targets were presented in only one of the four screen corners. This was the training location where adaptive motor learning was induced by an intrasaccadic target displacement. After several adaptation trials targets were again shown in every corner of the screen. This method allowed to determine the amount of adaptation transfer to saccade targets at different screen positions. In separate sessions reactive and scanning saccades were performed in either leftward or rightward direction. In each session saccades were adapted in either inward or outward direction. Additionally, we also ran sessions in which a localization task was included before and after adaptation. With these sessions we wanted to find out whether adaptation-induced mislocalization can be modulated by changes in eye position.

5.2.1 Reactive saccades in rightward direction

Saccades with an amplitude size of 15 deg were tested. A trial started with the presentation of a fixation point on which the subject should establish and maintain fixation. Fixation points were shown either in the bottom left corner of the screen (12.5 deg to the left of and 14 deg below the screen center), in the bottom right corner of the screen (horizontal position at screen center and 14 deg below the screen center), in the top left screen corner (12.5 deg to the left of and 14 deg above the screen center) or in the top right screen corner (horizontal position at screen center and 14 deg above the screen center). Figure 19 shows the positions of the fixation point and the saccade target in each of the four corners. After 1000 ms the fixation point was lit off and a saccade target appeared simultaneously. In sessions in which rightward saccades were tested the saccade target always appeared 15 deg to the right of the fixation point. After 1200 ms the saccade target was extinguished and the next fixation point appeared in one of the four screen corners. In 80 pre-adaptation trials saccades were tested 20 times in each of the four screen corners in a pseudorandom order. The next 270 trials were adaptation trials. In these trials the fixation point always appeared in the bottom left corner of the screen. In 2/3 of all adaptation trials the saccade target was presented 15 deg to the right of the fixation point. In 1/3 of the adaptation trials the saccade target was presented 15 deg above the fixation point in order to avoid that subjects could anticipate the next saccade target location. These trials were pseudorandomly intermixed in the adaptation-trials and were not used for analysis. Saccade adaptation was induced following the paradigm of McLaughlin (1967). Gaze position was measured online. When gaze was detected 2.5 deg to the right of the fixation point the saccade target was displaced 5 deg. In inward adaptation sessions the saccade target was displaced to the left of its initial position. In outward adaptation sessions the saccade target was displaced to the right of its initial position.

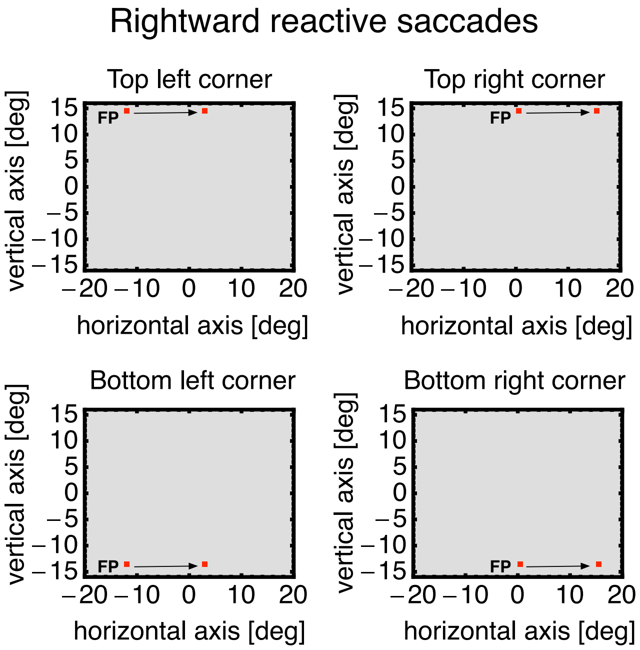

Figure 19: Target positions for reactive saccades. Each panel shows the position of the fixation point and the saccade target in one of the four corners of the screen. The fixation point was shown for 1000 ms. Simultaneously with the extinction of the fixation point the saccade target appeared and the subject was required to perform a saccade. Then the next fixation point appeared. In pre and post adaptation trials the positions at which the fixation points appeared were pseudorandomly selected. In adaptation trials of rightward saccades the fixation point always appeared in the bottom left corner and the saccade target could appear either rightwards or upwards. In adaptation trials of leftward saccades the fixation point always appeared in the top right corner and the saccade target could either appear leftwards or downwards.

In the last 180 trials saccades were again tested in all four corners of the screen. These trials consisted of 20 blocks with 9 trials each. In one block three test-saccades were performed, one in the bottom right corner, one in the top left corner and one in the top right corner. To ensure that these test-saccades did not evoke de-adaptation 6 trials of each block were adaptation-trials in the bottom left corner of the screen. Trials within one block were pseudorandomly ordered. To determine the amount of saccade adaptation we built the median over the saccade amplitudes from the pre and post trials for each corner. Then we subtracted the median post-adaptation amplitude from the median pre-adaptation amplitude for each corner.

5.2.2 Reactive saccades in leftward direction

The positions of the targets in leftward reactive saccade sessions were the same as the positions in rightward reactive saccade sessions. However, target positions in which a saccade target was presented in rightward sessions were used for the fixation point in leftward sessions. Likewise, the saccade target in leftward sessions was presented at the same position where the fixation point was presented in rightward sessions. Except this difference the sequence of pre-trials followed the same scheme as in rightward sessions. In adaptation trials the fixation point appeared in the top right corner of the screen. In 2/3 of all trials a saccade target was presented 15 deg to the right of the fixation point. In 1/3 of all trials the saccade target was presented 15 deg below the fixation point. These trials were pseudorandomly intermixed in the adaptation trials and not used for analysis. In inward adaptation sessions the saccade target was displaced to the right of its initial position. In outward adaptation sessions the saccade target was displaced to the left of its initial position. The last 180 trials were arranged in 20 blocks of 9 trials each as in the rightward trials.

For instance, scanning saccades in the top left corner started with the presentation of a fixation point 2.5 deg rightwards of and 14 deg above the center of the screen.

5.2.3 Scanning saccades in rightward direction

Scanning saccades were performed to four permanently visible targets. Scanning saccades were tested in the four corners of the screen (Figure 21).

The subject had to scan the four targets in clockwise order starting at the

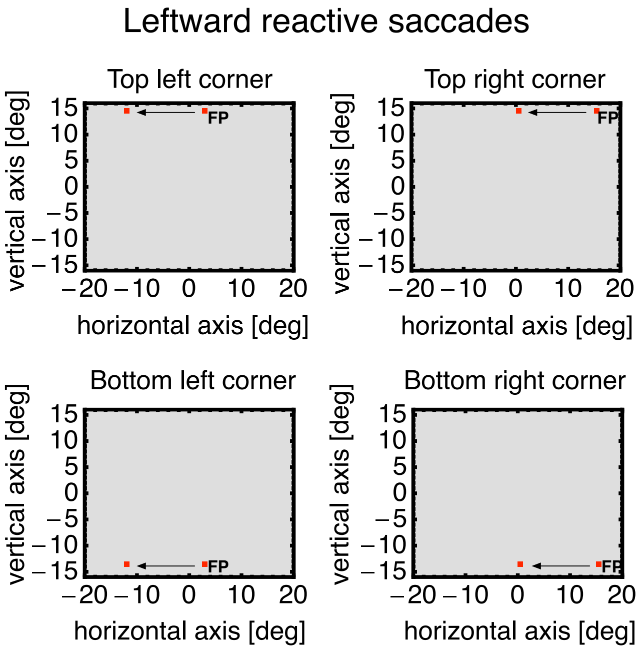

Figure 20: The procedure for triggering reactive leftward saccades was mainly the same as for rightward saccades. The fixation point was now placed where the saccade target had been in rightward sessions. The saccade target was placed where the fixation point had been. For adaptation of leftward saccades the fixation point was presented in the top right corner. The saccade target could be either to the left of or below the fixation point.

fixation point. Subjects were instructed to start the scanpath with a vertical saccade. Thus, when the targets appeared in the top left or in the top right corner of the screen scanning started with a saccade in downward direction. When targets appeared in the bottom left or in the bottom right corner of the screen scanning started with a saccade in upward direction. The rationale behind this was that the last saccade in the scanpath was a rightward saccade. These saccades were used for analysis. The targets of the last saccade in the scanpath in each corner were placed such that they matched the positions of the corresponding targets in the reactive saccade sessions. For example the starting point of the last saccade of the scanpath in the top left corner of Figure 21 was at a screen position of 15 deg to the left and 14 deg above the screen center. At the same screen position the fixation point in the reactive saccade sessions was presented as shown in the top left corner of Figure 21. The subject had to establish fixation on the fixation point and to start the trial when ready by pressing the space button on the keyboard. Then, with the next frame four saccade targets were visible. When gaze had arrived on the last target the subject had to press the mouse button to end the trial. Then, the next fixation point appeared in one of the four screen corners.

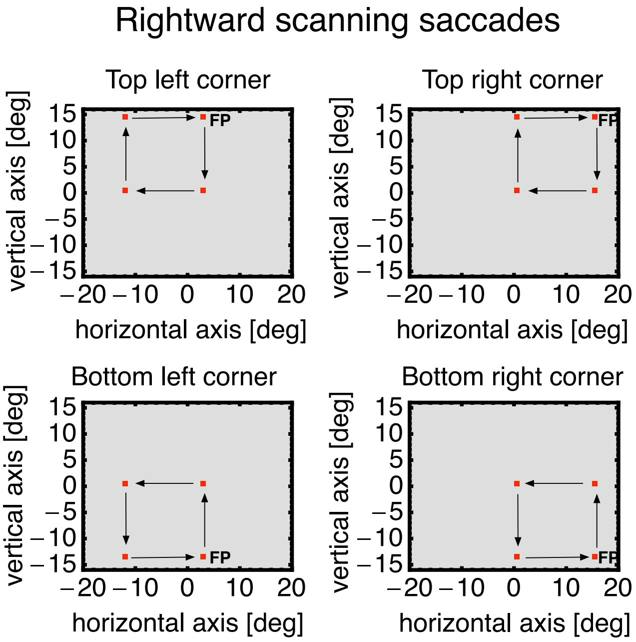

Figure 21: A trial started with the presentation of a fixation point. When the subject pressed the space button on the keyboard four targets were shown, which were permanently visible. The subject had to scan these targets in a counterclockwise manner. Saccade adaptation was induced for the last saccade of the scanpath which in this case was a rightward saccade. When the execution of the last saccade was detected all four saccade targets stepped either 5 deg inward or outward.

In 40 pre-adaptation trials saccades were tested 10 times in each corner in a pseudorandom order. Trials 41 to 220 were adaptation-trials. In the adaptation-trials saccade targets always appeared in the bottom left corner of the screen. Saccade adaptation was induced when the last saccade of the scanpath, a 15 deg rightward saccade was performed. When gaze was detected 2.5 deg to the right of the fixation point the saccade target was displaced 5 deg. In inward adaptation sessions the saccade target was displaced to the left of its initial position. In outward adaptation sessions the saccade target was displaced to the right of its initial position. In the last 90 trials saccades were again tested in all four corners of the screen. These trials consisted of 10 blocks with 9 trials each. In one block three test-saccades were performed, one in the bottom right corner, one in the top left corner and one in the top right corner. To ensure that these test-saccades did not evoke de-adaptation 6 trials of each block were adaptation-trials in the bottom left corner of the screen. Trials within one block were pseudorandomly ordered.

5.2.4 Scanning saccades in leftward direction

The positions of the targets in leftward scanning saccade sessions were the same as the positions in rightward scanning saccade sessions as can be seen in Figure 22. Since the last saccade of the scanpath should now be a leftward saccade the fixation point was placed in the left part of the scanpath and the subject had to scan the target counterclockwise.

The procedure was the same as for scanning rightward saccades. In inward adaptation sessions the saccade target was displaced to the right of its initial position. In outward adaptation sessions the saccade target was displaced to the left of its initial position.

5.2.5 Localization procedure before and after outward adaptation of reactive saccades and scanning saccades

A localization task was included in reactive rightward saccade adaptation sessions and in scanning rightward saccade adaptation sessions. All sessions

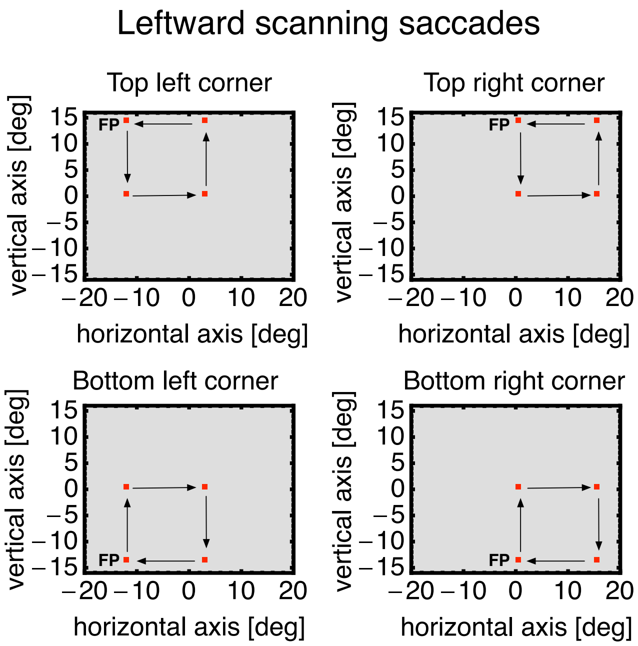

Figure 22: The procedure was the same as for scanning saccades in rightward direction. Now subjects had to scan the four targets in clockwise manner.

containing localization trials were conducted in complete darkness. To avoid visibility of the screen borders the display monitor was covered with a transparent foil that reduced the luminance by about 2 log units. In 55 pre-trials localization and saccades were tested in all four corners. Localization was tested 5 times in each corner. In a localization trial the fixation point was presented in green color. Green fixation points signalized to the subjects to keep fixation during the whole trial and to avoid any eye movement. The fixation point was shown for 1000 ms. After the fixation point was extinguished the screen was blank for 100 ms. Then a small bar (0.3 deg x 4 deg, luminance 0.2 cd/m^2) was flashed for 20 ms. The bar was flashed 15 deg to the right of the fixation point at the same position where the saccade target was presented in saccade trials. When the bar was lit off the screen was blank again for 500 ms. Then a mouse pointer appeared which the subject should use to indicate the perceived position of the bar. The pointer appeared 1000 ms after the saccade near the bottom of the screen at a randomly assigned horizontal position between 35 deg and 40 deg. The localization error was calculated as the deviation of the mouse click position from the position where the bar was presented. To determine the amount of mislocalization we calculated the median over the localization errors from the pre and post trials for each corner. Then we subtracted the median post-adaptation localization error from the median pre-adaptation localization error for each corner. In case the fixation point was red the subject should perform a saccade. In reactive saccade adaptation sessions the trial was as described in section 5.2.1 and in scanning saccade adaptation sessions the trial was as described in section 5.2.3. Saccades were tested 5 times each in the bottom right, the top left and the top right corner. Saccades were tested 15 times in the bottom left corner to obtain a baseline for the adaptation trials. Localization and saccade trials were presented in pseudorandom order. In 270 adaptation trials saccades were adapted. The last 90 trials were arranged in 10 blocks of 9 trials each. Subjects absolved each session twice in order to collect enough trials.

5.2.6 Saccade latencies

We used latency differences as a test of whether we were successful in eliciting different saccade types. Saccade latencies in reactive saccade sessions were calculated as the time interval between onset of the saccade target and detection of the saccade. Since in scanning saccade sessions all saccade targets are visible from trial start on saccade latency was calculated as the time interval between the previous fixation and detection of the saccade. Reactive saccade latencies were very small: Latencies from inward adaptation sessions (144 ± 12.15 ms for rightward saccades and 148 ± 6.9 ms for leftward saccades) were similar to latencies from outward adaptation sessions (138 ± 8.38 ms for rightward saccades and 141 ± 5.12 ms for leftward saccades). Scanning saccade latencies were much higher: Latencies from inward adaptation sessions (388 ± 51.15 ms for rightward saccades and 396 ± 53.63 ms for leftward saccades) and latencies from outward adaptation sessions (436 ± 54.95 ms for rightward saccades and 408 ± 61.18 ms for leftward saccades) were comparable. To test whether reactive and scanning saccade latencies were significantly different at the four screen corners a two-way repeated measures ANOVA was conducted. Leftward and rightward saccade sessions were analyzed separately because the adaptation training location in these sessions was at different screen positions (as shown in Figures 19, 20, 21 and 22). Data from inward and outward adaptation sessions were pooled. Latencies between reactive and scanning saccades differed significantly for leftward saccades ($F = 30.643$, $p = 0.003$) and for rightward saccades ($F = 28.253$, $p = 0.003$).

Participants

Six subjects, 1 male, 5 female (1 author, 5 naive subjects, mean age = 23 years) participated in all of the experiments. All subjects were students from the Psychology Department and had normal or corrected-to-normal vision. Subjects gave informed consent. All subjects underwent all experimental conditions. The experiments were carried out along the principles laid down in the declaration of Helsinki.

5.3 Results

The influence of eye position on the magnitude of saccade adaptation was tested. In separate sessions leftward and rightward saccades were adapted each in inward and in outward direction. Additional sessions also tested the influence of eye position on adaptation-induced mislocalization. We will first report the effect of eye position on saccade adaptation.

5.3.1 Eye position effects on saccade adaptation in inward direction

Figure 23 shows saccade amplitudes over a single session of reactive rightward saccade adaptation in inward direction. The saccade adaptation training location was in the bottom left corner of the screen. Trials 1 - 80 were pre-adaptation trials in which the saccade target was shown 15 deg to the right of the fixation point. In the pre-adaptation trials saccades were tested in all four corners of the screen. Median saccade amplitudes in the pre-adaptation trials of saccades performed in the training location of the bottom left corner was 14.45 ± 0.79 deg for this subject. From trial 81 saccade adaptation was induced with an intrasaccadic target displacement of 5 deg. The target was displaced in inward direction, i.e. to the left of its initial position. Trials 351 -530 were post-adaptation trials. In the post-adaptation trials saccades were tested in all four corners of the screen as in the pre-adaptation trials. Median saccade amplitudes in the post-adaptation trials of saccades performed in the training location was 10.43 ± 0.68 deg for this subject. The amount of adaptation was calculated as the difference between pre- and post-adaptation trials. The amount of adaptation in the bottom left corner was 4.02 deg. To determine the effect of eye position on saccade adaptation the amount of adaptation in the training location was compared to the amount of adaptation in the remaining corners. Adaptation magnitude of saccades performed in positions distant from the training location was reduced: In the bottom right corner the amount of adaptation was 1.93 deg, in the top left corner it was 2.31 deg and in the top right corner it was 1.07 deg.

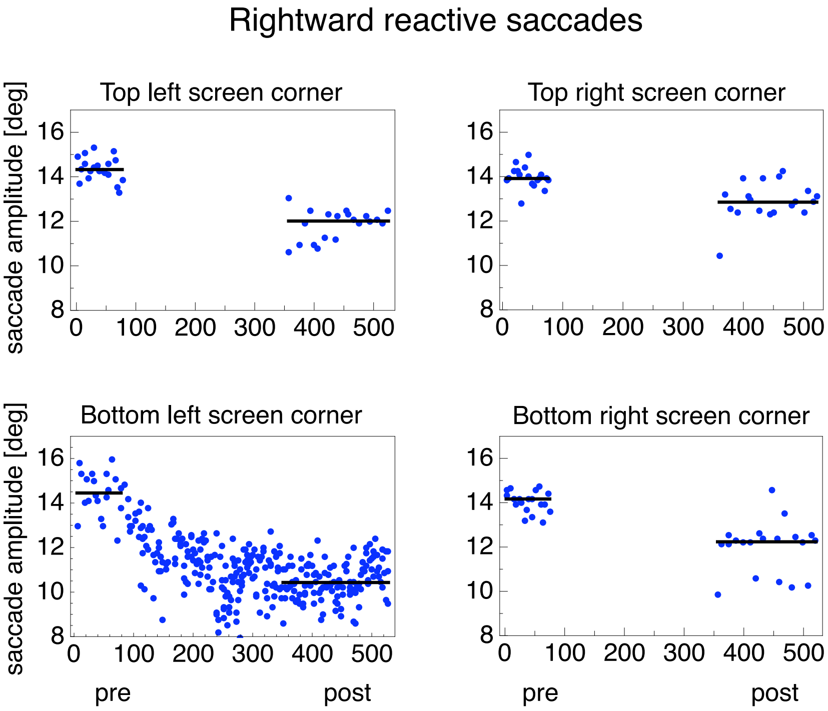

Figure 23: Saccade amplitudes (blue points) of a single subject from a session in which rightward reactive saccades where adapted in inward direction. The saccade adaptation training location was in the bottom left corner of the screen. The adaptation curve is shown in the bottom left panel. The other panels show pre- and post- adaptation saccade amplitudes tested at the corresponding screen locations. The black lines indicate the median saccade amplitude.

Saccade amplitudes over a single session of scanning leftward saccade adaptation in inward direction are shown in Figure 24. The saccade adaptation training location was the top right screen corner. The first 40 trials were pre-adaptation trials. Median saccade amplitude in the pre-adaptation trials of saccades performed in the training location was 12.92 ± 0.47 deg for this subject. From trial 41 on the saccade target in the top right corner was displaced in inward direction to the right of its initial position. Trials 221-330 were post-adaptation trials in which the amount of adaptation was tested in all four corners of the screen. In the post-adaptation trials median saccade amplitude in the training location was 10.27 ± 0.81 deg. The amount of adaptation in the training location was therefore 2.65 deg. Adaptation magnitude declined at other positions: In the top left corner was 2.26 deg, in the bottom right corner 1.37 deg and in the bottom left corner -1.0 deg.

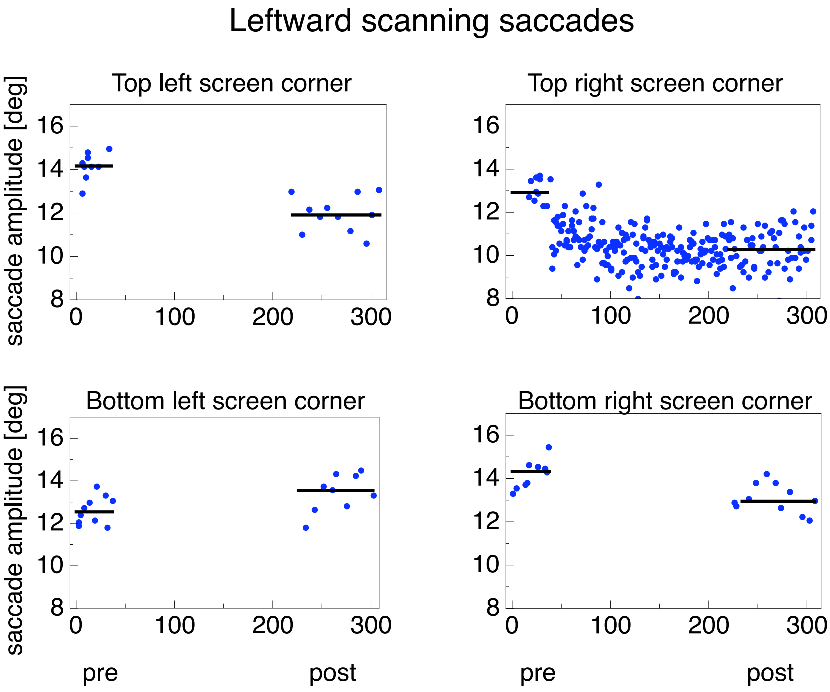

Figure 24: Saccade amplitudes (blue points) of a single subject from a session in which leftward scanning saccades where adapted in inward direction. The saccade adaptation training location was in the top right corner of the screen. The adaptation curve is shown in the top right panel. The other panels show pre- and post- adaptation saccade amplitudes tested at the corresponding screen locations. The black lines indicate the median saccade amplitude.

The amount of inward adaptation averaged over all subjects is shown in Figure 25. The diameter of each inner circle (in black) represents the mean adaptation magnitude in the corresponding corner of the screen. The diameters of the outer circles reflect the size of the standard error. Results from leftward saccade adaptation sessions are shown in Panel A for reactive saccades. The amount of adaptation in the training location in the top right corner was 3.45 ± 0.27 deg. Adaptation magnitude of saccades tested at other screen positions was reduced as can be seen by the smaller size of the circles. In the top left screen corner adaptation magnitude was 1.86 ± 0.15 deg, in the bottom right corner it was 1.55 ± 0.57 deg and in the bottom left corner it was 1.07 ± 0.29 deg. The amount of saccade adaptation therefore depends on the position of the eye in the orbita. A very similar result was observed after adaptation of leftward scanning saccades which is shown in Panel B of Figure 25. Adaptation magnitude was highest in the training location (2.95 ± 0.33 deg) and declined at the other screen positions: in the top left screen corner adaptation magnitude was 2.05 ± 0.31 deg, in the bottom right corner it was 0.89 ± 0.21 deg and in the bottom left corner 0.29 ± 0.19 deg. The results from sessions inducing rightward saccade adaptation are shown in Panel C for reactive and in Panel D for scanning saccades. The training location was in the bottom left screen corner. Also for rightward saccades adaptation magnitude was highest at the training location for reactive (3.02 ± 0.36 deg) as well as for scanning saccades (2.9 ± 0.5 deg) and declined at other screen positions. In reactive rightward saccade sessions adaptation magnitude in the bottom right corner was 1.38 ± 0.28 deg, in the top left corner it was 1.59 ± 0.25 deg and in the top right corner 0.99 ± 0.16 deg. In scanning rightward saccade sessions adaptation magnitude in the bottom right corner was 2.04 ± 0.54 deg, in the top left corner it was 0.64 ± 0.33 deg and in the top right corner 0.01 ± 0.15 deg.

In order to quantify the change in eye position we calculated the euclidean distance between the adapted saccade target and the test saccade targets. For instance, when saccades were adapted in the bottom left corner the nearest saccade target was in the bottom right corner with a distance of 12.5 deg.

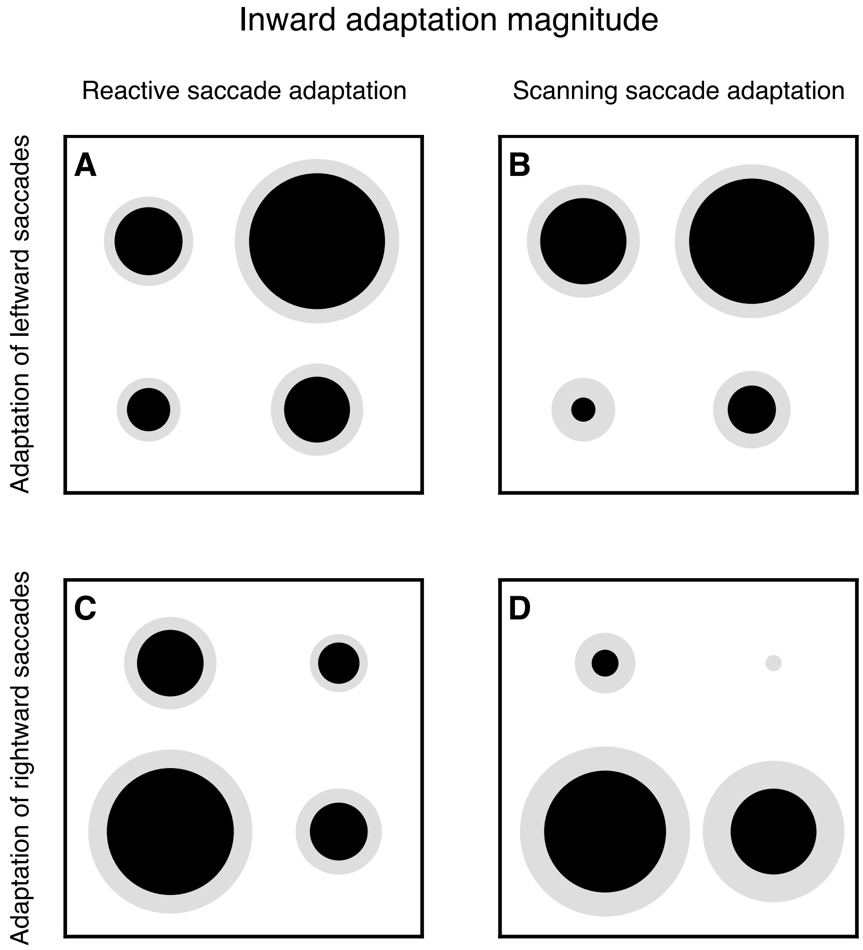

Figure 25: Average amount of reactive and scanning saccade adaptation in inward direction. The diameter of each inner circle represents the adaptation magnitude at the corresponding screen position. The diameter of the outer circles represents the standard error of the sample mean at each corresponding screen position. Adaptation magnitude was calculated as the difference between median amplitude sizes from pre- and post-adaptation trials. Panel A: Adaptation magnitude of reactive leftward saccades. Panel B: Adaptation magnitude of scanning leftward saccades. Panel C: Adaptation magnitude of reactive rightward saccades. Panel D: Adaptation magnitude of scanning rightward saccades.

The saccade target in the top left corner then was 28 deg distant and the saccade target in the top right corner was 30.7 deg distant. In inward as well as in outward adaptation sessions no differences in the data from leftward and rightward saccade sessions were observed. Data from these sessions was therefore pooled (Figure 26).

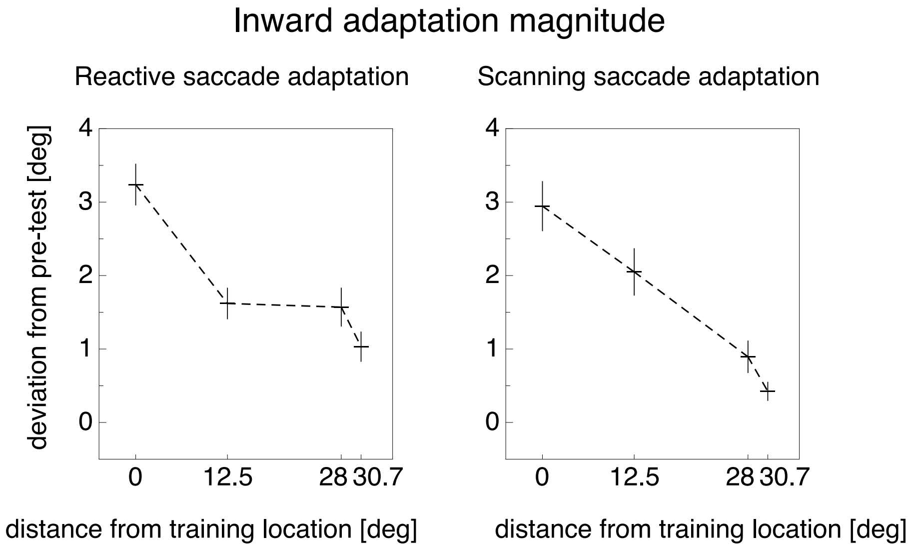

Figure 26: Average amount of reactive and scanning saccade adaptation in inward direction. Adaptation magnitude is shown against the euclidean distance from the training location where saccade adaptation was induced. The amount of adaptation was calculated as the difference between pre and post-adaptation trials. Error bars are standard errors.

Adaptation magnitude was reduced at screen positions distant from the training location. For reactive saccade adaptation this effect was nearly constant over the different screen positions. Scanning saccade adaptation however decreased more linearly as a function of distance from the training location. For reactive and scanning saccades adapted in inward direction a two-way ANOVA was calculated with the factors "saccade type" (reactive / scanning) and "screen positions" (all four corners). A significant main effect for the factor "screen positions" was revealed (F = 45.011, p = 0.001) confirmed eye position effects on saccade adaptation in inward direction. Bonferroni post-tests revealed that saccades performed at all screen locations distant from the training location were significantly less affected by saccade adaptation than saccades performed in the training location. A significant interaction effect (F = 4.330, p = 0.038) showed that eye position modulated reactive and saccade differently.

5.3.2 Eye position effects on saccade adaptation in outward direction

Saccade amplitudes over a single session of reactive leftward saccade adaptation in outward direction are shown in Figure 27.

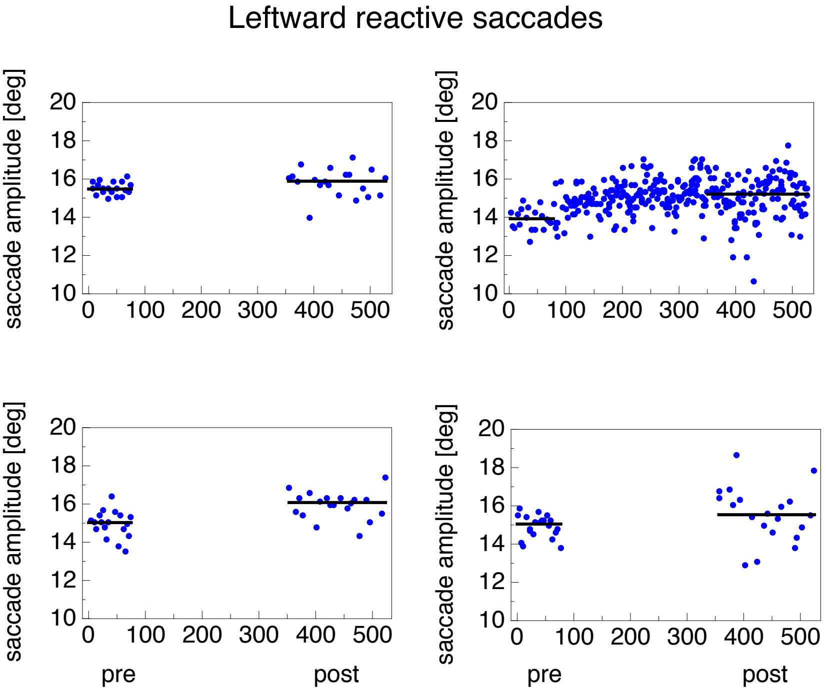

Figure 27: Saccade amplitudes over a single session of reactive leftward saccade adaptation in outward direction. The saccade adaptation training location was in the top right corner of the screen. The adaptation curve is shown in the top right panel. The other panels show pre- and post- adaptation saccade amplitudes tested in the corresponding screen locations. The black lines indicate the median saccade amplitude.

The data derive from the same subject as those shown in Figure 23. The saccade adaptation training location was in the top right corner of the screen. In the pre-adaptation trials (trials 1 - 80) the saccade target was presented 15 deg to the left of the fixation point. In the pre-adaptation trials the median amplitude size in the training location was 13.9 ± 0.47 deg. From trial 81 on a 5 deg target displacement in outward direction induced saccade adaptation. The median saccade amplitude of saccades performed in the training location in the post-adaptation trials (trials 351 - 530) was 15.21 ± 0.84 deg. The saccade target displacement thus induced 1.29 deg adaptation in this subject. The amount of adaptation in the top left corner was 0.41 deg, in the bottom right corner it was 0.48 deg and in the bottom left corner 1.05 deg.

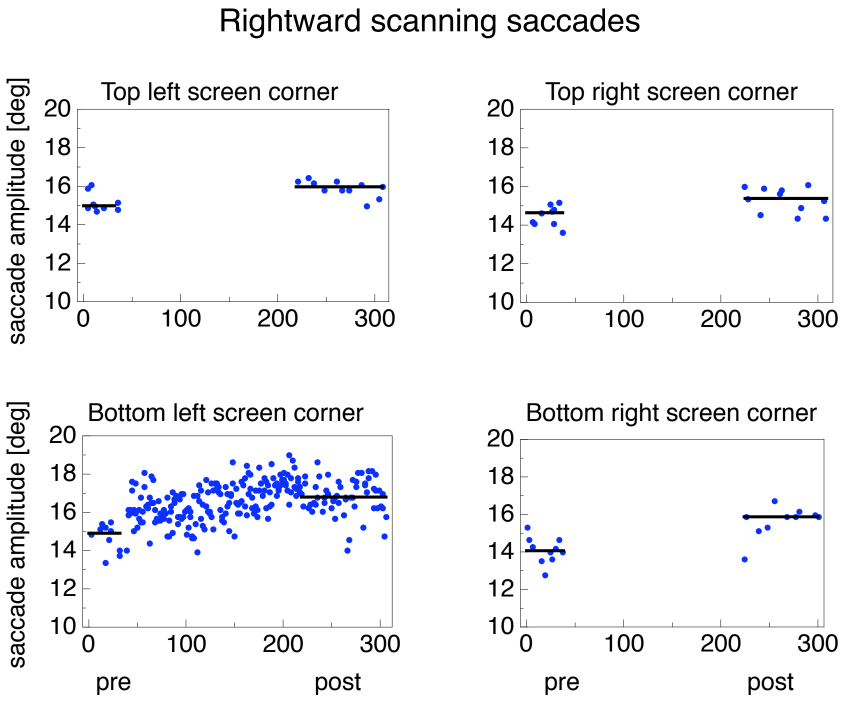

Figure 28: Saccade amplitudes over a single session of scanning rightward saccade adaptation in outward direction. The saccade adaptation training location was in the bottom left corner of the screen. The adaptation curve is shown in the bottom left panel. The other panels show pre- and post- adaptation saccade amplitudes tested in the corresponding screen locations. The black lines indicate the median saccade amplitude.

Saccade amplitudes over a single session of scanning rightward saccade adaptation in outward direction are shown in Figure 28. In this session the saccade adaptation training location was the bottom left screen corner. Median saccade amplitudes in the pre-trials (trials 1 - 40) of saccades performed in the training location was 14.91 ± 0.56 deg for this subject. From trial 41 on the saccade target in the bottom left corner was displaced in outward direction to the right of its initial position. Trials 221-330 were post-adaptation trials in which the amount of adaptation was tested in all four corners of the screen. Median saccade amplitude in the training location was 16.8 ± 0.69 deg. The amount of adaptation in the training location therefore was 1.89 deg. Adaptation magnitude of saccades performed in other screen locations was reduced: In the top left corner it was 1.81 deg, in the bottom right corner 0.99 deg and in the bottom left corner 0.74 deg.

The amount of outward adaptation averaged over all subjects is shown in Figure 29. Results from leftward saccade outward adaptation sessions are shown in Panel A for reactive and in Panel B for scanning saccades. The training location in these sessions was the top right screen corner. Adaptation magnitude in the training location was 1.51 ± 0.2 deg for reactive and 1.79 ± deg for scanning saccades. The intrasaccadic target displacement in outward direction therefore induced less adaptation than in inward direction (which was 3.45 ± 0.27 deg for reactive and 2.99 ± 0.33 deg for scanning leftward saccades). But similar to inward adaptation the amount of adaptation declined at other screen positions. For leftward reactive saccade sessions adaptation magnitude in the top left screen corner was 0.49 ± 0.22 deg, in the bottom right screen corner it was 1.08 ± 0.31 deg and in the bottom left screen corner 0.89 ± 0.23 deg. For leftward scanning saccade sessions adaptation magnitude in the top left screen corner was 0.91 ± 0.29 deg, in the bottom right screen corner it was 0.32 ± 0.26 deg and in the bottom left screen corner 0.43 ± 0.24 deg. Adaptation in outward direction was

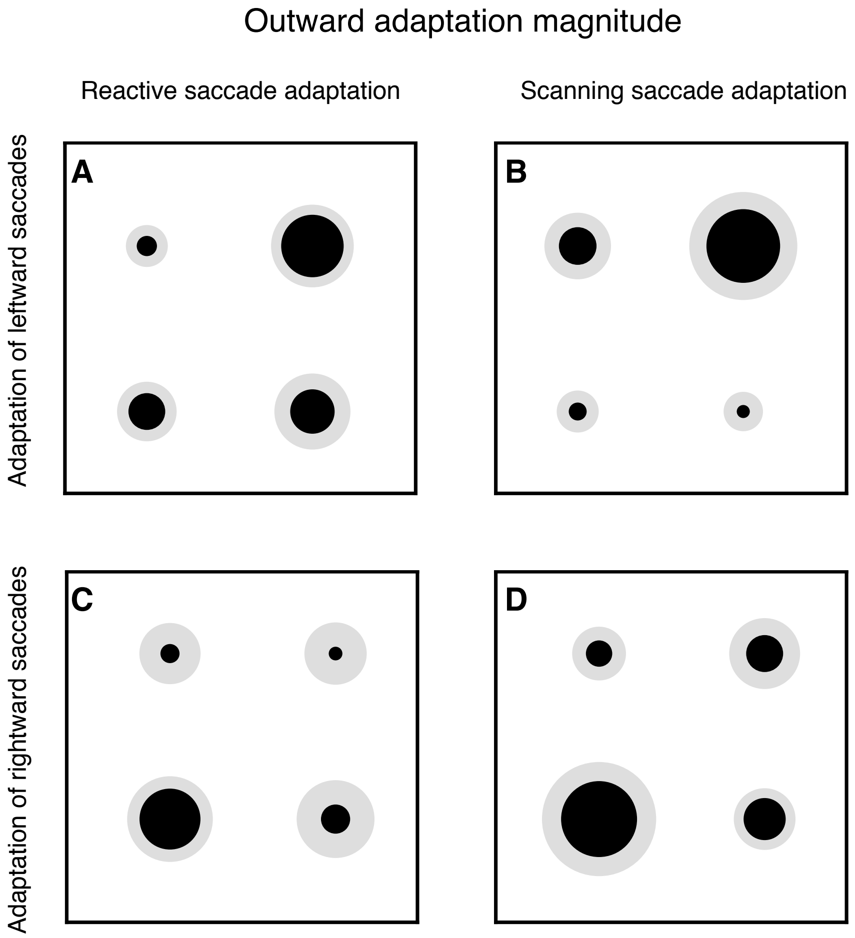

Figure 29: Average amount of reactive and scanning saccade adaptation in outward direction. The diameter of each inner circle represents the adaptation magnitude at the corresponding screen position. The diameter of the outer circles represents the standard error of the sample mean at each corresponding screen position. Adaptation magnitude was calculated as the difference between median amplitude sizes from pre- and post-adaptation trials. A: Adaptation magnitude of reactive leftward saccades. B: Adaptation magnitude of scanning leftward saccades. C: Adaptation magnitude of reactive rightward saccades. D: Adaptation magnitude of scanning rightward saccades.

therefore dependent on eye position. Results from rightward saccade outward adaptation sessions are shown in Panel C for reactive and in Panel D for scanning saccades. The saccade adaptation training location was the bottom left screen corner. Adaptation magnitude in the training location was 1.48 ± 0.25 deg for reactive and 1.84 ± 0.38 deg for scanning saccades. Also for rightward saccades the target displacement in outward direction induced less adaptation than in inward direction (which was 3.02 ± 0.36 deg deg for reactive rightward saccades and 2.9 ± 0.5 deg deg for scanning rightward saccades).

Figure 30 shows adaptation magnitude plotted against distance from the training location. Data from leftward and rightward sessions are pooled. Adaptation magnitude of rightward saccades adapted in outward direction was reduced at screen positions distant from the training location. For rightward reactive saccades adaptation magnitude in the bottom right screen corner was 0.71 ± 0.48 deg, in the top left corner it was 0.46 ± 0.41 deg and in the top right corner 0.33 ± 0.48 deg. For rightward scanning saccades adaptation magnitude in the bottom right screen corner was 1.02 ± 0.19 deg, in the top left corner it was 0.64 ± 0.27 deg and in the top right corner 0.89 ± 0.34 deg.

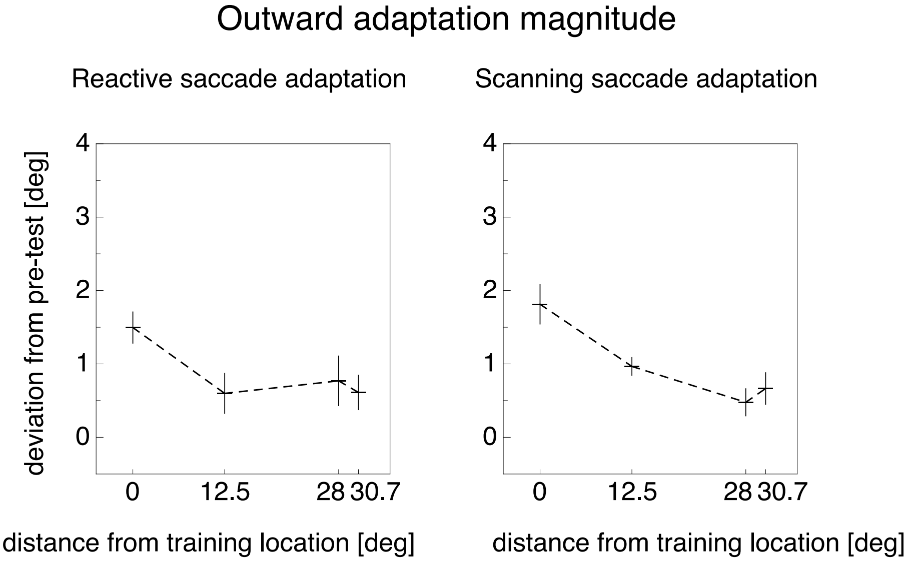

Figure 30: Average amount of reactive and scanning saccade adaptation in outward direction. Errors bars are standard errors.

For reactive and scanning saccades adapted in outward direction a two-way ANOVA was calculated with the factors "saccade type" (reactive / scanning) and "screen position" (all four screen corners). A significant main effect for the factor "screen positions" was revealed (F = 12,797, $p = 0.001$). Bonferroni post-tests revealed that adaptation magnitude in screen positions distant from the training location was significantly smaller than adaptation magnitude in the training location. The analysis confirms that also outward adaptation depends on the position of the eye in the orbita. However, no difference between reactive and scanning saccade outward adaptation was found. We checked for differences between outward and inward adaptation separately for reactive and scanning saccades. Significant less adaptation was found after outward than after inward adaptation for reactive (paired t-test, $p < 0.001$) and for scanning saccade (paired t-test, $p < 0.001$). This result confirms data from section 3 as well as from earlier reports (Miller et al., 1981; Straube et al., 1997b; Noto et al., 1999; Bahcall and Kowler, 2000; Robinson et al., 2003). We also tested whether eye position effects were different after outward than after inward adaptation. For every screen corner distant from the training location we calculated the amount of transfer from the training location. This was done by dividing for every session the adaptation magnitude at screen locations distant from the training location by the amount of adaptation at the training location. Separately for reactive and scanning saccades a two-way ANOVA was calculated over these values with the factors "adaptation direction" (inward / outward) and "screen position" (the three corners distant from the training location). A significant main effect of the factor "screen positions" ($F = 35.351$, $p < 0.001$) revealed that in scanning saccade sessions the adaptation transfer from the training location was differently pronounced over the screen location. Bonferroni post-tests confirmed that adaptation magnitude declined with distance from the training location. No significant effect was found for reactive saccade sessions.

5.3.3 Eye position effects on mislocalization after saccade adaptation in outward direction

In separate sessions we also tested the influence of eye position on adaptation-induced mislocalization. These sessions were run in complete darkness to avoid that localization could be influenced by visual landmarks. Visual localization was tested after adaptation of reactive and of scanning saccades. Adaptation was induced in outward direction since the results of section 4 showed that with the standard adaptation method only outward adaptation was accompanied by mislocalization. Both, localization and saccade amplitudes were tested in each session to compare the effects of eye position. This procedure also allowed to estimate whether the results from the previous sections also apply to saccades performed in darkness. Subjects absolved the sessions at least twice to obtain enough data for statistical analysis. Data from these sessions were then averaged for each subject.

Figure 31 shows localization errors from a single session of rightward reactive saccade adaptation in outward direction. Localization errors were calculated as the difference between the position where the probe bars were presented and the position where the subject indicated the perceived position of the bar. The saccade adaptation training location was the bottom left corner of the screen. The bottom left panel of Figure 31 shows pre - and post-adaptation localization errors tested in the bottom left corner of the screen. The median localization error in the pre-trials was -3.58 ± 2.04 deg and in the post-trials -2.1 ± 0.69 deg. Saccade adaptation thus induced mislocalization of 1.48 deg for this subject. In the bottom right corner of the screen mislocalization was

1.05 deg, in the top left corner it was 1.75 deg and in the top right corner 2.4 deg.

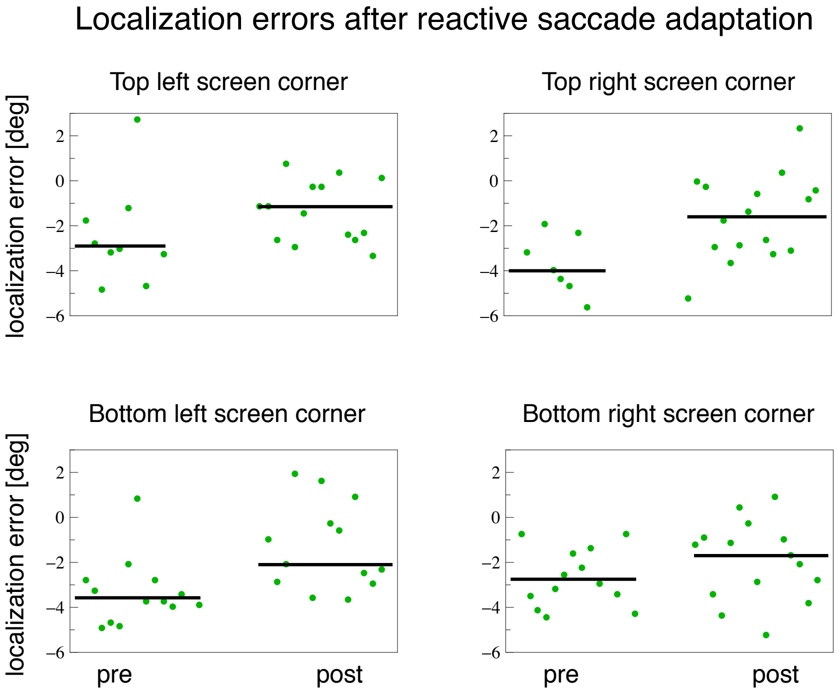

Figure 31: Pre - and post - adaptation localization errors from a single session of reactive rightward saccade adaptation in outward direction. The saccade adaptation training location was the bottom left corner of the screen. The black lines indicate the median localization error.

Figure 32 shows average mislocalization and average adaptation after reactive saccade outward adaptation. At the training location in the bottom left screen corner probe bars were 1.08 ± 0.53 deg mislocalized. The amount of mislocalization declined at other screen positions. Mislocalization magnitude in the bottom right screen corner was 0.58 ± 0.35 deg, in the top left screen corner it was 1.44 ± 0.2 deg and in the top right screen corner 1.24 ± 0.5 deg. Adaptation magnitude was highest in the training location (1.47 deg ± 0.26). In the bottom right screen corner adaptation magnitude was 1.28 ±

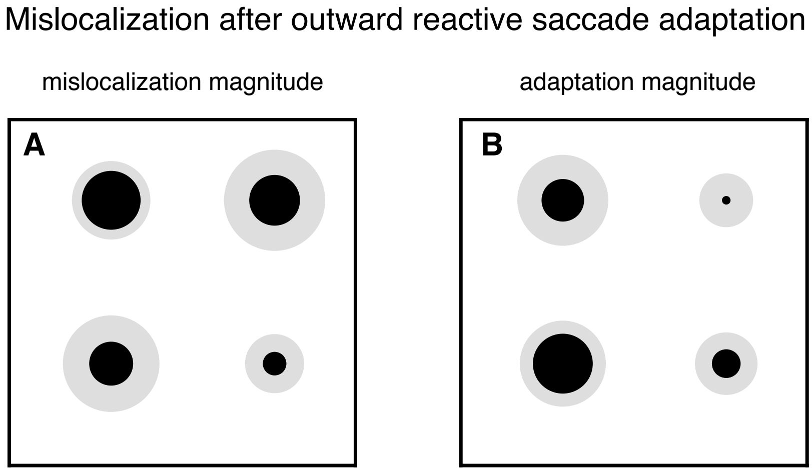

Figure 32: Adaptation and mislocalization results after reactive saccade adaptation in outward direction averaged over all subjects. A: Mislocalization magnitude of probe bars tested at all four screen positions. B: Reactive saccade outward adaptation magnitude of saccades tested at all four screen positions

0.28 deg, in the top left corner it was 1.04 ± 0.49 deg and in the top right screen corner 0.21± 0.45 deg.

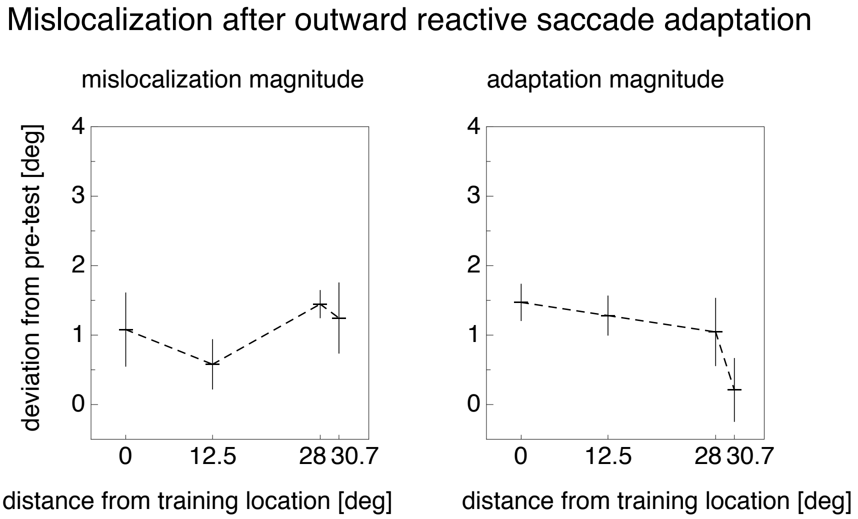

Figure 33: Average amount of reactive saccade adaptation in outward direction and mislocalization. Adaptation and mislocalization magnitude is shown against distance from the training location where saccade adaptation was induced. The amount of adaptation was calculated as the difference between pre and post-adaptation trials. Error bars are standard errors.

Reactive saccade outward adaptation magnitude was comparable to the sessions measured in dim light condition (Figures 29 and 30). In Figure 33 mislocalization magnitude and adaptation magnitude are plotted against distance from training location. For the amount of adaptation and mislocalization after saccade adaptation in outward direction a two-way ANOVA was calculated. A significant main effect for the factor "screen position" was revealed (F = 13.44, p = 0.03). Mislocalization and adaptation magnitude therefore were modulated by eye position.

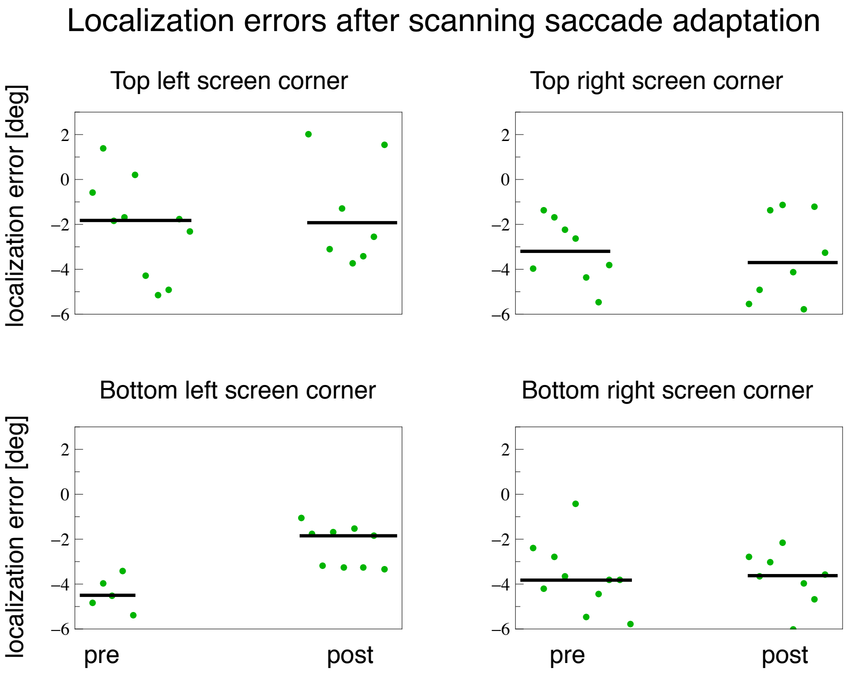

Figure 34: Pre - and post - adaptation localization errors from a single session of scanning rightward saccade adaptation in outward direction. Saccades were adapted in the bottom left corner of the screen. The black lines indicate the median localization error.

Figure 34 shows localization errors from a single session of rightward scanning saccade adaptation in outward direction. Data from the same subject as in Figure 31 are shown. Saccades were adapted in the bottom left corner of the screen. The bottom left panel of Figure 31 shows pre - and - post adaptation localization errors tested in the bottom left corner of the screen. In the pre-trials the median localization error in the training location was -4.5 ± 0.6 deg and in the post-trials -1.85 ± 0.79 deg. Saccade adaptation thus induced mislocalization of 2.65 deg for this subject. At other screen positions the amount of mislocalization was drastically reduced. In the bottom right corner of the screen mislocalization magnitude was 0.2 deg, in the top left corner it was -0.1 deg and in the top right corner -0.5 deg. Average mislocalization measured in scanning saccade outward adaptation sessions is shown in Figure 35. In the training location in the bottom right screen corner probe bars were 1.25 ± 0.36 deg mislocalized. A clear reduction of mislocalization magnitude was observed for saccades tested at screen positions distant from the training location: In the bottom right screen corner mislocalization magnitude was 0.85 ± 0.34 deg, in the top left screen corner it was 0.19 ± 0.26 deg and in the top right screen corner 0.35 ± 0.26 deg.

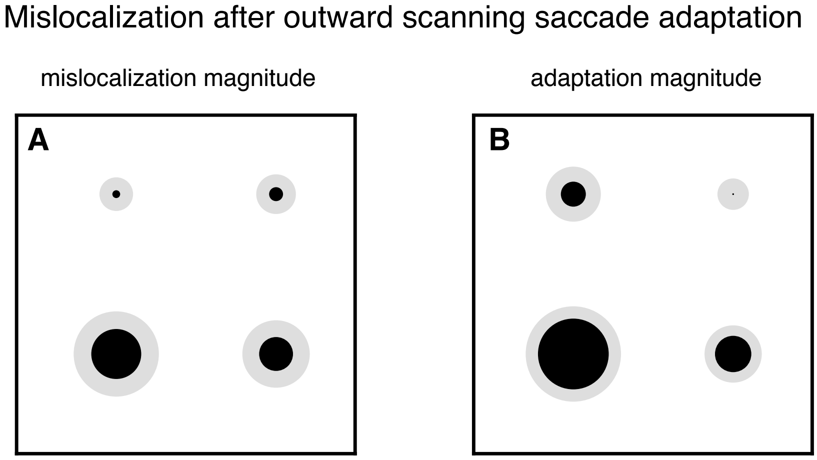

Figure 35: Adaptation and mislocalization results after scanning saccade adaptation in outward direction averaged over all subjects. A: mislocalization magnitude of probe bars tested at all four screen positions. B: reactive saccade outward adaptation magnitude of saccades tested at all four screen positions

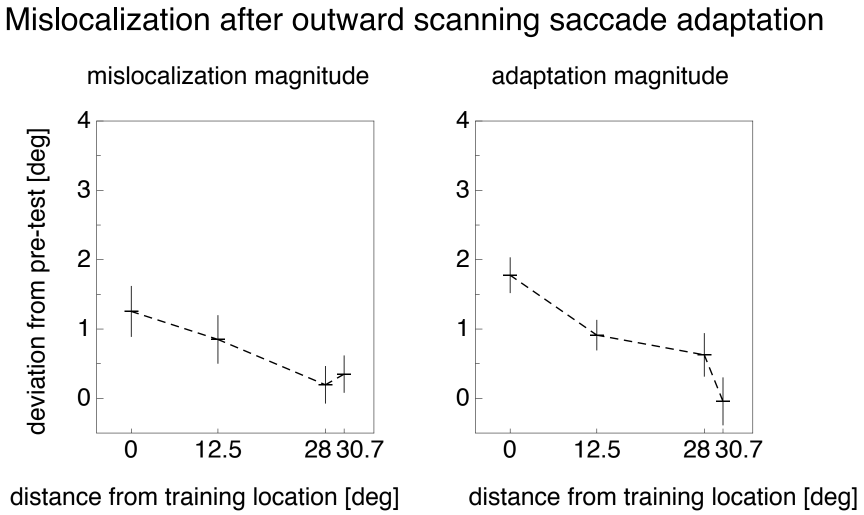

Figure 36: Average amount of scanning saccade adaptation in outward direction and mislocalization. Error bars are standard errors.

Scanning saccade outward adaptation magnitude for rightward saccades was comparable to the sessions measured in the dim light condition (Figures 29 and 30). Adaptation magnitude in the training location was 1.77 ± 0.255 deg, in the bottom right location it was 0.91 ± 0.21 deg, in the top left location it was 0.62 ± 0.3 deg and in the top right location 0.04 ± 0.33 deg. Figure 36 shows mislocalization magnitude and scanning saccade adaptation magnitude plotted against distance from training location. For the amount of adaptation and mislocalization after saccade adaptation in outward direction a two-way ANOVA was calculated. A significant main effect for the factor screen positions was revealed (F = 2.677, p = 0.001).

5.4 Discussion

Eye position affected reactive and scanning saccade adaptation in inward as well as in outward direction. Adaptation magnitude was decreased for saccades tested in different screen position than the training location in which saccade adaptation was induced. These results contradict the assumption that saccade adaptation is coded in purely retinal coordinates. The present data rather suggest that both saccade adaptation types are coded in multiple coordinate systems which are mutually supportive. A retino-centered coordinate system would predict that adaptation magnitude remains constant irrespective of eye position. For inward adaptation the amount of reactive saccade adaptation was reduced relative to the training location but remained nearly distant at all positions distant from the training location. The eye position specificity of scanning saccade adaptation differed slightly from reactive saccade adaptation. Scanning adaptation magnitude decreased proportionally to the distance from the training location and was more reduced than reactive saccade adaptation at the most distant position. This form of eye position specificity might indicate a stronger contribution of a head-centered coding. A head-centered coordinate system would predict that adaptation magnitude can be modulated by variations in eye position. Adaptation magnitude should then decrease as a function of distance from the training location. This interpretation is consistent with a computational model assumption by Gancarz and Grossberg (1999). In this model the adaptation of voluntary saccades is achieved in a head-centered coordinate system whereas reactive saccade adaptation is based on cerebellar learning.

A reason for a different relative contribution of coordinate systems might be that to code a saccade target in a head-centered reference frame takes a certain period of time. Since saccadic reaction times to suddenly appearing targets are faster they might be triggered by an immediate response in an eye-centered coordinate system. Scanning saccade reaction times are higher and the processing of their targets might be long enough to be transformed into a head-centered reference frame. This explanation fits nicely with the assumptions of two computational models: The "gain-field model" (Andersen et al., 1985) suggests that head-centered coordinates are implicitly represented in populations of neurons that have eye-centered receptive fields. The "conversion on command" model (Henriques et al., 1998) assumes that saccade target positions are first coded in eye-centered coordinates and will be transformed on demand into the task-relevant coordinate system.

Earlier studies measured eye position effects on saccade adaptation and found different results. Semmlow et al. (1989) found a slight reduction of adaptation magnitude at screen positions distant from the training location for inward adaptation. The reduction was constant over all tested screen positions. For outward adaptation, however, the reduction of adaptation magnitude was proportional to the distance from the adaptation site. This difference between inward and outward reactive saccade adaptation was not observable in our data. The amount of inward and outward reactive saccade adaptation was constantly reduced at different eye positions. However, Semmlow et al. (1989) used target displacements of different sizes for inward (25 percent of the required saccade amplitude) and outward adaptation (100 percent of the required saccade amplitude). We used a target displacement size of 33 percent of the required saccade amplitude for inward as well as for outward adaptation. Frens and Van Opstal (1994) measured eye position specificity of reactive saccade inward adaptation. Although not statistically significant in two of the three subjects the adaptation magnitude was reduced at different eye positions. Also in the data from Deubel (1995a) a slight trend of eye position specificity of reactive saccade inward adaptation could be seen. Albano (1996) tested eye position dependency of reactive saccade adaptation in inward and outward adaptation at a very small range. For adaptation in inward and outward direction adaptation magnitude was reduced at some positions and at others not.

Both, reactive and scanning saccade adaptation induced changes in visual localization. The modulation of mislocalization magnitude through eye position signals was very similar as that of the according saccade adaptation for reactive as well as scanning saccades. The eye position specificity of mislocalization magnitude was different after reactive saccade adaptation than after scanning saccade adaptation. In sections 3 and 4 we showed that reactive and scanning saccade adaptation induces changes in visual localization. Here we tested the eye position specificity of adaptation-induced mislocalization during continuous fixation. Mislocalization after reactive saccade adaptation was hardly affected by eye position. Mislocalization after scanning saccade adaptation however decreased proportionally to the distance from the training location. As for scanning saccade adaptation magnitude this result indicates a stronger contribution of a head-centered coding. This could explain the different mislocalization of flashed and stationary bars after reactive and scanning saccade adaptation (as described in section 3).

We conclude that different coordinate systems have different relative contributions in the adaptation of reactive and scanning saccades. The metrics of reactive and scanning saccades selectively contribute to the perception of visual objects in space.

6 General Discussion

The general hypothesis underlying my thesis was that action and perception share a common representation. Sensorimotor theories claim that the spatial perception of objects is constituted by the coordinates which control motor activities to that object. In this view, the same metrics which are used for reaching an object provide the signals for visual localization of that object. The problem of sensorimotor coordination is most intensively exemplified in saccadic eye movements because visual localization is most often associated with a saccade to that object. To test the predicted reliance of visual localization on motor coordinates we asked three general questions: How do the adaptation of reactive and scanning saccades change visual localization? Does saccade adaptation change visual localization even during continuous fixation? In which coordinate systems are saccade adaptation and adaptation-induced localization changes coded?

6.1 How do reactive saccade adaptation and scanning saccade adaptation affect visual localization?

In the first study we investigated changes in visual localization after adaptation of different saccade types. Previous studies demonstrated that reactive and voluntary saccade types can be adapted independently from each other. We asked whether adaptation of both saccade types induce changes in visual localization. We used briefly presented localization probes which should resemble the suddenly appearing reactive saccade targets and we used permanently visible probes which should mimic the scanning saccade targets. We adapted reactive and scanning saccades selectively. Reactive saccades were performed to suddenly appearing saccade targets whereas scanning saccades were performed to continuously visible targets. The selective adaptation of these saccade types had differential effects on visual localization. Scanning saccade adaptation induced mislocalization for briefly presented as well as for permanently visible localization probes. Reactive saccade adaptation however induced mislocalization only for briefly presented bars. The adaptation selectivity in the motor range is thus reflected in the perception of visual space. The pathway in which saccades to briefly presented targets are generated may also be the pathway which establishes the localization of briefly presented objects. The pathway responsible for the generation of scanning saccades contributes to the spatial perception of both permanently visible and briefly presented objects. Since perceived bar positions were reported after execution of a saccade reference-object theories (McConkie and Currie, 1996; Deubel et al., 1996, 2002) would predict that the saccade target is used as a landmark for localization. Indeed, a small part of mislocalization was due to the visibility of the saccade target. However, the main part of mislocalization was also observed when the saccade target was extinguished during execution of the saccade. In some studies it has been proposed that the efference copy, i.e. a copy of the motor command, is used for post-saccadic localization. To explain the results this way one has to assume one efference copy for reactive saccades which is used only for flashed bars and another efference copy for scanning saccades which is used for both flashed and stationary bars. However, this proposal makes a prediction, which can be easily falsified: After saccades to suddenly appearing events, stationary objects should be perceived shifted. But this is clearly not the case. An efference copy therefore cannot explain the localization results in this study. The amount of mislocalization depended on the saccade type that was executed. In trials where one saccade was adapted but the opposite saccade type was performed mislocalization magnitude was reduced. This can be explained by the lower adaptation magnitude of saccades executed in the transfer-trials. This explanation however would imply that the main part of the mislocalization measured in this study critically depends on the execution of an adapted saccade. The results therefore raise the question of whether saccade adaptation changes visual localization even during continuous fixation.

6.2 Do modifications in saccade metrics change visual localization even during continuous fixation?

To find out whether modifications in saccade metrics induce mislocalization even when the eye is not moving we measured visual localization during continuous fixation. Saccade amplitudes were adapted in inward and in outward direction. The perceived position of briefly presented localization bars was clearly shifted in the adaptation direction. Inward adaptation left localization completely unaffected. The results confirm predictions of recent computational modeling, which is based on optimal control theory (Ethier et al., 2008b). In this framework two different mechanisms are supposed to adapt saccades. On the one hand, a forward model predicts the sensory consequences of the motor command. Systematic mismatches between the predicted and the sensory feedback induce adaptive changes in saccade dynamics such that the saccade lands on its target correctly. On the other hand a change in the saccade target representation from, for instance, a 10 deg target position to a 16 deg target position could reduce post-saccadic visual errors as they occur in the saccade adaptation paradigm. The dynamics of this saccade should then be identical to an unadapted saccade to a target at 16 deg. The oculomotor system then faces a credit assignment problem

(Kording et al., 2007): Is the discrepancy between the observed and the predicted sensory feedback due to a change in the saccade target position or due to incorrect saccade dynamics? If credit is assigned to a change in the target position, then the saccade target representation should be modified. If however credit is assigned to an incorrect motor command the forward model should modify saccade dynamics. The model simulations of Chen-Harris et al. (2008) revealed for large post-saccadic visual errors, credit is assigned to a change in the saccade target position. When the errors then however are small through adaptive changes, credit is assigned to the motor command. Peak velocity results of data from the second study are fully consistent with this framework. The peak velocities of saccades adapted in inward direction were reduced compared to peak velocities of unadapted saccades with the same amplitude size. The peak velocities of saccades adapted in outward direction however were nearly identical to peak velocities of unadapted saccades with the same amplitude size. Adaptation in inward direction was faster and more complete than adaptation in outward direction. The post-saccadic visual errors of saccades adapted in inward direction were thus small. Adaptation of these saccades should be mainly achieved through a change in the saccade motor command. Since outward adaptation was slower and less complete, larger post-saccadic visual errors remained. Adaptation therefore should be achieved through a modification in the saccade target representation. Mislocalization was observed only after adaptation in outward direction in agreement with the main idea of my thesis that modifications in saccade metrics induce changes in visual localization. We tested this account more explicitly by using an adaptation method which applied a constant visual error after every trial. The magnitude of the localization change scaled with the size of the post-saccadic visual error. With constant visual error adaptation, mislocalization could be observed after inward adaptation.

6.3 In which coordinate system are saccade adaptation and adaptation-induced localization changes coded?

The results of the first study suggested that reactive and scanning saccades might be coded in different coordinate systems. To determine which coordinate system codes the adaptation of reactive and scanning saccades we investigated the dependency of saccade adaptation on the position of the eye in the orbita. Saccade adaptation was induced in one single location on the screen. After adaptation saccades were tested at different positions on the screen and thereby at different eye positions. If saccade adaptation is coded in a retinal coordinate system the amount of adaptation should be independent from eye position. However, eye position clearly modulated adaptation magnitude. These results therefore contradict the widely accepted assumption that saccade adaptation is coded in a purely retino-centered coordinate system. Differences in the eye position specificity between reactive and scanning saccade adaptation suggest that at least partially different coordinate systems might be involved in their coding. Since scanning saccade adaptation magnitude decreases as a function of distance from the training location a stronger contribution of a head-centered coordinate system is possible.

Outward adaptation of both saccade types induced changes in visual localization, which in the training location was nearly as large as the amount of adaptation. The amount of localization change was affected by eye position in a way very similar to the adaptation magnitude. After reactive saccade adaptation in outward direction mislocalization magnitude varied slightly when tested at different screen positions. After scanning saccade adaptation in outward direction however mislocalization magnitude decreased with distance from the training location. For reactive and scanning saccades the eye position specificity of mislocalization was thus very similar to that of adaptation. This is therefore additional evidence that saccade metrics are used for visual localization.

6.4 Implications for future studies

Visual localization can be modified by changes in saccade motor metrics. A common spatial representation of action and perception highlights once more the active and dynamic nature of visual perception. In this view, vision is constantly adapted to the behavioral dispositions instead of being a static and isolated capacity. The next logical step would be to identify the neural network controlling oculomotor and visual plasticity inside the oculomotor system. Since my thesis presents evidence that visual localization and saccade motor metrics share a common representation one should expect to find the origin of the visual plasticity at the site where the oculomotor plasticity takes place. The selectivity of reactive and scanning saccade adaptation indicates that these saccade types are adapted in different locations of the brain. However, which areas might be involved is still controversivly discussed.

Due to the different saccade reaction times the processing duration of the saccade target position is longer for scanning than for reactive saccades. A stronger contribution of a retino-centered coordinate system in reactive saccade adaptation and a stronger contribution of a head-centered coordinate system in scanning saccade adaptation was suggested by the results of my first (described in section 3) and my last study (described in section 4). The reason for this difference may be the different processing duration of the saccade target. Indeed, Deubel (1995a) found evidence for effects of saccade latency on adaptation transfer. Saccade latency was determined in the overlap paradigm by systematically varying the duration of the overlap interval, which is the duration in which fixation point and saccade target are visible simultaneously. There was strong adaptation transfer from reactive saccades to overlap saccades with short latencies (~ 250 ms). However, no or only small adaptation transfer from reactive saccades to overlap saccades with longer latencies (> 500 ms) was observed. Future studies could systematically test whether the presentation duration of the saccade target in the overlap paradigm can modulate in which coordinate system the target position is coded. The kind of coordinate system which codes the target position could be tested by measuring saccade adaptation magnitude at different screen positions. Saccade adaptation with trials in which the fixation point is extinguished late should then show a higher dependency on eye position as saccade adaptation with trials in which the fixation point is extinguished early.

The idea that stimuli with longer presentation durations will be represented in a head-centered coordinate system might also explain the mislocalization of stationary bars after scanning saccade adaptation. Stationary bars should then also be mislocalized when presented during continuous fixation. Experiments could be run following the same procedure described in section 5.3.3. If the contribution of a head-centered coordinate system is stronger in scanning than in reactive saccade adaptation stationary bars should be mislocalized after scanning but not after reactive saccade adaptation. Additionally, the presentation duration of the probes could be systematically varied. Mislocalization magnitude after reactive saccade adaptation should be anti-proportional to the presentation duration of the probe bars.

The results of my thesis allow some speculations about which brain structures induce the changes in saccade motor metrics. First, the adaptation-induced changes in visual localization suggest that saccade adaptation occurs in brain structures which have connections to visual areas. This makes adaptation on the brainstem level very unlikely. Because of the predominant role of the parietal cortex for the representation of space (Husain and Nachev, 2007) structures in the parieto-tectal pathway would be well suited to generate changes in saccade metrics as well as in visual space perception. Electrical stimulation of the SC deeper layers demonstrates that signals from the SC in principle can induce saccade motor learning (Kaku et al., 2009). Neurons which change their firing pattern after saccade adaptation have indeed been found in the superior colliculus (Takeichi et al., 2007). However, many current studies suggest that saccade adaptation takes place in the cerebellum. The oculomotor vermis is a likely location to induce saccade motor learning. Saccade adaptation is impaired in patients suffering from vermal pathology (Golla et al., 2008). Surgical ablation of the cerebellar vermis in monkeys prevents saccade adaptation (Optican and Robinson, 1980; Takagi et al., 1998; Barash et al., 1999). Also lesions in the cerebellum in humans impairs saccade adaptation (Optican et al., 1985; Waespe and Baumgartner, 1992; Straube et al., 2001). Population bursts of Purkinje cell simple spikes might provide the different mechanisms of adaptation in inward and outward adaptation (Catz et al., 2008). Further research has to clarify the contributions of the SC and the oculomotor vermis to saccadic adaptation.

Second, the selectivity of reactive and scanning saccade adaptation suggested that different brain areas adapt different saccade adaptation types. Most experiments which were devoted to find the physiological basis of saccade motor learning only investigated reactive saccade adaptation (but see (Alahyane et al., 2008)). Future studies should investigate the neuronal locus of voluntary saccade adaptation.

Third, the neuronal locus for reactive and for scanning saccade adaptation must contain eye position signals. Saccade-related eye position effects have been found at several stages in the oculomotor system: in the monkey in superior colliculus (Opstal et al., 1995; Paré and Munoz, 2001), the frontal and supplementary eye fields (Russo and Bruce, 1993) and in areas LIP and 7a (Andersen et al., 1990). Following the results of my thesis it is probable that the neural locus for scanning saccade adaptation contains a head-centered representation of targets or at least receive eye position signals.

Insights into the neural origin of saccade adaptation-induced changes in visual perception would allow a broader understanding of space perception in general.

6.5 General Conclusion

The results of my thesis demonstrate that modifications in the motor coordinates of saccadic eye movements produce homogeneous adjustments in the perception of visual space. Systematic post-saccadic visual errors between the intended and the actual saccade targeting lead to adaptive changes in saccade amplitudes as well as in localization. We therefore conclude that the same spatial representation which guides motor behavior also constitutes the perception of visual space.

6.6 Zusammenfassung

In meiner Dissertation habe ich untersucht, ob die räumliche Lokalisation visueller Objekte auf den motorischen Koordinaten der Sakkadengenerierung beruht. In drei Experiment-Reihen wurde mit psychophysischen Methoden untersucht, ob und inwieweit sich Modifikationen in den Sakkaden-Koordinaten auf die visuelle Lokalisation auswirken. Zur Modifikation der Sakkaden-Koordinaten wurde das Paradigma der Sakkaden-Adaptation eingesetzt. Durch Sakkaden-Adaptation kann eine bestimmte Sakkaden-Amplitude entweder vergrößert oder verringert werden. Die Lokalisation wurde getestet, indem kleine Balken präsentiert wurden, deren räumliche Position die Versuchsperson mit dem Mauszeiger angeben sollte. Die Lokalisationsaufgabe wurde jeweils einmal vor und einmal nach der Sakkadenadaptation durchgeführt. Die Experimente waren nach drei generellen Fragestellungen ausgerichtet. Die Ergebnisse der Experimente werden im Folgenden dargestellt.

Wie beeinflusst die Adaptation reaktiver und scanning Sakkaden die visuelle Wahrnehmung?

In Kapitel 3 wurden Experimente beschrieben, in denen der Einfluss der Adaptation verschiedener Sakkadentypen auf die Lokalisation untersucht wurde. Dabei wurden reaktive Sakkaden, die zu plötzlich erscheinenden Zielen ausgeführt werden, und scanning-Sakaden, die zu permanent sichtbaren Zielen ausgeführt werden, selektiv adaptiert. Bei diesen beiden Sakkadentypen besteht ein asymmetrischer Adaptationstransfer: Nach Adaptation reaktiver Sakkaden sind scanning Sakkaden kaum adaptiert, wohingegen sich nach Adaptation von scanning Sakkaden ein gewisser Betrag von Adaptation reaktiver Sakkaden zeigt. Der Einfluss der Adaptation dieser beiden Sakkadentypen wurde anhand von kurzzeitig präsentierten und stätionären Lokalisations-Stimuli untersucht. Kurzzeitig präsentierte Stimuli sollten dabei die Eigenschaften reaktiver Sakkadenziele imitieren. Die Stimuli wurden vor Beginn einer Sakkade präsentiert und verschwanden spätestens während der Ausführung der Sakkade. Nach der Adaptation von reaktiven Sakkaden wurden kurzzeitig präsentierte Stimuli fehllokalisiert, nicht jedoch stationäre Stimuli. Nach der Adaptation von scanning Sakkaden wurden beide Arten von Stimuli fehllokalisiert. Somit bewirkt die Adaptation im okulomotorischen System eine gleichartige Veränderung in der räumlichen Lokalisation. Dieses Ergebnis legt nahe, dass derjenige Pfad im okulomotorischen System, der Sakkaden zu kurzzeitig präsentierten Zielen generiert, ebenfalls die räumlichen Parameter für die Lokalisation kurzzeitig präsentierter Objekte bereitstellt. Der Pfad hingegen, in dem scanning Sakkaden generiert werden, trägt zur Lokalisation stationärer sowie kurzzeitig präsentierter Objekte bei.

Bewirken Modifikationen in den Sakkadenkoordinaten Veränderungen der visuellen Wahrnehmungen auch während Fixation?

In Kapitel 4 wurde eine Reihe von Experimenten dargestellt, die adaptationsbedingte Fehllokalisationseffekte während kontinuierlicher Fixation untersucht haben. Wenn die Modifikation der Sakkaden-Koordinaten durch Adaptation die Raumwahrnehmung beeinflusst, dann sollten Fehllokalisationseffekte auch bei unbewegtem Auge auftreten. Die Sakkaden-Adaptation wurde über einen langen Zeitraum (1000 Durchgänge) durchgeführt. Vor und während der Adaptation gab es Durchgänge, in denen kurzzeitig präsentierte Balken lokalisiert werden mussten. Diese Abfolge wurde in separaten Experimenten für Amplitudenverlängerung und Amplitudenverkürzung durchgeführt. Nach Amplitudenverlängerung gab es Fehllokalisation von der gleichen Größe wie die Adaptation. Nach Amplitudenverkürzung hingegen gab es keine Fehllokalisation. Die adaptive Amplitudenverlängerung ist langsamer und unvollständiger als die Amplitudenverkürzung. der post-sakkadische visuelle Fehler zwischen intendierter und tatsächlicher Augenlandeposition ist deswegen in der Amplitudenverlängerung größer. Um den Einfluss des visuellen Fehlers auf die Fehllokalisation direkt nachweisen zu können, wurde in zusätzlichen Experimenten eine Adaptationsmethode eingesetzt, bei der der Fehler zwischen der geplanten und der tatsächlichen Augenlandeposition in jedem einzelnen Durchgang konstant gehalten werden konnte. Dabei zeigte sich, dass die Größe der Fehllokalisation abhängig ist von der Größe des visuellen Fehlers. Daher konnte mit dieser Methode auch Fehllokalisation für Amplitudenverkürzung induziert werden.

In welchem Koordinatensystem sind die Sakkaden-Adaptation sowie die adaptations-induzierte Fehllokalisation kodiert?

Mit der dritten Reihe von Experimenten (Kapitel 5) wurde untersucht, inwieweit Sakkaden-Adaptation abhängig ist von der Position des Auges in der Orbita. Die Ergebnisse der ersten Studie hatten nahe gelegt, dass reaktive und scanning Sakkaden in unterschiedlichen Koordinatensystemen kodiert sein könnten. Wenn Sakkaden-Adaptation in einem rein retinalen Koordinatensystem kodiert wäre, müsste die Stärke der Adaptation unabhängig von der Position der Augen sein. In den Experimenten der dritten Studie zeigte sich jedoch ein deutlicher Effekt der Augenposition auf die Größe der Adaptation. Diese Ergebnisse widersprechen daher der allgemein akzeptierten Annahme, dass Sakkaden-Adaptation in einem rein retinalen Koordinaten-System kodiert sei. Unterschiede in der Abhängigkeit der Adaptationsstärke von der Augenposition zwischen reaktiven und scanning Sakkaden legen nahe, dass deren Adaptation zum Teil durch unterschiedliche Koordinatensysteme kodiert wird. Sakkaden-Adaptation wurde an einer fixen Bildschirmposition, dem Trainingsort, adaptiert. Nach Adaptation wurde an verschiedenen Bildschirmpositionen die Adaptationsstärke getestet. Da die Adaptationsstärke von scanning Sakkaden mit der Distanz zum Trainingsort abfiel, ist eine stärkere Beteiligung eines kopfzentrierten Koordinatensystems möglich. Die adaptive Sakkadenverlängerung beider Sakkadentypen beeinflusste die visuelle Lokalisation. Am Trainingsort war die Fehllokalisation vergleichbar zur Adaptationsstärke. Die Größe der Fehllokalisation war beeinflusst durch die Augenposition in ähnlicher Weise wie die Adaptation. Nach der Adaptation reaktiver Sakkaden variierte die Größe der Fehllokalisation an den verschiedenen Bildschirmpositionen ein wenig. Jedoch nach Adaptation von scanning Sakkaden stand die Größe der Fehllokalisation in direkter Abhängigkeit zur Entfernung vom Trainingsort. Sowohl für reaktive als auch für scanning Sakkaden war der Einfluss der Augenposition auf die Fehllokalisation vergleichbar zum Einfluss der Augenposition auf die Adaptation. Diese Ergebnisse zeigen, dass verschiedene Koordinatensysteme unterschiedlich stark an der Adaptation reaktiver und scanning Sakkaden beteiligt sind. Die Koordinaten von reaktiven und scanning Sakkaden tragen unterschiedlich zur Lokalisation visueller Objekte im Raum bei.

In meiner Dissertation habe ich gezeigt, dass Modifikationen in den Zielkoordinaten sakkadischer Augenbewegungen die visuelle Raumwahrnehmung beeinflussen. Systematische post-sakkadische visuelle Fehler zwischen der geplanten und der tatschlichen Sakkade bewirken adaptive Veränderungen in der Sakkadenamplitude sowie in visueller Lokalisation. Daraus lässt sich folgern, dass die räumliche Repräsentation der Augenbewegungskoordinaten ebenfalls die Wahrnehmung visuller Objekte im Raum ermöglicht.

List of abbreviations

API = Application programming interface

BBG = Brainstem burst generator

cMRF = central mesencephalic reticular formation

CRT = Cathode ray tube

FEF = Frontal eye field

LGN = Lateral geniculate nucleus

Open GL = Open Graphics Library

PEF = Parietal eye field

PPRF = paramedian pontine reticular formation

SC = Superior colliculus

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