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Psychophysical studies on the peri-saccadic perception of space, time, and object features

Psychophysische Studien zur peri-sakkadischen Wahrnehmung von Raum, Zeit und Objekteigenschaften

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DAS JAHR GEHT ZU ENDE

Wieder schwand ein Jahr —
und ich trage immer noch
Pilgerhut und -schuh.[1]

Matsuo Bashô (1643–1694)

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[1] Pilgerhut und -schuh: Das Menschenleben ist eine Pilgerschaft

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Part I

General introduction

Chapter 1

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1.1 Introduction

In humans, the visual sense is the most important sensory system for orientation and navigation in space. Humans are able to visually detect and identify potentially relevant items, and to gather information supporting social interaction, such as body postures and facial expressions. Consequently, the visual system is the most advanced sensory system.

Inconsistent with our intuition, perception—and visual perception in particular—is not just a passive accumulation of incoming information. It is a rather active and dynamic process, driven by intrinsic motivation and shaped by assumptions and expectations. Instead of being an objective and veridical reflection of the outside world, perception is highly subjective and creative. Therefore, perception is rather being *constructed* than reproduced by the visual system.

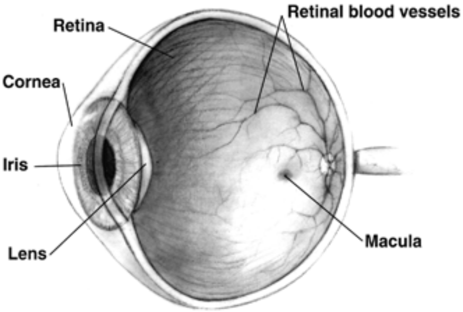

Figure 1.1: The human eye in cross-sectional view. The fovea, the region with the highest cone photoreceptor density, is located on the macula. Image courtesy of *NIH National Eye Institute*, USA.

Reception of visual information begins in the eye. After crossing the optic system of the eye, i. e. cornea, iris, lens, and vitreous body, light is detected by photoreceptors on the retina. See Figure 1.1 for an illustration of the human eye. There are two different types of photoreceptors: *rods* and *cones*. These photoreceptors are nonuniformly distributed across the retina. The cones are predominantly accumulated in a small pit named *fovea centralis*, or just fovea. Away from the fovea, cone receptor density declines sharply. There are three subtypes of cones, each being tuned to a certain wavelength of light, thereby providing the basis for color vision. Rods are more uniformly distributed across the retina, except that there are virtually no rods in the central area of the fovea, the so-called *foveola.* Rods have lower response thresholds compared to cones, thus responding better to less luminant light (e.g., see Kirschfeld, 1996). Moreover, rod photoreceptors do not respond differentially to light of different wavelengths. Thus, color vision is not possible in the periphery of the retina. Convergence between photoreceptors and ganglion cells is higher for rods compared to cones. Thus, sensitivity is increased at the expense of losing spatial resolution.

The retina is optimized in many respects. At the fovea photoreceptor density is optimal in terms of the optic properties of the eye. Here, spatial resolution is maximal. With increasing eccentricity *neural resolution* largely decreases, together with the *optical resolution* of the optic system, due to spheric and chromatic aberration (Frisen and Glansholm, 1975; Kirschfeld, 1996). A resolution as high as that implemented at the fovea would neither be possible nor necessary for the complete visual field. The particularly high receptor density at the fovea is only possible because of the fovea showing the form of a pit. A higher resolution in the periphery would cost additional resources. Moreover, it would also result in a dramatically increasing amount of information. This information would be in parts redundant or irrelevant with regard to the necessity to (re-)act.

As a consequence the gaze has to be frequently shifted in order to thoroughly explore the visual field. Thus, this exploration is—to some extent—sequential. By shifting the gaze, the image on the retina is correspondingly shifted and new parts of the visual scene are then projected onto the fovea. Eye movements are the most efficient way for shifting the gaze, due to their minimum effort as well as both their high velocity and accuracy. For large amplitudes eye movements are combined with head or body movements.

1.2 Eye movements

Six extra-ocular muscles (EOM) are sufficient for rotating the eyes along each of the three axes. These muscles are the *lateral*, *medial*, *inferior*, and *superior rectus*, and the *inferior* and *superior oblique* muscle. An illustration of these muscles in the orbit of one eye can be found in Figure 1.2.

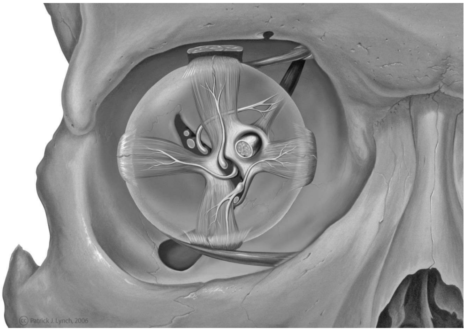

Figure 1.2: Anterior view of the eye and orbit anatomy with the extra-ocular muscles and motor nerves. Picture courtesy of Patrick J. Lynch, medical illustrator, and C. Carl Jaffe, MD.

There are different kinds of eye movements: *smooth pursuit*, *vergence movements*, the *optokinetic nystagmus* (OKN), the *vestibulo-ocular reflex* (VOR), *saccades*, and the so-called *fixational eye movements*. Fixational eye movements are only ostensibly a contradiction. They comprise *microsaccades*, *drift*, and muscle *tremor*. Although being subject to discussions, fixational eye movements prevent the image on the retina from being degraded due to habituation. For a review, see Fischer (1999). From these different kinds of eye movements, only saccades are of major relevancy for the experiments described in this thesis.

1.3 Saccadic eye movements

Saccades are used for sequentially sampling different locations in a visual scene. Due to the different photoreceptor systems described above, color vision, i. e. the extracting of wavelength information, is only possible at the fovea. Furthermore, spatial resolution decreases considerably with eccentricity. This effect is additionally strengthended by the so-called *cortical magnification factor*. The cortical magnification factor specifies the number of neurons in a visual brain area that are responsible for a stimulus of a certain size as a function of eccentricity. In early visual areas the fovea is considerably over-represented compared to peripheral locations (see Hoffmann and Wehrhahn, 1996). Due to these inhomogeneities, only the fovea has the properties necessary for providing the visual system with the desirable degree of detail, for instance, high spatial resolution, and the ability to process color information. Therefore, the gaze has to be moved rapidly to thoroughly analyze different locations in successions. This is illustrated in Figure 1.3. Note that visual information is gathered predominantly during fixations, not during the saccades.

Figure 1.3: Two successive fixations on a movie scene. Illustrated are the estimated effects of differential photoreceptor types and photoreceptor density, and of the convergence of visual information. At the fovea, spatial resolution is high and color vision is possible. Towards periphery color information is reduced together with spatial resolution. The distortion effect around the fovea symbolizes the cortical magnification factor. Stills from the motion picture *The Shining* (Kubrick, 1980).

In contrast to other types of eye movements, saccades are particularly fast, and large in amplitude. On average, saccades of several degrees of visual angle, most frequently less than 10 °, are conducted several times per second, typically about three to five. Unusually larger saccades, up to more than 50 ° of 60 ° are as well possible. The maximum velocity of saccades is about 600 °/s, depending on saccade amplitude, with higher maximum velocities for saccades with larger amplitudes. Saccade duration is typically around 25 ms for saccades of less than 10 °, and longer for larger saccades. Saccade duration is not direct proportional to its amplitude, since during larger saccades the eyes move faster (see Fischer, 1999).

Furthermore, saccades are so-called “ballistic” movements, indicating that saccades are completely planned previous to the start of the movement. During a saccade no changes or corrections of any kind, for example in direction and amplitude, are possible. Due to this saccade planning, there is a certain reaction time, referred to as *saccade latency*, necessary before motion onset. Saccade latency averages around 150 ms to 200 ms, depending on many internal and external factors. So-called *express saccades* might take only about 100 ms for preparation.

1.4 Brain areas involved in saccade generation

The optomotoric cycle, i. e. the alternation between fixation and saccades, is controlled by complex and multi-layer brain structures. In most stages of these control structures a clear differentiation between *afferent* sensory systems on the one hand, and *efferent* motor systems on the other hand is not possible.

Visual information from the retina is relayed in two pathways: directly to the *superior colliculus* (SC), and via the *lateral geniculate nucleus* (LGN) to the *primary visual cortex* (V1). The direct projections from the retina to SC are the shortest route for saccade generation. Visual information from V1 is processed in parallel *and* in hierarchical manner in many different visual areas. Generally speaking, there are two major pathways of visual processing, the *ventral* and the *dorsal stream.* The ventral stream projects towards the *inferior temporal cortex* (IT) and processes information on object features, such as color and shape. The dorsal stream projects towards the parietal cortex and predominantly processes information on motion and space. To assume a definite separation between these two pathways would be too simplistic, since areas of both pathways interact significantly (Hoffmann and Wehrhahn, 1996). For more information on the two visual pathways also see Chapter 7 on page 91.

The *frontal eye field* (FEF) in the frontal cortex is a key structure for programming voluntary—as opposed to reflexive—saccades. The FEF projects down to the SC, and to the *paramedian pontine reticular formation* and the *mesencephalic reticular formation* (PPRF and MRF, respectively) in the brain stem (Sommer and Tehovnik, 1997; Sommer and Wurtz, 2000), but there are also recursive projections from the SC to FEF (Sommer and Wurtz, 2000). Via the *caudate nucleus* and the *substantia nigra pars reticulata*, both being located in the basal ganglia, the FEF can affect the inhibition of saccade generation in the SC. Before and during saccades, this inhibition is intermitted (Hikosaka and Wurtz, 1983). Activity of the *supplementary eye field* (SEF) in the dorsomedial frontal cortex is also related to the maintenance of saccades. A different population of cells in SEF encodes eye position in the orbit (Schlag et al., 1992). The *lateral intraparietal area* (LIP) is involved in space representation, target selection and saccade planning, and the deployment of visual attention (see Colby and Goldberg, 1999, for a review). The activity of neurons in LIP is as well modulated by eye position (Bremmer et al., 1997).

The *superior colliculus* plays a central role in the generation of saccades. On one hand the SC receives direct visual input from the retina. On the other hand it receives input from the frontal cortex, the most important area being FEF, both direct and indirect via the caudate nucleus and the substantia nigra pars reticulata, as described above. The SC is organized in layers, the superficial layers receiving visual information, the intermediate, visuomotor layers receiving signals from FEF, SEF and the substantia nigra pars reticulata. In the rostral parts of the intermediate layers there are fixation cells that are active as long as fixation is maintained, independently of visual stimulation (Munoz and Wurtz, 1993b,a; Sumner et al., 2006). In the caudal parts, planned saccades are encoded in a retinotopic map (Wurtz and Optican, 1994; Munoz and Wurtz, 1995a,b; Munoz et al., 1996). Impending saccades are population-coded, potentially rather as the desired saccade vector than to a specific target (Mays and Sparks, 1980; Sparks, 1999). The deep layers are thought to implement premotor functions (see Fischer, 1999). The SC projects, amongst others, to *omnipause neurons* in the oculomotor brain stem and to the PPRF.

In the brain stem the PPRF and MRF generate the activation actually representing the horizontal and vertical component of an impending saccade. Activation has the form of a pulse/step combination, with the height of the pulse, and the height and duration of the pulse determining amplitude, speed, and duration of a saccade, respectively. The nuclei of the motor neurons innervating the extraocular muscles are also located in the brain stem. These are the *oculo-motor*, the *trochlear*, and the *abducens* nerve, corresponding to the cranial nerves III, IV, and IV.

A brain area that has not been mentioned yet is the *cerebellum*. The cerebellum is not directly involved in saccade generation but modifies the motor parameters of saccades. Being the most important structure for motor learning of different kinds, the cerebellum also adjusts saccades to maintain accuracy. The cerebellum receives input from the SC via the *nucleus reticularis tegmentis pontis* (NRTP) and projects to the oculomotor brain stem via the *fastigial nucleus* (see Dean et al., 1994). The cerebellum is particularly relevant for *saccadic adaptation* (Robinson and Fuchs, 2001; Robinson et al., 2002; also see Chapter 6 on page 53).

Chapter 2

Perceptual stability

Contents

2.1 Introduction

As described in the previous chapter, the gaze is frequently being shifted in order to explore the visual scene.

Due to the movement of the eyes, the retinal image after a saccade differs considerably from that previous to a saccade—for large saccades this difference in retinal image becomes dramatic. Unlike the film from a video camera being panned around, there is no impression of motion in visual perception across eye movements. Although the retinal image is shifted by a certain amount, the visual system does not interpret this image motion as the outside world being rotated with respect to the observer, i. e. relative to the position of the head or the body. Therefore, the movement of the eyes has to be taken into account. This ability of the visual system, to construct or maintain the percept of spatial relations remaining constant across eye movements, is referred to as *spatial stability* or *space constancy.*

During saccades the eyes move extremely fast, thereby inducing retinal motion with high velocity. This retinal motion is usually not noticed by humans. Moreover, in many cases even the eye movement itself remains unnoticed, since saccades are frequently elicited unconsciously. Albeit their high velocity, saccades require considerable time intervals for completion. However, these time intervals are also unnoticed, generating the impression of a continuous, uninterrupted stream of visual information. This percept is referred to as *temporal stability.*

2.2 Spatial stability

2.2.1 Coordinate systems

To construct a stable representation of spatial relations, a constant coordinate system is necessary. A coordinate system that is not affected by movements of the eyes or the body is referred to as being *world-centered.* A relatively stable coordinate system would allow for reliable orientation in our environment and for sophisticated interaction with objects from this environment. The image on the retina does not meet these requirements. The retinal image changes with every movement of the eyes. Taking account of the movements of the eyes results in a head-centered coordinate system. This head-centered coordinate system is yet affected by movements of the body. Only by additionally including the movements of all relevant body parts, a self-contained, internal, world-centered coordinate system could be generated and sustained. More different coordinate systems than the three mentioned above—retinal, head-centered, and world centered—are possible. Potentially, additional coordinate systems are implemented in the visual system (see Fischer, 1999).

Effectively, the visual system compensates for virtually all self-generated movements. Space constancy *is* actually maintained across eye movements. However, up to now it remains unknown in which brain structures and how these coordinate transformations are accomplished.

2.2.2 Maintaining spatial stability across saccades

Different theories have been proposed on how spatial stability is maintained across saccades. Among these theories, two fundamentally different groups can be differentiated, *cancellation theories* and *reference theories*. These are explained in the following.

Cancellation theories

Cancellation theories are among the first theories on spatial stability. They suggest the existence of a signal comprising the relevant information on the eye movement, and used by the visual system to compensate for all perceptual consequences of an eye movement. Theoretically, the displacement of the retinal image could be compensated by subtracting the vector of the corresponding saccade.

Proprioceptive information gained from the muscle spindles of the extra-ocular eye muscles suggests itself as a candidate for such a signal. Proprioceptive signals could carry sufficient information on saccade amplitude and direction. However, proprioceptive information could be gathered at the earliest during the actual movement. Together with subsequent processing stages, proprioceptive signals would be considerably delayed. As a consequence, proprioception does not fulfill the requirements for immediately compensating for all occurring eye movements.

A different source of information could be the plan for moving the eyes, i. e. a copy of the motor command sent to the oculomotor plant. This idea traces back to the *effort of will* ("Willensanstrengung") proposed by von Helmholtz (cited from von Holst and Mittelstaedt, 1950). Later, von Holst and Mittelstaedt (1950) and Sperry (1950) coined the terms *efference copy* ("Reafferenz") and *corollary discharge*, respectively. This efference copy would be available some time before the actual movement. A premise for these theories is the actual existence of an efference copy signal in the brain. For a long time this could not be verified. Recently, a signal thought to represent a corollary discharge was found in the thalamus (Sommer and Wurtz, 2006). Furthermore, in parietal area LIP neurons have been found that "update" their receptive fields immediately prior to a saccade (Duhamel et al., 1992; Colby et al., 1995; Heiser and Colby, 2006). Consistent results were derived from experiments using fMRI in humans (Merriam et al., 2003). Is is suggested that These receptive field shifts are thought to accomplish the *spatial updating*, analog to the coordinate transformations described in the previous Section 2.2.1 on page 12. But also see Bays and Husain (2007) and Bridgeman (2007) for different interpretations.

Reference theories

Reference theories comprise the *saccade target theory* (McConkie and Currie, 1996; Currie et al., 2000) and the *reference object theory* (Deubel et al., 1996, 1998, 2002; Deubel, 2004). Both theories emphasize the role of visual information, and post-saccadic visual references in particular. Pre-saccadically, a limited amount of visual information is stored from an area around the future saccade target. This information is used for a post-saccadic comparison, especially with respect to the spatial relations between the saccade target and nearby objects, so-called *landmarks*. This comparison relies on retinal rather than on extra-retinal information. If the pre-saccadically stored and the post-saccadically available information match to a certain degree, spatial stability is assumed.

Recently, Hamker et al. (2007) suggested a quantitative model combining both an oculomotor feedback signal, i. e. a corollary discharge, with outcomes of the saccade target theory. Therein, the corollary discharge, being directed to the location of the future saccade target, is supposed to cause the preferential processing of visual information at or around saccade target. Furthermore, this model predicts receptive field shifts as that found in area LIP (Sommer and Wurtz, 2006; also see Section 2.2.2 on page 13).

2.3 Temporal stability

As stated above, the retinal motion during saccades is usually not perceived. This is due to *peri-saccadic suppression*, an effect suppressing visual information processing around the time of saccades. This suppression selectively affects the processing along the *magnocellular pathway* (Burr et al., 1994). Input from the retina via the magnocellular pathway is further processed along the dorsal stream, and comprises predominantly motion and positional information (see Hoffmann and Wehrhahn, 1996). By selectively suppressing the magnocellular pathway, erroneous and potentially distracting image motion is eliminated.

Saccade execution requires a variable time interval, mainly depending on saccade amplitude. While small saccades of only a few degrees might take about 25 ms from on- to offset, larger saccades of, for example, 25 degrees may take 60–70 ms. These are temporal dimensions that are—under specific conditions—readily noticeable. However, neither the period of peri-saccadic suppression nor the actual period of the eye movement are consciously perceived. Instead, the subjective impression of a continuous and uninterrupted stream of visual information is retained—the temporal stability.

In contrast to spatial information, there are no sensory systems for the direct registration of elapsed time (for a review on the neural basis of interval timing see Buhusi and Meck, 2005). Yarrow et al. (2001, 2004a,b) found a specific overestimation of time intervals immediately following saccades. They proposed a general mechanism, referred to as *chronostasis*, compensating for the time interval during saccades. Following their line of arguments, the first visual percept subsequent to a saccade is "antedated" to a point in time immediately previous to the saccade, thereby cutting out the epoch around the eye movement.

Chapter 3

Objectives

Contents

3.1 Preface

The objectives of the individual experiments are extensively described in the corresponding introductory sections, together with the related background information. Thus, the general objectives are only briefly reviewed in the following.

3.2 The peri-saccadic perception of time

In Chapter 5 on page 29 ff we addressed humans' subjective perception of a stable and continuous visual world in the context of saccadic eye movements. Although visual perception is impaired by high image motion during saccades as well as actively suppressed in the time around saccades, humans do not perceive an interruption in the stream of subjective visual impressions. Investigating the peri-saccadic perception of time also alludes to the topic of relating voluntary actions to their perceptual consequences. It had been hypothesized that there are active mechanisms linking voluntary actions to their expected sensory consequences, thereby shortening the perceived time interval between these two events. A specific, compensatory mechanism was postulated for the case of saccadic eye movements. This mechanism was termed *chronostasis*. We aimed at improving the notion of this effect by demonstrating that chronostasis is not a global misperception of time, antedating a complete visual scene before entering awareness, but rather a potentially attention-driven effect, restricted to the region of the saccade target.

3.3 Perceptual consequences of saccadic adaptation

In Chapter 6 on page 53 ff we investigated a different aspect related to the perceptual consequences of voluntary actions. While we discussed the maintaining of *temporal* stability in the experiment described above, we here addressed the maintaining of *spatial* stability. Again, we used saccadic eye movements as an example for voluntary actions. To preserve spatial stability across saccades, an integration mechanism is necessary for converting retinal information gathered from successive fixations into one common, stable, and head- or body-centered reference system. Therefore, information on the saccade metrics are required. Saccadic adaptation is a mechanism proposed to adjust saccade amplitude in order to accurately reaching saccade targets. Under laboratory conditions it is possible to artificially induce a short-term saccadic adaptation. This short-term saccadic adaptation has consequences for the trans-saccadic integration of positional information. We aimed at characterizing these perceptual consequences of short-term saccadic adaptation, and at revealing the mechanisms underlying these perceptual effects.

3.4 The peri-saccadic representation of object features

For creating rather than maintaining the subjective impression of a stable, continuous world, not only spatio-temporal stability, as addressed in the aforementioned experiments, has to be achieved. Moreover, meaningful information, such as from object recognition, has to be integrated into a coherent whole. This information has to be maintained across saccades to preserve object identity. Or, alternatively, pre-saccadically gathered object information has to be linked to information post-saccadically available. Even for this linkage, limited information on object features and object identity has to be integrated across saccades. And indeed, certain different object features have been demonstrated to be peri-saccadically retained. We aimed at extending these findings by utilizing *motion* as an object feature that had not been investigated yet. In contrast to other object features, motion information is processed in areas along the so-called dorsal stream, which is known to be heavily affected by peri-saccadic perceptual effects.

3.5 Affective saccade targets

In the last series of experiments, described in Chapter 8 on page 119 ff of this thesis, we conducted an exploratory study investigating the potential impact of emotionally relevant pictures on saccade planning and execution, and on peri-saccadic localization. Thereby, the involvement of spatial attention constitutes the common thread between emotional pictures, saccade planning and execution, and peri-saccadic localization. Potential emotional stimuli attract attention with the utmost probability. Saccade target selection and saccade planning also necessitate the pre-saccadic shift of spatial attention to the intended saccade target. Moreover, abrupt stimulus onsets, such as briefly presented localization stimuli, also attract spatial attention. In our experiments the emotional pictures at the same time constituted saccade targets. Around the time of the saccade towards these pictures, subjects were instructed to solve a localization task. We aimed at recording a variety of motor and perceptual parameters, being subject to the emotional content of the target pictures.

Part II

Experimental section

Chapter 4

General methodology

Contents

4.1 Eye movement recording

The *EyeLink* systems (*SR Research, Inc.*, Canada) used in our experiments described below are video-based eye tracking systems. The eye tracking system consists of three high-speed, infrared (IR) cameras mounted to a headband. Two of these cameras keep track of one eye each, the third camera tracks four IR markers attached to the corners of the monitor screen. By this means the movements of the eyes relative to the headband and the movement of the head relative to the monitor are recorded. Each of the eye tracking cameras has two built-in IR light-emitting diodes (LED), illuminating the eyes with light in an almost invisible spectrum. The *EyeLink II* is pictured in Figure 4.1.

Figure 4.1: The *EyeLink II* system with headband and two eye cameras. The third camera is integrated in the forehead part. Courtesy of *SR Research, Inc.*, Canada.

Before each experimental session the system was calibrated. Therefore, subjects consecutively fixated nine targets, arranged on a 3×3 grid on the monitor and presented one after another in random order. Calibration was subsequently validated by fixating the same monitor positions. During calibration and validation the *EyeLink* system selects the subject's dominant eye for calculating gaze position. During normal viewing in only one depth plane—the monitor screen in our experiments—, no vergence movements are necessary. Hence, eye movements are usually conjugated under such conditions, and gaze position of both eyes is nearly identical.

Gaze position is sampled with high frequency. Individual samples are stored as well as analyzed on-line. Eye movement events (saccades, fixations, blinks) are automatically inferred from sample data. The on-line parser detects saccade onsets when eye velocity and eye acceleration crossed thresholds of 22 °/s and 4000 $°/s^2$, respectively. Eye movement events were also stored to a data file.

4.1.1 EyeLink I

The *EyeLink I* system samples eye position at a frequency of 250 Hz, corresponding to one measurement every 4 ms. Pupil detection is used to infer gaze position. In our experiments, only one camera was functional, i. e., always the position of the left eye was tracked, irrespective of eye dominance. In theory, the *EyeLink I* system achieves a spatial resolution of less than 0.01 °, velocity noise of less than 3 °/s, and average gaze position accuracy of less than 0.5 °, as given in the manufacturer's technical specifications. In praxis, performance might be impaired by suboptimal calibration and validation procedure, head movements, vibrations, or headband slippage.

4.1.2 EyeLink II

The *EyeLink II* system is able to sample eye position at a frequency of up to 500 Hz, corresponding to one measurement every 2 ms. It can use pupil detection as well as a measurement of corneal reflection to interpolate and extrapolate gaze position. Using both algorithms, pupil detection and corneal reflection, increases spatial acuity but reduces sampling rate to 250 Hz. In our experiments only pupil detection was employed, resulting in the higher temporal resolution of 500 Hz at the potential expense of loosing some spatial acuity. The technical specifications of accuracy and noise levels are identical to those of the *EyeLink I* system, except for the higher sample rate.

4.2 Computer monitors

Two different cathode-ray tube (CRT) monitors were used in the experiments described below.

iiyama Vision Master Pro 450

The *iiyama Vision Master Pro 450* has a 19" CRT with a visible screen size of 18" (45.5 cm). Maximum vertical frequency was 144 Hz at a resolution of 800 × 600 pixels. This monitor was used in experiments described in Chapter 5 on page 29.

iiyama Vision Master Pro 514

The *iiyama Vision Master Pro 514* is a 22" monitor with a visible screen size of 20" (50.8 cm). Maximum vertical frequency was 200 Hz at a resolution of 800 × 600 pixels, used in experiments described in Chapter 6 on page 53 and Chapter 7 on page 91. At a resolutions of 1280 × 1024, used in the experiments described in Chapter 8 on page 119, maximum vertical frequency was 120 Hz.

4.3 Software

4.3.1 Stimulus presentation

Different combinations of custom-made computer programs and open-source software libraries allowed for high-performance stimulus presentation and control of the experimental procedure.

For the *EyeLink I* system, used in experiments described in Chapter 5 on page 29, basic software was provided by the manufacturer.

Experiments were written in C using an older version of *Microsoft Visual Studio*, an integrated development environment (IDE), running under Windows 95. Experimental programs linked *Simple DirectMedia Layer* (SDL), an open-source software library written in C, for governing monitor presentation.

In the experiments described in Chapter 6 on page 53 the *EyeLink II* system was used. Experimental programs were written in C++ using the *Xcode* (Version 2.4.1) IDE running under Mac OS X. Software packages provided by *SR Research, Inc.*, were adapted. The experimental programs also linked SDL for controlling monitor presentation.

Experiments described in Chapter 7 on page 91 and in Chapter 8 on page 119 were also conducted with the *EyeLink II* system. Experimental programs were written in C++ and Objective-C, using the *Xcode* IDE and involving the *CoCoA* application programming interface (API), both running under Mac OS X. These experimental programs were not based on provided software but were rather in-house applications. They linked OpenGL (Open Graphics Library) instead of SDL to govern monitor presentation.

4.3.2 Data analysis

Data analysis was carried out with *Mathematica*, Versions 5.2 and 6.0 (*Wolfram Research, Inc.*). All programs for the reading in of data files, analyzing of results and calculating of statistical analyses were self-programmed.

Standard statistical analyses were applied, including parametric (t-test, standard ANOVA), and non-parametric tests (Fisher's randomization test, Friedman test, Kruskal-Wallis/H-test, and the Wilcoxon-Wilcox test).

4.4 Subjects

A total of 30 subjects, including the author, performed the experiments described in this thesis. Their age ranged from 20 to 38 years. Most of them were either students or employees at the Department of Psychology at the University of Münster, and most were female. All of them gave informed consent. The experiments have been carried out along the principles laid down in the Declaration of Helsinki (2004 edition). All subjects had normal or corrected-to-normal vision.

Chapter 5

Peri-saccadic perception of time

Contents

5.1 Abstract

Visual perception is being suppressed during fast, saccadic eye movements. This saccadic suppression prevents erroneous and distracting motion percepts resulting from saccade induced retinal slip. Although saccadic suppression occurs over a substantial time interval around the saccade, there is no “perceptual gap” during saccades. The mechanisms underlying this temporal perceptual filling-in are unknown. When subjects are asked to perform temporal interval judgments of stimuli presented at the time of saccades, the time interval following the termination of the saccade appears longer than subsequent intervals of identical length. This illusion is known as “chronostasis”, because a clock presented at the saccade target seemingly stops for a moment. Two series of experiments dedicated to this effect are described in this chapter. In the first, we test whether chronostasis is a global mechanism that may compensate for the temporal gap associated with saccadic suppression. We show that a clock positioned halfway between the initial fixation point and the saccade target does not exhibit prolongation of the interval following the saccade. The characteristical distortion of temporal perception occurred only in the case of a clock being located at the saccade target. In the second experiment, aiming at specifying the location-dependence of the observed effect in more detail, we use additional clock positions spread across the horizontal axis. Although the results of the second experiment remain ambiguous to some extent, the results suggest a local, object-specific mechanism underlying the stopped clock illusion that might originate from a shift in attention immediately preceding the eye movement.

5.2 Introduction

From their personal experience, many people are familiar with the so called “stopped clock” illusion. Observing a clock with a silently moving second hand, the second hand sometimes seems to take longer than just one second to move immediately after a saccade, depending on the timing of the eye movement relative to the second hand movement. The mechanisms underlying the perception of time are largely unknown (Buhusi and Meck, 2005). A number of substantially different models of time perception have been proposed, ranging from a central internal clock to sensory timing (Allan, 1979; Mauk and Buonomano, 2004). Among several different illusions relating to perception of time (Rose and Summers, 1995), the “stopped clock” phenomenon is one that relates to eye movements. No time misjudgement is observed when the eyes rest on the clock. Time misjudgements may occur while fixating, but they are different from the “stopped clock” illusion (Rose and Summers, 1995; Tse et al., 2004).

The proposed mechanism underlying the “stopped clock” illusion has been named *chronostasis* (Yarrow et al., 2001). It implies a process of active antedating or redrafting of post-saccadic perceptual impressions in order to bridge the “perceptual gap” (Yarrow et al., 2006) that is supposed to emerge from the peri-saccadic suppression (Burr et al., 1994). By the way, this notion fits in the theory of Libet (2005), who argues that conscious perception lags physical events by about 400 ms. Such a delay between subjective and objective timing would theoretically render possible an antedating process like that claimed for chronostasis. Chronostasis has been reported across different types of saccades (Yarrow et al., 2004b) and across a series of different stimulus durations (Yarrow et al., 2004a). Moreover, chronostasis-like phenomena can also be observed with other voluntary actions and sensory modalities such as key presses and voice commands (Park et al., 2003), voluntary arm movements and tactile stimuli (Yarrow and Rothwell, 2003), and manual responses and auditory stimuli (Hodinott-Hill et al., 2002). In all these cases, the temporal intervals are defined at least partly by voluntary actions or their sensory consequences. Thus, saccades may cause a distortion in time perception in a similar manner to other voluntary actions.

One may speculate that the perceived duration of these temporal intervals relate to shifts of attention associated with the action. Although several studies trying to rule out spatial attention as a possible mechanism underlying chronostasis, preferring arousal instead, these studies only cover the auditory modality (Hodinott-Hill et al., 2002; Alexander et al., 2005). However, the auditory system differs from the visual system amongst other things by different magnitudes in spatial and temporal resolution, what might be of particular relevance, since relatively small spatial and temporal differences are investigated in these experiments. A general linkage between voluntary actions and the perceived timing of their sensory consequences might attract the two events so that they appear closer together in time (Haggard et al., 2002), although there are also explanations for distortions of perceived timing that are independent of motor acts (Hodinott-Hill et al., 2002; Alexander et al., 2005).

The objective of our first experiment was to test the hypothesis of a global mechanism underlying the distortion of perceived timing in the original chronostasis experiment. Yarrow et al. (2001) proposed that chronostasis arises from a mechanism that compensates for the perceptually suppressed epoch during saccadic suppression. For this purpose, this mechanism should be global in a sense that it affects the complete visual field, image motion being suppressed not only in the center but also in the periphery (Ross et al., 2001a). This notion has recently been challenged by Ross et al. (2007), providing evidence that the timing of brief visual events is achieved by neural structures with spatially limited receptive fields. Thus, the authors argue against a global, centralized, and multi-modal clock. However, their experiment involved the adaptation to moving gratings at different positions during fixation and were therefore, amongst others, difficult to compare to the chronostasis experiments.

In our second experiment, after falsifying the hypothesis of chronostasis being a global mechanism, we aimed at specifying its spatial extent in more detail. Therefore, the counter stimulus constituting the temporal intervals for the discrimination task was presented at various positions relative to saccade target.

5.3 Methods

5.3.1 Experiment 1: Spatial restrictiveness of saccade-induced chronostasis

Experiment 1 compares three different conditions of temporal duration judgements. Firstly, a fixation control condition in which a clock moved at saccadic speed towards the fixation point. Secondly, the original chronostasis condition in which a saccade was made towards the clock. These two conditions served as baseline for the third condition, the very condition we wanted to test. This third condition tested whether chronostasis is a global effect. Instead of presenting the clock at the saccade target, we presented it halfway between the fixation point and the saccade target.

Subjects

Six subjects, four of them naïve to the aims of the experiment, and one an author, performed the experiment. All of them gave informed consent.

Apparatus

The *EyeLink I* system (*SR Research, Inc.*, Canada) was used, sampling eye position at a frequency of 250 Hz. For more information see Section 4.1 on page 24.

The visible size of the used monitor, an *iiyama Vision Master Pro 450*, was 36.5 × 27.3 cm, with a resolution of 800 × 600 pixel, running with a vertical frequency of 144 Hz (for more details see Section 4.2 on page 26).

Data analysis

During the trials, eye position was continuously monitored. Trials in which the gaze position deviated from the fixation point more than 2 ° between the presentation of the tone and the beginning of the forth time interval were discarded. For analysis, we correlated the responses of each subject ("First interval shorter" or "First interval longer") to the difference in duration between *test* stimulus (the '1') and *reference* stimuli (subsequent digits). The durations of the test stimuli were uniformly distributed over the variation range. Hence, the data was binned regarding the presentation duration of the test stimulus. For each bin the proportion of trials in which the first interval appeared shorter was calculated. A cumulative gaussian curve was fitted to the data, the *point of subjective equality* (PSE) was evaluated by determining the duration at the interpolated 50 % value percentage of the curve.

Experimental conditions

No eye movement As outlined above, the first condition served as a baseline for temporal interval judgement in the absence of a saccade. Subjects fixated a small disc (diameter 1 ° visual angle), 8° to the left of the center of the screen, throughout the trial. The clock was presented 16 ° to the right of the fixation point, and initially consisted of a counter displaying the digit '0', presented in about the same size as the fixation target. This counter moved with saccadic speed (about 330 °/s, estimated from data of pilot experiments) towards the fixation point. A tone alerted the subjects to the impending movement of the clock stimulus. The stimulus movement began between 200 ms and 300 ms after the tone. When the counter reached the fixation point, it switched to '1' and subsequently incremented up to '4'. The '1' was visible for a random interval of 400 to 1600 ms, the subsequent digits for 1000 ms each without an inter-stimulus interval. After the last digit was displayed, the subject indicated whether the first interval appeared to be shorter or longer than the subsequent ones in a two-alternative forced-choice (2AFC). An experimental block comprised 100 trials. A simplified illustration of the screen presentation and experimental procedure in a single trial is depicted in Figure 5.1 on the next page.

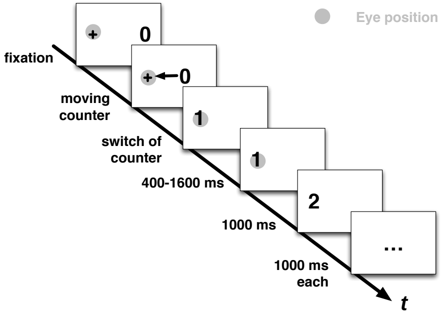

Figure 5.1: Diagram of the screen presentations in the condition with no eye movement. In the beginning the subject fixates the fixation point and the counter at 16 ° to the right shows a ‘0’. 200 to 300 ms after a tone occurs, the counter moves to the fixation point with saccadic speed (about 330 °/s). When reaching the fixation point, the counter changes to ‘1’. The ‘1’ is visible for about 400 to 1600 ms, then the counter increments up to ‘4’, every subsequent digit visible for 1000 ms with no inter-stimulus interval. After complete stimulus presentation a response screen containing two dots is displayed.

Counter at saccade target In the two remaining conditions, subjects in addition to fixating the fixation point at the beginning of each trial, had to make a saccade to the target. In the original chronostasis condition, the counter was again visible 16 ° to the right of the fixation mark and initially consisted of the digit ‘0’. The counter also served as the saccade target. An acoustic cue signaled the beginning of a trial. The subject was free to conduct a voluntary saccade to the target anytime after the tone. Eye position was tracked online. Shortly (about 6 to 14 ms) after the eyes passed the horizontal center of the screen, the counter switched to ‘1’. This switch occurred approximately two-thirds through the saccade duration and varied slightly from trial to trial, whereby the ‘1’ then was visible for a random interval of about 300 to 1700 ms from the time the eyes landed, estimated *a priori*, from the average latency of the eye tracking system, monitor refresh rate, and typical saccade duration. After the '1' had disappeared, the counter progressed consecutively to '4', with each digit being visible for 1000 ms without an inter-stimulus interval. Due to saccadic suppression (Ross et al., 2001a), it is unlikely that the counter change could be noticed by the subject during the saccade. We confirmed suppression in a separate control experiment described below. For a trial to be included in the data anaylsis, the post-saccadic eye position had to be within 5 ° from the saccade target, the counter switch had to be completed during the eye movement and fixation had to be maintained throughout the *reference* intervals. On average, 135 valid trials per subject and condition were included in this experiment. Since the number of accepted trials varied highly across subjects and experimental blocks, subjects did between two and six blocks each. A simplified illustration of the screen presentation and experimental procedure in this condition is depicted in Figure 5.2.

Counter between fixation point and saccade target In the third condition, we presented the same stimuli and procedure as in the original chronostasis condition but the counter was located halfway between the fixation point (8 ° left) and the saccade target (8 ° right, same appearance as the fixation point). The counter initially showed a '0'. The subject had to execute a voluntary saccade from the initial fixation point to the target. As in the previous condition, the counter switched to '1' when the eyes moved about two thirds of the distance and subsequently incremented up to '4'. The '1' was visible for about 300 to 1700 ms, the subsequent digits for 1000 ms each. Timing and accuracy of eye movements were controlled offline. An illustration of the screen presentation and experimental procedure in this condition is depicted in Figure 5.3.

Control experiment Saccadic suppression had to be confirmed for our experimental conditions. Therefore, two of the six subjects

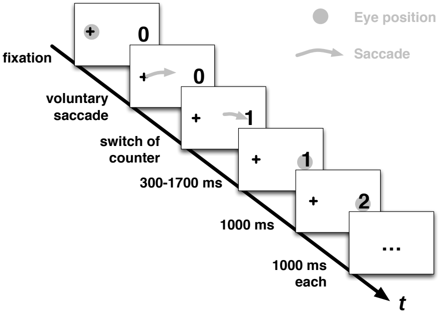

Figure 5.2: Diagram of the screen presentations in the saccade condition with the counter at saccade target. In the beginning the subject fixates the fixation point and the counter at the saccade target shows a ‘0’. After a tone occurs, the subject is free to saccade to the counter (amplitude 16 °) when ready. While the eyes are moving, the counter changes to ‘1’. The ‘1’ is visible for about 300 to 1700 ms from the time the eyes are landing, then the counter increments up to ‘4’, every subsequent digit visible for 1000 ms with no inter-stimulus interval. After complete stimulus presentation a response screen containing two dots is displayed.

participated in an additional suppression experiment. They had to detect a short, intra-saccadic counter switch. The experimental setup resembled very much the saccade condition with the counter at saccade target. The counter initially showed a ‘0’, but switched to a ‘1’ in 50 % of the trials (pseudo-randomized) during the saccade. After one monitor frame (7 ms), it switched back to ‘0’. When the eyes were landing, a ’0’ was visible in every trial. The subjects were asked to indicate if they had noticed a counter switch during the saccade in a two-alternative forced-choice (2AFC).

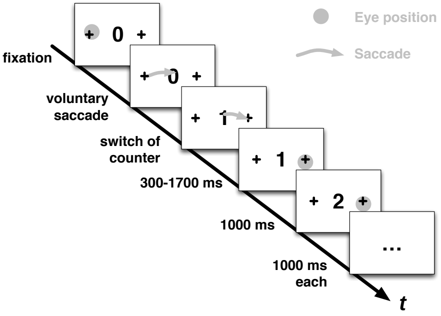

Figure 5.3: Diagram of the screen presentations in the saccade condition with the counter intermediate between fixation point and saccade target. In the beginning the subject fixates the fixation point and the counter shows a '0'. After a tone occurs, the subject is free to saccade to the saccade target (amplitude 16 °) when ready. In all other respects this condition resembles the condition with the counter at saccade target (see Figure 5.2).

5.3.2 Experiment 2: Estimating the spatial extent of saccade-induced chronostasis

After finding spacial constraints of the perceived distortion of subjective timing in Experiment 1, the objective of Experiment 2 was to broaden the findings of by characterizing its spatial distribution in more detail. Assuming that the shift of spatial attention to the future saccade target immediately before a saccade is the mechanisms underlying chronostasis allows for several predictions. Firstly, the perceived duration of events presented after a saccade should prove to be correlated—at least to some extent—to the time course of the shift of spatial attention before the respective saccade. Secondly, the spatial extent of the focus of attention should confine the spatial extent of the chronostasis effect to some region, presumably centered at or around saccade target. The first prediction has not been tested directly, but is consistent with chronostasis effects being largely independent of saccade size, saccade duration (Yarrow et al., 2001), saccade type (Yarrow et al., 2004b), and stimulus duration (Yarrow et al., 2004a). Experiment 1 already gave evidence corroborating the second prediction of chronostasis being spatially confined. Experiment 2 further tests this prediction and aimed at specifying these spatial confinements. Experiment 2 was conducted in only one condition but with several stimulus positions spread along the horizontal axis, randomly intermixed independently in every trial.

Subjects

Five subjects participated in this experiment, four of them naïve to the specific aims of this experiment, and one an author. Three of them previously participated in Experiment 1.

Apparatus

The apparatus, i. e. eye tracking system and stimulus presentation monitor, was the same as in Experiment 1 (see Section 5.3.1 on page 33).

Procedure

Stimulus presentation resembles Experiment 1, except that in Experiment 2 a square probe stimulus, alternately being filled and empty, served as a counter. Furthermore, the duration of the *reference* stimuli was only 500 ms, the duration of the *test* stimuli being adjusted accordingly. Initially, subjects fixated a small cross of 0.7 ° width, located 10 ° to the left of the center of the screen. Additionally, the saccade target—of the same appearance as fixation mark but located 20 ° to the right of that—, and the counter—initially an empty square of 2.6 ° side length—were already visible on the screen. An acoustic cue signaled the beginning of each trial. The subject was free to conduct a voluntary saccade to the target anytime after the tone. Eye position was tracked online. About two-thirds through the saccade duration the counter became a filled square. The filled square was then visible for a random interval of about 100 to 900 ms from the time the eyes landed, and representing the *test* interval. After this time, the counter started alternating between being empty and being full three more times at regular intervals of 500 ms, the *reference* intervals. 500 ms after the last alternation, a mouse pointer appeared. Subjects indicated on a response screen whether the *test* interval appeared to be shorter or longer than the subsequent *reference* intervals in a two-alternative forced-choice. An experimental block comprised 100 trials. In each trial, the position of the counter was pseudo-randomly chosen from one of seven possible positions, 0 °, 10 °, 15 °, 17.5 °, 20 °, 22.5 or 25 ° to the right of the fixation mark. In the case of the counter being located at 0 °, the empty square en-framed the fixation mark, the full square hence occluding it. In the case of the counter being located at 20 °, the same was true for the saccade target instead.

For a simplified illustration of the screen presentation and experimental procedure in a single trial see Figure 5.4.

Data analysis

Data analysis was similar to that in the Experiment 1 (Section 5.3.1). For a trial to be included in the data analysis, the counter switch had to be completed during the eye movement and fixation had to be maintained throughout the *reference* intervals. Single trials were discarded if the post-saccadic eye position deviated more than 1.25 ° from the saccade target in any direction. This is more strict than in Experiment 1, since the minimum distance between adjacent counter positions around saccade target was only 2.5 °. Subjects did between four and 22 blocks each. For analysis, we correlated the responses of each subject ("First interval shorter" or "First interval longer") to the difference in duration between *test* interval and *reference* intervals. Data were binned regarding the presentation duration of the test stimulus. For each bin the proportion of trials in which the first interval appeared shorter was calculated. A cumulative gaussian

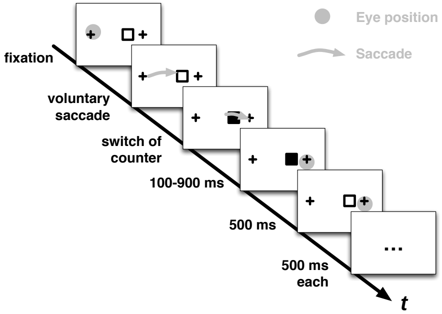

Figure 5.4: Diagram of the screen presentations for one probe position. In the beginning the subject fixates the fixation point, saccade target and probe stimulus already being visible. The probe, initially an empty rectangle, is located at a randomly chosen position 0 ° (i. e., fixation point), 10 °, 15 °, 17.5 °, 20 ° (i. e., saccade target), 22.5 °, or 25 ° to the right. After a tone occurs, the subject is free to saccade to the saccade target (amplitude 20 °). While the eyes are moving, the probe stimulus becomes a filled rectangle and remains unchanged for about 100 to 900 ms from the time the eyes are landing. After this, the counter alternates three times between being empty and filled, every subsequent state lasting 500 ms with no inter-stimulus interval. After complete stimulus presentation a response screen containing two dots is displayed.

curve was fitted to the data, the PSE was evaluated by determining the duration at the interpolated 50 % value percentage of the curve.

5.4 Results

5.4.1 Spatial restrictiveness of saccade-induced chronostasis

No eye movement The results of the baseline condition are shown in the first column (dark gray) of Figure 5.5 on the following page. There was a minor overestimation (median 75 ms) of the first interval if compared to the veridical duration. Thus, the *point of subjective* *equality* (PSE) was reached when the first interval was presented for 925 ms. This agrees in principle with results of Rose and Summers (1995), who found an overestimation of the first stimulus in a sequential train of identical stimuli, although their effect was more pronounced.

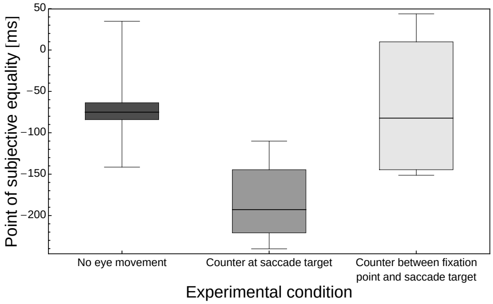

Figure 5.5: Results of the three experimental conditions. Dark grey the baseline condition with the moving counter and no eye movement; medium grey the saccade condition with the counter as saccade target; light grey the saccade condition with the counter halfway between the fixation point and the saccade target. Data consists of the 6 subjects that participated in all three conditions. Box-Whisker-Plots show median, quartiles and variation range. The median in the saccade condition with the counter at saccade target is significantly ($\alpha = 5\,\%$) lower than in the other two conditions. There is no significant difference between the results of the baseline condition and the saccade condition with the intermediate counter position.

Counter at saccade target The result of the original chronostasis condition with the counter at saccade target is shown in the second column (medium grey) of Figure 5.5. Consistent with earlier reports (Yarrow et al., 2001), there was a distinct overestimation of the time interval immediately following the saccade, the median of this overestimation being 193 ms. Thus, the interpolated PSE is reached when the first interval following the saccade lasts for 807 ms. This value must be compared to the baseline condition, because there are already misestimations of time intervals during steady fixation. The difference between the median PSE in the saccade condition and in the baseline condition—the value that is referred to as chronostasis—is 118 ms and differs significantly from zero ($\alpha = 5\,\%$), tested with *Fisher's randomization test*. The value is within the range of the results of earlier experiments (Yarrow et al., 2001, 2004a,b).

Counter between fixation point and saccade target The results of the experimental condition with the counter halfway between fixation and target are shown in the third column (light grey) of Figure 5.5. The median overestimation of the first interval was 82 ms, the corresponding PSE was 918 ms. This value was not significantly different from the baseline condition with no eye movement, but was significantly different from the original chronostasis condition with the counter at the saccade target ($\alpha = 5\,\%$ with *Fisher's randomization test*).

Control experiment Mean detection rate of the intra-saccadic counter switch for the two subjects was 9.7 % (6.4 % and 13.0 %, respectively), the mean false alarm rate was 2.8 % (1.9 % and 3.7 %), sensitivity indices d' for the two subjects resulted in 0.66 and 0.55, respectively. We thus conclude that the intra-saccadic counter switch is not noticed in the vast majority of trials. Consequently, detecting the veridical time of the intra-saccadic counter switch could not explain our results from the two saccade conditions with the counter at saccade target and the counter between fixation point and saccade target.

5.4.2 Estimating the spatial extent of saccade-induced chronostasis

The results for all five subjects that participated in Experiment 2 are shown in Figure 5.6 on the next page. For all seven counter positions, the individual PSEs are pictured. Gray lines represent individual results, the black line represents the median and interquartile deviation across subjects. Negative values indicate an overestimation of the *test* interval compared to the *reference* intervals.

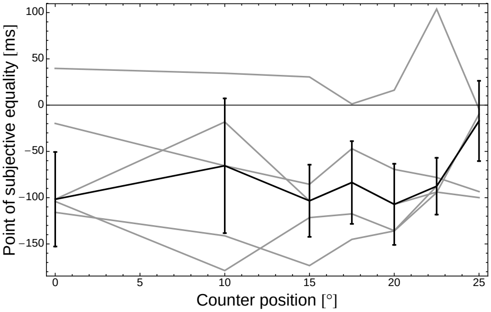

Figure 5.6: Spatial dependence of saccade-induced chronostasis. Fixation point is at 0 °, saccade target at 20 °. Gray lines represent the results of the individual subjects. The black line represents the median across subjects, error bars indicate quartile deviation. The Friedman test reveals significant differences for counter position ($p < .01$). The median PSE for the counter at 25 ° differs significantly from the medians for all other counter positions; median PSE for 22.5 ° significantly differs from that for 15 ° and 20 ° (Wilcoxon-Wilcox test, $\alpha = 5\,\%$). All other differences do not reach significance.

The data show a very high inter-subject as well as intra-subject variability that hinders interpretation. This might in some respect be similar to Experiment 1, where a variation range of about 200 ms nevertheless resulted in significant differences, because all subjects—no matter what there amount of chronostasis was in the condition without eye movements—showed the same dependence on experimental condition, with a more negative PSE in the condition with the counter at saccade target than in both other conditions. Here the data is less uniform. While some subjects show a decline in PSE in the range between 15 ° and 22.5 °, others do not and show more irregular behavior. What could be expected from Experiment 1 was a decline in PSE at or around the saccade target at 20 °—that is, an overestimation of stimuli presented at the corresponding location. Analysis of variance (ANOVA) was used to assess potential systematic differences between counter positions. The non-parametric Friedman test was applied since normal distribution could not be assumed. While the Friedman test revealed a significant effect of counter position, subsequently calculated multiple comparisons with the Wilcoxon-Wilcox test did not give a uniform picture. Only the median at counter position 22.5 ° differed significantly ($\alpha = 5\%$) from the medians at 15 ° and 20 °. No other differences reached significance.

Misjudgment at the counter position of 0 °, i. e. the fixation point, differed largely across subjects. This might be—at least to some extent—due to different intra-individual internal criteria in different subjects. In other words, subjects might be differentially biased, resulting in largely unequal baseline performance in temporal interval judgments as required here. Unlike Experiment 1, there is no condition with steady fixation in Experiment 2 that allowed to assess the proportion of this bias that is independent of eye movements. To reduce inter-subject variability, the results of Experiment 2 were re-evaluated. Data of single subjects were standardized by subtracting the PSE at the fixation point (counter location 0 °) from the PSE at all other positions. Figure 5.7 on the following page shows the re-evaluated results. Again, gray lines represent individual data, the black line and error bars represent the median and quartile deviation, respectively.

ANOVA revealed a significant effect of counter position on PSE (Friedman test, $\alpha = 5\%$). Subsequently calculated Wilcoxon-Wilcox tests proved significant differences between the median PSEs at 10 °, 15 °, 17.5 °, and 20 °, and the medians at all other positions (0 °, 22.5 °, 25 °). No other differences reached significance.

Results differ in many aspects from the results of Experiment 1. Firstly, and most important, chronostasis is clearly smaller in Experiment 2 than in Experiment 1. While in Experiment 1 overestimation

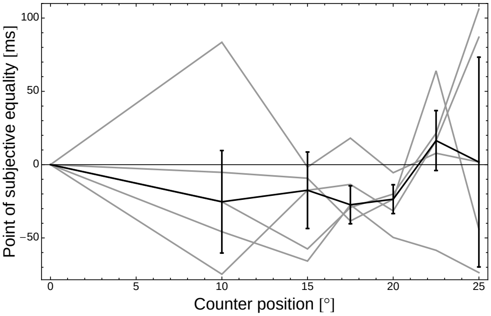

Figure 5.7: Re-plotted data from Figure 5.6 on page 44 after standardization of each individual subject's data to its corresponding PSE with the counter at the fixation point. Fixation point is at 0 °, saccade target at 20 °. Gray lines represent the results of the individual subjects. The black line represents the median across subjects, error bars indicate quartile deviation. The median PSEs for the counter positions 10 °, 15 °, 17.5 °, and 20 ° (i.e., saccade target) all differ significantly from the medians for all other positions (Wilcoxon-Wilcox test, $\alpha = 1\,\%$). All other differences do not reach significance.

of the first interval after a saccade averages at about 200 ms in total—about 100 ms if compared to baseline condition—overestimation is only about 50 ms in Experiment 2. There is no applicable baseline condition in Experiment 2, but compared to the counter position at the fixation point, overestimation is only about 50 ms. From results of previous studies (Yarrow et al., 2001, 2004a), we expected a similar amount of chronostasis in both of our experiments, independent of saccade type and stimulus duration. Moreover, in Experiment 1 there was a significant difference between the amount of chronostasis at the saccade target and at a position halfway between saccade target and fixation point. This difference does not become apparent in Experiment 2. Instead, there is a significant difference between counter positions from 10 ° to 20 ° and all other counter positions, i. e. the fixation point, and positions more eccentric than the saccade target.

Different sources of this differences between Experiment 1 and

Experiment 2 are possible. Potentially, counter positions were too eccentric in Experiment 2. With higher eccentricities, the counter becomes increasingly difficult to recognize. A counter-argument would be that variability does not increase with eccentricity (see Fig. 5.6). Eccentricity does not inherently influence chronostasis (Yarrow et al., 2001). Furthermore, the counter switch could have been theoretically been noticed in Experiment 2. In Experiment 2, counter appearance considerably differed from the counter used in Experiment 1. The potential influence of counter appearance has not been tested separately. However, if subjects explicitly noticed the counter change, a better performance with PSEs close to veridical was expected. From the data at hand, the inconsistencies between Experiment 1 and Experiment 2 cannot be solved.

5.5 Discussion

From the results of Experiment 1 we conclude that there is a distortion of perceived timing at the location of the saccade target but not at a location halfway between the initial fixation point and the saccade target. Accordingly, it is implausible that the distortion of perceived timing at the location of the saccade target is a global effect. Our results suggest a local effect, instead, presumably centered at or around the saccade target. If one takes into account that a potential mechanism compensating for saccadic suppression does not necessarily need to be global in the sense that it compensates for every detail of the visual world—because only a relatively sparse set of information is integrated trans-saccadically—, this local distortion of perceived timing as shown here might still suffice therefore. Experiment 2 did not succeed in circumscribing the region in which this local distortion is operative in more detail.

In Experiment 1, a difference between the third experimental condition and the baseline condition is the location of the counter. In the baseline condition, as well as in the saccade condition with the counter at the saccade target, the duration of the first interval is judged when the counter is on the fovea. In the saccade condition with the counter halfway between fixation point and saccade target, the duration of the counter is judged 8 ° peripheral. However, it has been shown that the eccentricity of the counter does not influence the duration judgement systematically (Yarrow et al., 2001). In a control condition and a further control experiment—both described in their Experiment 1—, they directly compare two conditions of duration judgement with a peripheral (22 ° and 55 °) and a foveal counter, respectively, and found no significant differences.

The question is, why the time misjudgement is confined to the saccade target area. We believe that a combination of saccade-related attention shifting and a misperception of the time of saccade onset may explain our result. Spatial attention is known to be shifting mandatorily to the location of the saccade target just prior to a saccade (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996; Irwin and Gordon, 1998; Peterson et al., 2004; Baldauf and Deubel, 2008). Furthermore, observers have been shown to misjudge the exact time of moving their eyes (Volkmann and Moore, 1978; Deubel and Schneider, 1996; Deubel et al., 1999). Volkmann and Moore (1978) found a substantial overestimation of the period the eyes are moving. While their results can be interpreted as revealing a general uncertainty of subjects about when there eyes actually move, Deubel et al. (1999) showed that, under some conditions, subjects judge events that occur before a saccade as occurring after it. They asked subjects whether a probe stimulus occurred before or after a voluntary saccade. Subjects judged the time of their saccade by about 145 ms too early if the test stimulus occurred at the location of the saccade target, presumably because attention shifted there before the saccade. However, in the case of the test stimulus occurring at the fixation point, the saccade onset was judged only 45 ms too early. Put differently, subjects reported that their gaze was already at the saccade target from 145 ms before saccade onset, and, in the second condition, reported that their gaze was at the fixation point up to 45 ms before the saccade. This reveals a difference of 100 ms in the perceived timing of saccade onset between the two probe locations.

Our hypothesis is based on the assumptions that, firstly, subjects misjudge the time of their eye movement and, secondly, subjects do not explicitly notice the counter change due to saccadic suppression. There is evidence for both assumptions.

In our chronostasis condition, subjects cannot notice the first change of the counter during their eye movement because of saccadic suppression, as corroborated in our control condition. Note that in previous experiments on chronostasis (Yarrow et al., 2001, 2004a,b) this has not been ascertained yet. Perceptibility of the counter change probably depends on a combination of eccentricity, size, and contrast of the counter. Under certain conditions subjects are able to reliably detect an intra-saccadic counter change (Hunt et al., 2008). However, in our experiments subjects have no explicit perception of the onset of the test interval. They may correctly interpret this onset as having occurred during the saccade and before their gaze reached the counter. As subjects perceive their gaze to be at the saccade target well before the saccade, the onset of the test interval would also be misjudged as too early, if the stimulus defining the interval is presented at the saccade location. For a clock at the fixation position or at an intermediate position, the onset of the test interval should be perceived more correctly because the onset of gaze shift is perceived more correctly. The differences found between the onset judgements of stimuli presented at saccade target and fixation point (Deubel et al., 1999) quantitatively matches the differences in perceived timing in our data.

Attentional explanations for our results could include a contribution of *inhibition of return* (IOR). We may speculate that the task-relevant counter likely attracts attention in the beginning of the trial. Shortly before the saccade, attention must be shifted to the future saccade target (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996; Peterson et al., 2004). Therefore, IOR may occur at the counter location, i. e. the previous locus of attention, and may contribute to a delayed processing of visual information from that location. Whether or not this is the case, however, cannot be concluded from the present experiments. We explain the distortion of perceived timing around saccades by hypothesizing that subjects mistake the time of the premotor attention shift with the time of the actual eye movement. The possible involvement of inhibition of return—as an effect arising from a shift of spatial attention—does not undermine our hypothesis at all, since the exact parameters of this mechanism are not exactly clear at the moment. Moreover, Hunt and Kingstone (2003) found a dissociation between the attentional and the oculomotor components of IOR, suggesting an at least partially independence of both components.

Attention is shifted in a matching time range before a saccade and can be validated amongst others with a pre-saccadically enhanced discrimination performance at the future saccade target (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996; Godijn and Theeuwes, 2003; Gersch et al., 2004; Baldauf and Deubel, 2008). Physiological correlates of spatial attention have been shown in brain areas as early as V1 (Yeshurun and Carrasco, 1998, 2000), yet enhanced neuronal activity has been demonstrated in visual areas of different levels of processing (Brefczynski and DeYoe, 1999; Müller and Kleinschmidt, 2003; Müller et al., 2003; Müller and Kleinschmidt, 2004; Müller et al., 2005). Information from attended locations might be weighted differently, but the quality of processing remains unchanged (Eckstein et al., 2002). This focus of spatial attention is delimited, albeit it is variable in size and thereby capable of adapting to different tasks (Handy et al., 1996; Madelain et al., 2005; Belopolsky et al., 2007). In the first 100 ms after target onset, covert attention and saccade planning are coupled (Peterson et al., 2004), as assessed psychophysically. Following Tse et al. (2004), attention takes about 120 ms to be re-allocated. In a sequence of saccades, Gersch et al. (2004) found visual enhancements at the very next saccade target 150 ms after offset of the previous saccade. Deubel and Schneider (1996) found enhanced discrimination performance at the future saccade target with stimuli presented 60–180 ms after the signal to start a saccade. More recently, Baldauf and Deubel (2008) found enhanced discrimination performance for stimuli presented 50–110 ms after target onset—corresponding to about 120–180 ms before onset of the first saccade—at all future targets of a sequence of saccades. Carlson et al. (2006) measured the latency of attention shifts and found 140 ms for peripheral cues, rendering findings of Cheal and Lyon (1991) more precisely, who previously found latencies of about 100 ms. Nakayama and Mackeben (1989) showed a peak in discrimination performance if the cue preceded the target array by 70–150 ms. Moreover, the speed of attention is independent of the distance in the visual field (Eriksen and Webb, 1989). Weichselgartner and Sperling (1987) found considerably longer time courses for shifting spatial attention (300-400 ms), but this difference could also be attributed—at least in part—to the so-called attentional blink (see Peterson and Juola, 2000). Weichselgartner and Sperling (1987) also characterized the dynamics of two distinct attentional processes: a fast, automatic, and effortless process and a second slower, effortful, and consciously controlled process. This is also in line with findings of Cheal and Lyon (1991) and Carlson et al. (2006), who found much longer latencies (300 ms and 240 ms, respectively) for attentional shifts elicited by central, symbolic cues. Also neurophysiologically, larger responses are found about 100 ms after spatial cuing in different areas of the visual cortex Müller and Kleinschmidt (2007). Summarizing the above, most psychophysical studies show that attention takes between 60 ms to 180 ms to be re-allocated. There is reasonable evidence for further narrowing this down to about 60 ms to 120 ms. This is also corroborated by neurophysiological findings. Since saccadic latencies vary across subjects and depend on the particular experimental setup, the exact time of the attention shift relative to saccade onset cannot be inferred from the above-mentioned studies. Nevertheless, the estimated interval between the pre-saccadic attention shift and the actual saccade onset—sometime between about 50 ms and 150 ms—is consistent with our assumption that the shift of spatial attention and the overestimation of the post-saccadic time interval are correlated.

Yarrow et al. (2001) argued against an involvement of attention, because chronostasis occurred also in a control condition in which subjects had to voluntarily shift their attention to the saccade target some time prior to the saccade. However, it is possible that, even if explicit attention is shifted to the saccade target early on, implicit attentional ressources are recruited around saccade onset, as the association between eye movements and attention shifts is not consciously detachable (Peterson et al., 2004; Hoffman and Subramaniam, 1995; Kowler et al., 1995). Moreover, this would be consistent with the notion of two different attentional processes (Weichselgartner and Sperling, 1987; Cheal and Lyon, 1991; Carlson et al., 2006), one consciously controllable, the other potentially stimulus-driven and probably coupled with the preparation of eye movements.

Morrone et al. (2005b) recently provided evidence of an effect different to the distortion of perceived timing described above. Their test intervals were only 100 ms long, involving the discrimination of temporal intervals between two flashing stimuli around saccade onset. They found a pronounced *compression* of temporal perception around the time of saccades, accompanied by a perceived inversion of temporal order. This compression of time has approximately the same time course as the saccadic compression of space, from shortly before to shortly after the saccade, reaching its maximum at the beginning of the saccade. Furthermore, this effect seems to be global, insofar as Morrone et al. used peripheral stimuli that covered the whole monitor width, as well as smaller stimuli closer to the saccade target. Note that in their experiments subjects do not necessarily need knowledge about their actual or subjectively perceived gaze position over time to solve the tasks. Because of both, its different time course—maximal at saccade onset and swiftly diminishing toward saccade end—and its global effect, we think that the compression of perceived timing is caused by a mechanism different from chronostasis. Unlike this compression of perceived timing we showed chronostasis to be a local, and presumably attention-related, phenomenon.

Chapter 6

Perceptual consequences of saccadic adaptation

Contents

6.1 Abstract

Short-term saccadic adaptation is a mechanism that adjusts saccade amplitude to accurately reach an intended saccade target. Short-term saccadic adaptation induces a shift of perceived localization of objects flashed before the saccade. This shift, being detectable only before an adapted saccade, disappears at some time around saccade onset. Up to now, the exact time course of this effect has remained unknown. In previous experiments, the mislocalization caused by this adaptation-induced shift was overlapping with the mislocalization caused by a different, saccade-related localization error, the peri-saccadic compression. Due to peri-saccadic compression, objects flashed immediately at saccade onset appear compressed towards the saccade target. A priori, we tested whether the adaptation-induced shift and the peri-saccadic compression were either independent or related processes. We performed experiments with two different contrast conditions to separate the adaptation-induced shift and the peri-saccadic compression. Human subjects had to indicate the perceived location of briefly presented stimuli before, during or after an adapted saccade. Adaptation-induced shift occurred similarly in either contrast condition, with or without peri-saccadic compression. After validating the premise of both processes being independent and superimposing, we aimed at characterizing the time course of the adaptation-induced shift in more detail. Being present up to one second before an adapted saccade, the adaptation-induced shift begins to gradually decline from about 150 ms before saccade onset, and ceases during the saccade. A final experiment revealed that visual references make a major contribution to adaptation-induced mislocalization.

6.2 Introduction

Motor actions are continuously being monitored and adjusted by the nervous system. Movements are optimized by constantly comparing and calibrating motor commands and their sensory consequences. This is valid for a range of different types of movements, saccadic eye movements being one of those. Saccades are insofar special as they are 'ballistic' movements, i. e. they cannot be altered during the actual movement. Instead, they have to be programmed completely a certain time before movement onset. If saccades have not reached an intended target accurately for a number of times, saccadic adaptation modulates the amplitude of the saccade. Saccadic adaptation is thought to counter-act changes in saccade gain, i. e. the ratio between intended and actually executed saccade. Such changes can be caused by growth, injuries, diseases or exhaustion (Vilis et al., 1983; Optican et al., 1985). The error signal driving saccadic adaptation is visual, not motor, and no corrective saccades are necessary for adaptation to occur (Wallman and Fuchs, 1998). To be effective, the visual error signal has to be available immediately after the saccade (Shafer et al., 2000).

Saccadic adaptation is investigated in humans and monkeys by means of computer-based psychophysical experiments. Therein, the target of a saccade is displaced during the eye movement. Consequently, the initial saccade target visible before the saccade, referred to as T1, is visible at a different location after the saccade, referred to as T2. Due to saccadic suppression, this displacement is not noticed by subjects. Instead, the oculomotor system gradually adapts the amplitude of the saccades to the target displacement, such that the displaced target, T2, will be reached even though it does not match the eccentricity of the initially visible target, T1. In the course of this procedure saccade amplitude can be increased or decreased by several degrees. In monkeys, saccadic adaptation develops within 1,000–1,500 trials (Fuchs et al., 1996), with rate constants ranging from several hundred to about a thousand trials (Straube et al., 1997; Scudder et al., 1998). In humans, saccadic adaptation is much faster: About 50 trials are sufficient (Deubel et al., 1986), with rate constants of about 30–60 trials (Deubel et al., 1986; Frens and van Opstal, 1994; Albano, 1996). Because of this significant difference in adaptation rate the adaptation in humans is named short-term saccadic adaptation.

In humans, several different mechanisms of saccadic adaptation occur at different levels of the oculomotor system (Deubel, 1995; Albano, 1996; Alahyane and Pelisson, 2003; Alahyane et al., 2007). Nerve palsy and prism adaptation, for example, lead to long-term adaptation that is both, disconjugate and dependent on eye position, but not dependent on saccade amplitude (Hopp and Fuchs, 2004). In contrast, short-term adaptation is conjugate (Albano and Marrero, 1995; Das et al., 2004), direction- and amplitude-specific (Straube et al., 1997; Watanabe et al., 2003), and dependent on eye displacement vector rather than eye position (Albano, 1996). Different types of saccadic adaptation may be driven by different processes, for example a slower, long-lasting motor adaptation, and a faster, short-lasting, possibly higher cognitive or perceptual process.

The possibility of a cognitive or perceptual process in particular should be taken into account because saccadic adaptation shows perceptual consequences: It affects the localization of stimuli presented in the adapted space. Moidell and Bedell (1988) described that saccadic adaptation induced apparent shifts of localization targets that were briefly presented in the vicinity of the saccade target. These shifts were small in amplitude (about 0.5 °) but occurred during fixation when subjects were previously adapted. Bahcall and Kowler (1999) found a more pronounced effect when comparing the perceived location of stimuli presented at the saccade target before and after an adapted saccade. Awater et al. (2005) reported a large, adaptation-induced localization shift of stimuli presented in the area between T1 and T2. When visible between 300 and 100 ms before the execution of an adapted saccade, stimuli presented in this area were perceived shifted in the direction of adaptation. Stimuli presented after an adapted saccade were localized correctly. Recently, a similar effect of saccadic adaptation has been demonstrated for open-loop pointing movements (Bruno and Morrone, 2007). We refer to this error in localization of pre-saccadically presented stimuli, specifically caused by saccadic adaptation, and shifting localization in the direction of adaptation, as *adaptation-induced shift* throughout this chapter.

In the time range from about 100 ms before the saccade to the end of the saccade, the time course and magnitude of adaptation-induced shift could not be studied. In this epoch, *peri-saccadic compression* occurred. Peri-saccadic compression is a specific error in the localization of stimuli presented briefly around the time of a saccade. Stimuli are perceived shifted towards the location of the saccade target (Ross et al., 1997; Morrone et al., 1997; Lappe et al., 2000; Kaiser and Lappe, 2004). In the experiments of Awater et al. (2005), both effects, the adaptation-induced shift and the peri-saccadic compression, occurred. Since both effects emerge in the temporal vicinity of a saccade and result in a distortion of perceived space, it remains unclear if the adaptation-induced shift and the peri-saccadic compression are entirely different effects or whether they interact with each other.

In addition to the aforementioned peri-saccadic compression, the *peri-saccadic shift* is another mislocalization effect around the time of saccadic eye movements. In contrast to peri-saccadic compression, however, the direction of this mislocalization is uniform throughout the visual field (Honda, 1991). Arising about 50 ms before saccade onset, the peri-saccadic shift reaches its maximum around saccade onset and decreases within 50 ms after saccade onset. Stimuli being presented briefly in this epoch are perceived shifted in the direction of the upcoming saccade. Typically, there is a transient undershoot short-time after saccade onset, resulting in a mislocalization in the opposite direction (Honda, 1989, 1991). This peri-saccadic shift is independent of stimulus position (Honda, 1991) and stimulus contrast (Michels and Lappe, 2004).

The experiments described below were designed to separate the adaptation-induced shift from other peri-saccadic localization errors. We aimed at replicating previous experiments (Awater et al., 2005), yet extending the findings over a wider range of presentation times and stimulus positions. Based on these findings, we wanted to address a series of questions:

(1) Are the adaptation-induced shift and the peri-saccadic com-

pression either independent or related processes? We varied stimulus contrast, thereby isolating the adaptation-induced shift from peri-saccadic compression, since the strength of the latter depends on stimulus contrast (Michels and Lappe, 2004). In the study of Awater et al. (2005), the adaptation-induced shift could not be examined separately.

(2) What is the time course of the adaptation-induced shift? After confirming the premise of both processes being independent and superimposing, we aimed at characterizing the time course of the adaptation-induced shift in more detail. Therefore, we conducted an experiment without previous saccadic adaptation, and without peri-saccadic compression. This permits quantifying the impact of the pure peri-saccadic shift. Subsequently, this peri-saccadic shift is subtracted from the data obtained in the adaptation experiment, thus eliminating both, the peri-saccadic compression and the peri-saccadic shift. Isolating the adaptation-induced shift should allow for studying the uncorrupted time course of this very effect, particularly the time course of its disappearance relative to saccade onset. From the data of Awater et al. (2005) this was impossible, since around the time of saccade onset it was intermingled with peri-saccadic shift and peri-saccadic compression. We aimed at differentiating between the possibilities of a pre- or an intra-saccadic disappearance, the former indicating the involvement of pre-saccadic perceptual processes, potentially related to saccade planning, the latter pointing at the relevance of motor processes generated during the execution of an adapted saccade.

(3) What is the temporal extent of the adaptation-induced shift? From the experiments of Awater et al. (2005) the adaptation-induced shift was already known to exist some time before the execution of an adapted saccade, and disappearing around saccade onset. Here, we wanted to further specify how long before saccade onset this shift is detectable, and in particular whether it is a transient effect, arising and diminishing before saccade onset. Therefore, we extended our previous experiments by very early pre-saccadic stimulus presentations, up to one second before saccade onset. Up to now, no

peri-saccadic effect is known to be operative such a long time before a saccade.

(4) Further on, we implemented a different, less stereotype way of establishing saccadic adaptation, thereby addressing possible issues of methodological validity and the general applicability of our results.

(5) In a final experiment, we examined the emerging of the adaptation-induced shift during the course of developing saccadic adaptation. Comparing changes in saccade amplitude with changes in peri-saccadic localization across successive trials allows for estimating symmetry and synchrony of the two parameters. If saccadic adaptation directly causes the adaptation-induced shift, both effects have to be tightly coupled over time.

6.3 Methods

6.3.1 Subjects

Seven subjects, two male and five female, participated in the study. All of them were students at the Department of Psychology and had normal or corrected vision. Their age ranged from 21 to 31 years. One subject was completely naïve to eye movement experiments. One subject was an author. The other subjects were experienced psycho-physical observers but naïve to the aims of the experiments. There were no qualitative differences ascertainable in the results of naïve and non-naïve subjects. All subjects gave informed consent.

6.3.2 Experimental setup

Two personal computers were running the experiments: a Windows PC sampling gaze position throughout the experiments and a Macintosh PC for stimulus presentation. The two computers were connected to each other via a dedicated ethernet connection. Subjects were seated about 45 cm distant from the stimulus screen. Their head was supported by a chin rest. The presentation monitor was a

22” (20” visible screen diagonal) *iiyama Vision Master Pro 514* with a vertical frequency of 200 Hz at a resolution of 800 × 600 pixels. In *high luminance-contrast* condition (see below) the monitor was additively darkened by means of a car-window foil that conducted only about 1% of light, thereby reducing luminance by about 2 log units.

6.3.3 Eye movement registration

Eye movements were recorded with the *EyeLink II* system (*SR Research, Ltd.*, Canada). Gaze positions were sampled and stored on the Windows PC with a frequency of 500 Hz. Eye movement events (saccades, fixations, and blinks) were detected online, stored, and sent to the stimulus computer via the ethernet connection. The eye-tracking computer calculated the gaze position from the camera data every 2 ms, detected saccades by comparing successive samples, and then sent a message to the Macintosh PC via Ethernet. For more information see Section 4.1 on page 24.

The delay of the availability of saccade information on the stimulus computer was in the range between 24 and 32 ms. On the Macintosh PC, the incoming eye movement event triggered the further stimulus presentation within the time of two monitor refreshes (less than 10 ms). At an average saccade duration of about 60 ms this was sufficient for complete intra-saccadic stimulus changes. For off-line analysis the data stored on the recording PC was used. Off-line data analysis confirmed that display changes occurred usually during saccades. Infrequent trials, in which the saccade detection was too slow to adjust the display during the saccade, were omitted from further analysis.

6.3.4 Experiments

Experiment 1: Main experiment

Six subjects, two male and four female, participated in Experiment 1. Before beginning the first experimental block, each subject received detailed instructions by the investigator and was allowed to perform some trials to familiarize with the task. At the beginning of each experimental block the eye-tracking system was calibrated and validated. The subject's dominant eye was used for tracking gaze position. Throughout the experiment the instructor was present in most of the blocks. Experiment 1 was carried out in two different contrast conditions (high and low luminance-contrast), conducted in separate blocks. Each subject participated in at least four blocks per contrast condition. An experimental block started with five regular saccade trials, in which the saccade target was not displaced intrasaccadically and no localization stimulus was shown. Subsequently, 50 adaptation trials and thereafter 200 localization trials followed. The precise structure of the foreground and background items differed with experimental condition (*high luminance-contrast* or *low luminance-contrast* condition) and is described separately.

Adaptation procedure. Each adaptation trial began with the presentation of a fixation point (a square of 1.25 ° by 1.25 ° visual angle) on an empty background. The fixation point was vertically centered and horizontally located 12.7 ° to the left of the center of the screen. After a random time of 1,100–2,100 ms, the fixation point disappeared. At the same time the initial saccade target (T1, same appearance as fixation point) was presented 25.0 ° to the right of the fixation point. Subjects were required to execute a saccade to T1 as fast as possible after its presentation. While the eyes were moving, T1 was replaced by T2, located 6.2 ° left of T1. Accordingly, the amplitude of the adapted saccade to T2 was decreased to 18.8 °, or about 75 % of the initial amplitude to T1. 1,000 ms after the intrasaccadic target displacement, T2 disappeared, and a new trial began with the presentation of the fixation point.

Localization procedure. The localization trials largely resembled adaptation trials. The presentation of the fixation point and T1 were identical, as was the target back-step, i. e. the distance between T1 and T2. In addition, at some predetermined time during a trial a localization stimulus was presented briefly (10 ms). The stimulus was a vertical bar of about 0.4 ° width, extending the height of the screen (37.5 °). The bar was presented at one of seven possible positions (15.8 °, 17.8 °, 19.9 °, 21.9 °, 24.0 °, 26.1 ° or 28.1 ° to the right of the fixation point). Stimulus presentation time ranged from about 200 ms before (referred to as −200 ms) to 200 ms after saccadic onset. After each localization trial, a mouse pointer appeared, and subjects had to indicate the perceived horizontal position of the stimulus. In case of a trial, in which subjects did not see the stimulus, they were instructed to click in the outermost right and lower corner of the screen. Those trials were discarded during later analysis.

A temporal scheme of the events in single trials can be found in Fig. 6.1 on the following page.

Fixation trials. In 10 % of the localization trials, pseudo-randomly intermixed, the fixation point did not disappear, no saccade target (neither T1 nor T2) was presented, and the subjects were requested not to elicit a saccade until they had indicated the perceived position of the localization stimulus by using the mouse pointer. The maintenance of fixation was monitored off-line. Trials in which fixation was broken were discarded from analysis.

Low luminance-contrast. In the low luminance contrast condition, the background of the screen presentation was medium gray. The fixation point, the saccade target, and the localization stimulus were blue. Their brightness was preliminarily adjusted to be roughly equiluminant to the background. Complete equiluminance was neither tested nor necessary, the aim was solely to largely reduce luminance contrast to result in a considerable amount of peri-saccadic compression. For the same reasons the background as well as the foreground items were structured by pseudo-randomly varying luminance by some amount between −20 % and +20 % independently

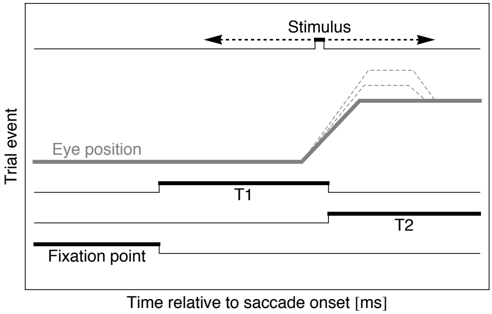

Figure 6.1: Temporal scheme of events during a single adaptation and localization trial. Initially, only the fixation point (FP) was visible and the subject fixated it. After a random time period of 1,100–2,100 ms the fixation point disappeared and at the same time the initial saccade target (T1) was presented. The subject conducted a saccade as fast as possible after appearance of the saccade target. While the eyes were moving (average saccade duration about 60 ms) T1 disappeared and the adaptation target (T2) appeared. Initially, saccades aim at T1, gradually adapting to T2 over successive trials (dashed gray lines). The next trial started 1,000 ms later. In localization trials, at some time before, during or after the saccade (from about 200 ms before to 200 ms after saccade start) a stimulus was presented briefly (10 ms). The next trial started after the subject had indicated the perceived position of the flashed stimulus by means of a mouse pointer that appeared after the trial.

for every pixel to increase positional uncertainty. Average luminance of the background and the foreground items was $5.0\,\mathrm{cd/m^2}$ and $3.8\,\mathrm{cd/m^2}$ respectively, resulting in a Michelson contrast (C_M) of 0.14. Due to color contrast and the remaining luminance contrast, the presented items were nevertheless clearly visible on the background. Ambient luminance was about $0.04\,\mathrm{cd/m^2}$.

High luminance-contrast. In the high luminance-contrast condition, the background was black, the fixation point and saccade targets were dark gray, the localization stimulus medium gray. The monitor screen was covered with a dark car window foil, reducing the total luminance of the presentation by about two log units. This was done to minimize the possible effect of phosphor persistence, and to reduce visible references from the monitor edges. Resulting luminance of the background was below 0.01 cd/m^2. Luminance of the saccade target and the stimuli was 0.08 cd/m^2 and 0.4 cd/m^2 respectively, resulting in a Michelson contrast of 0.78 and 0.95. The experimental room was almost completely dark (luminance below 0.01 cd/m^2). To avoid dark adaptation, the screen turned completely white for 150 ms after each trial.

Experiment 2: Non-adapted fixation condition

The non-adapted fixation condition served as a baseline for the localization trials described in Experiment 1, because even during fixation, localization of briefly flashed objects is not necessarily veridical (Müsseler et al., 1999).

All six subjects from Experiment 1 also participated in Experiment 2. Experiment 2 was carried out on separate days, and in both, the high and the low luminance-contrast condition. Each subject participated in between one and three blocks per condition. In this experiment, single blocks exclusively consisted of 210 fixation trials without a previous adaptation period. The single trials in Experiment 2 were identical to the intermixed fixation trials in Experiment 1.

Experiment 3: Non-adapted saccade condition.

The non-adapted saccade condition was conducted to estimate the amount and time course of the isolated peri-saccadic shift under conditions similar to Experiment 1. For this purpose, localization trials without previous adaptation were carried out, so there are no effects of adaptation in Experiment 3. Furthermore, Experiment 3 was conducted in high luminance-contrast condition only, so no peri-saccadic compression occurred.

Five subjects, two male and three female, participated in Experiment 3. All of them had also participated in Experiments 1 and 2. Experiments were executed on separate days, and in separate experimental blocks of 220 trials, consisting of 5 initial saccades and 215 localization trials without a previous adaptation period. The single localization trials resembled the localization trials in Experiment 1, except there was no intra-saccadic target displacement. Instead, T1 was presented at 18.8 °, the location of T2, and did not change during the eye movement.

Experiment 4: Early pre-saccadic presentation

From the experiments of Awater et al. (2005) the adaptation-induced shift is known to be present at least 200 ms preceding a saccade and disappearing before saccade onset. There are at least two possible explanations for these results. Firstly, the adaptation-induced shift is a transient effect, visible for a certain time before the planning or execution of an adapted saccade; or, secondly, it is an effect arising from an error in the processing of positional information across saccades, being visible at any time before an adapted saccade. We therefore conducted an experiment with much earlier pre-saccadic stimulus presentations.

Three subjects, one male and two female, participated in Experiment 4, all of them had also participated in Experiments 1 and 2. Experiment 4 was conducted in low luminance-contrast condition only. Each subject participated in between four and six blocks. Experiments were carried out on separate days, and in separate experimental blocks of 255 trials, consisting of 5 initial trials, 50 adaptation trials, and 200 localization trials. The single trials were identical to Experiment 1, with only the timing of the stimulus presentation in localization trials being modified. The localization stimuli were presented either peri-saccadically between −175 ms and 175 ms or about 400, 700 or 1,000 ms before saccade onset, each in 20 % of the trials. Note in the latter three cases the localization stimuli being presented even before presentation of T1. The remaining 20 % of the trials were fixation trials, and also identical to the fixation trials in Experiment 1.

Experiment 5: Alternative adaptation procedure

In Experiments 1 and 4, T1 and T2 always appeared at the same location on the monitor screen. By conducting an experiment with a less monotonic procedure we controlled for the potential impact of this stereotypical setup and subject's potential response strategies.

Four subjects, two male and two female, participated in Experiment 5; three of them had also participated in Experiments 1 and 2. Experiment 5 was conducted in low luminance-contrast condition only. Each subject participated in four blocks. In Experiment 5, single blocks consisted of 260 trials, comprising 10 initial trials, 50 adaptation trials and 200 localization trials. The single trials very much resembled Experiment 1, except all presented items—fixation point, T1, T2, and localization stimuli—were shifted as a whole to the left or to the right on the background independently in each trial. Thus, the complete layout was centered at one of seven equidistant monitor positions, spanning 15 ° visual angle. Geometric relationships between the individual items remained unchanged.

Experiment 6: Emerging of the adaptation-induced shift during the acquirement of saccadic adaptation

In the previous experiments, we examined the adaptation-induced shift under conditions of well-established short-term adaptation, since a large number of trials are necessary to give a comprehensive picture of this effect. In Experiment 6, we reduced the number of independent variables and simplified the procedure, so that an estimate of the emerging adaptation-induced shift could be derived from each trial. Furthermore, there is no separate adaptation procedure in this experiment. Instead localization stimuli are presented throughout the experiment.

Ten subjects, five male and five female, participated in Experiment 6; five of them also participated in previous experiments. Experiment 6 was conducted in low luminance-contrast condition only and resemble Experiment 5 insofar as the complete layout of presented items was shifted as a whole across the screen in each trial independently. Each subject participated in one experimental block only. Single blocks consisted of 200 trials, comprising of 50 initial trials, 100 trials with intra-saccadic target displacement, and 50 final trials. In the initial and final trials, T1 was presented without any intra-saccadic displacement. The middle 100 trials resembled the localization trials in Experiment 1, i. e. T1 was intra-saccadically replaced by T2. Thus, the first 50 trials provide a baseline for localization without saccadic adaptation. In the course of the next 100 trials, subjects acquired saccadic adaptation. In the final 50 trials, de-adaptation could take place. Note that in all 200 trials localization stimuli were presented. Stimulus presentation was limited to the epoch around 300 ms before saccade onset and to three stimulus positions between T1 and T2 (19.9 °, 21.9 °, and 24 °). In every trial, after the saccade, subjects indicated the horizontal position of the stimulus by means of the mouse pointer.

6.3.5 Data analysis

Data analysis was done in *Mathematica 5.2* (*Wolfram Research, Inc.*). For each experimental block, adaptation was verified by averaging the amplitudes of the localization trials. Data were discarded if the mean adapted landing position in a single block deviated more than 3.1 ° from the adaptation target or if the mean landing position of the first 10 trials (5 initial trials and the first 5 adaptation trials), did not differ significantly (t-test, $\alpha = .05$) from the mean landing position after adaptation. On average across subjects, adaptation was nearly complete, i. e. the adapted landing position of the eyes was mostly on or around the adaptation target. An example of the course of adaptation in a single experimental block is shown in

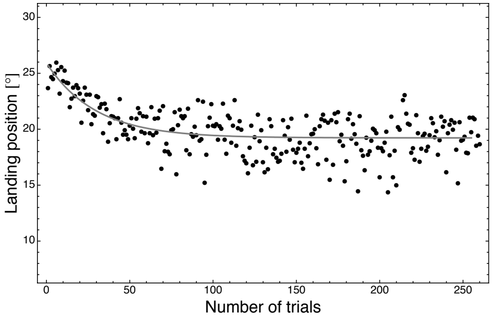

Figure 6.2: Time course of saccadic adaptation. Saccade amplitudes against trial numbers for every trial of a single experimental block. The block consists of 255 trials (5 saccade trials without target displacement, 50 adaptation trials, and 200 localization trials). T1 is at 25 °, T2 is at 18.8 °. Black dots represent single trials, the solid line an exponential decay curve fitted to the data ($f(x) = 19.2 + 6.7^{-0.049x}$, rate constant 20.3 trials, $r^2 = 0.17$).

Fig. 6.2.

In saccadic localization trials, single trials were discarded when the saccade target was missed by more than 6.2 °, the target displacement was not completed before the eyes had landed, or the subjects responded that they had not seen a localization stimulus. Fixation trials were discarded in response to a saccade occurring between the beginning of a trial and the mouse response, or subjects responding they had not seen a localization stimulus.

6.4 Results

6.4.1 Independence of adaptation-induced shift and peri-saccadic compression

In Experiment 1 we varied stimulus contrast in order to isolate the adaptation-induced shift from peri-saccadic compression. Successful adaptation was verified for each experimental block as described in the Data analysis section (Section 6.3.5 on the preceding page). Nine of the original 78 experimental blocks were discarded due to insufficient adaptation. Of the remaining blocks, 76 % of the saccade trials and only 33 % of the fixation trials reached the criteria specified above. The average rate constant of the exponential decay curve was 20 ± 7 trials (Mean ± SD) and 23 ± 6 trials in low and high luminance contrast condition, respectively. The amount of saccadic adaptation, i. e. the difference between mean landing positions of the five initial trials and of the localization trials, averages 4.8 ° (SD 0.7 °) and 4.3 ° (SD 0.8 °) across subjects for the low luminance-contrast condition and the high luminance-contrast condition, respectively. The results for both conditions are shown in Fig. 6.3 on the next page. The data was averaged in bins of 25 ms for each of the seven stimulus locations.

The low luminance-contrast condition (Fig. 6.3a) produces a large amount of peri-saccadic compression. Stimuli presented around the time of the saccade onset are localized incorrectly. The direction of mislocalization depends on the position of the localization stimuli. While stimuli presented between the fixation point and T2 appear shifted in the direction of the saccade, stimuli presented beyond T2 appear shifted in the opposite direction. Note that in both cases stimuli appear shifted towards T2. The focus of compression is T2, from which the actual landing position of the eyes does not differ significantly (adaptation target: 18.8°; mean landing position: 19.4 °, SD 1.1 °; t-test, $p > .05$). There is no compression towards T1, which is presented during saccade planning and onset. This reproduces the findings of Awater et al. (2005).

Stimuli presented before saccade onset are perceived systematically shifted in the direction of adaptation, while stimuli presented after saccade end are perceived roughly at the same positions as in the non-adapted fixation condition. The amount of this adaptation-induced shift is clearly smaller than the target back-step. While the target back-step is 6.2°, the mean adaptation-induced shift (well before the saccade compared to after the saccade) is 3.3 °. Thus, the adaptation-induced shift is also smaller than the amount of sacca-

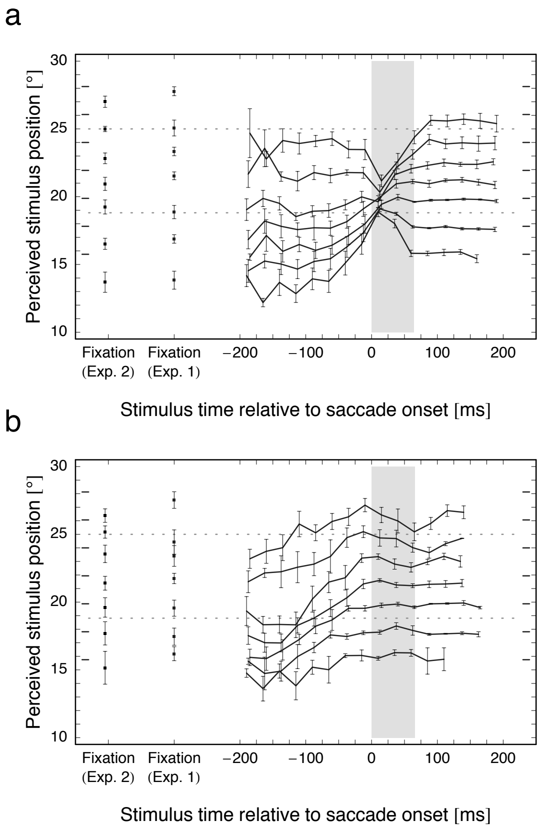

Figure 6.3: Peri-saccadic localization after adaptation in Experiment 1. **(a)** Low luminance-contrast condition. **(b)** High luminance-contrast condition. The vertical tick marks indicate the real stimulus positions, the horizontal dotted lines the positions of T1 and T2. The light gray area indicates the time of saccade start and average saccade termination. All results are means across subjects (N=6). Error bars indicate standard errors. The "Fixation" columns show the results of the fixation trials intermixed with saccade trials in Experiment 1 and of localization during non-adapted fixation in Experiment 2.

dic adaptation, which averages 4.8 ° (SD 0.7 °). Mean initial landing position is 24.2 ° (SD 1.7 °).

Intermixed with saccade trials were trials in which the subjects kept fixation, but were in the adapted state. In these trials subjects showed very little mislocalization confirming the previous observation that the actual execution of an adapted saccade is mandatory for the appearance of the adaptation-induced shift (Awater et al., 2005).

There is no qualitative difference between the results of the non-adapted fixation condition from Experiment 2, which was recorded in separate blocks, and the fixation trials that were recorded in the adapted state in Experiment 1. Results from Experiment 2 are integrated in Fig. 6.3.

While the low luminance-contrast condition largely reproduces earlier experiments, the high luminance-contrast condition (Fig. 6.3b), being described in the following, is a novel approach. In the high luminance-contrast condition, the mean initial and adapted landing positions were 23.2 ° (SD 1.1 °) and 18.9 ° (SD 1.0 °), respectively. The amount of saccadic adaptation was 4.3 ° (SD 0.8 °). No peri-saccadic compression is visible here. This absence of peri-saccadic compression was the incentive for chosing a relatively high luminance-contrast between the stimuli and the background. Nevertheless, the amount of adaptation-induced shift, 3.7 °, is qualitatively similar to that in the low luminance-contrast condition. Outside the time range in which peri-saccadic compression occurred (about −60 ms to 60 ms), the curves in Fig. 6.3a and 6.3b do not differ significantly.

To assess possible differences between conditions, a 2 (contrast condition) × 4 (saccade condition: adapted fixation, non-adapted fixation, pre-saccadic and post-saccadic stimulus presentation) × 7 (stimulus position) repeated-measures ANOVA was calculated. Pre- and post-saccadic stimulus presentation relates to each subject's earliest pre-saccadic and latest post-saccadic time bin, respectively. ANOVA revealed significant effects of saccade condition and stimulus position ($p < .01$ in both cases), but no significant effect of contrast condition ($p > .1$), thereby strengthening our premise of affecting peri-saccadic compression but not adaptation-induced shift with varying stimulus contrast. Only interaction between saccade condition and stimulus position reached significance ($p < .01$), pointing at the fact that stimuli presented between T1 and T2 are affected by the pre-saccadic adaptation-induced shift to a higher degree. Post-tests (Tukey's test, $\alpha = .01$) revealed significant differences between all seven stimulus positions. Furthermore, the pre-saccadic stimulus presentation differed significantly from all other saccade conditions (adapted fixation, non-adapted fixation, post-saccadic presentation). No other differences reached significance.

6.4.2 Time course of the adaptation-induced shift

In order to investigate the time course of the adaptation-induced shift we calculated at each point in time the difference between the localization in saccade trials from Experiment 1 and the localization in the non-adapted fixation condition from Experiment 2, averaged over the seven stimulus locations and the subjects. This was done for both contrast conditions. Fig. 6.4 shows the result. In both conditions, the saccade-induced shift is about 3 °, beginning to decrease between 150 and 100 ms before saccade onset. About 50 ms after saccade onset localization is correct, i. e. shift is zero. In the time around saccade onset, the curves differ because the peri-saccadic compression in the low luminance-contrast condition also influences the localization (dashed part of the black curve in Fig. 6.4). From the data in Fig. 6.4 it remains unclear whether the adaptation-induced shift reaches a stable level for stimuli presented earlier than 200 to 300 ms before saccade onset. This fact is explicitly addressed in Experiment 4.

However, the time course of the adaptation-induced shift near saccade onset in the high luminance-contrast condition is likely to be contaminated by a further saccade-related effect, the peri-saccadic shift. To determine the time course of the pure adaptation-induced

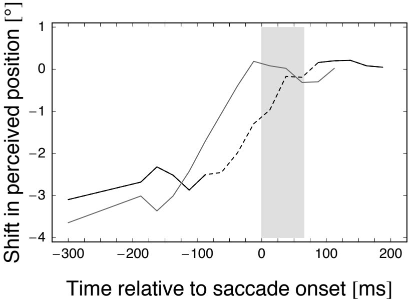

Figure 6.4: Time course of mean overall shift in low luminance-contrast condition (black) and high luminance-contrast condition (gray) from Experiment 1. X-axis shows the time of stimulus presentation relative to saccade onset. The overall shift is based on means across subjects (N=6) and is computed as the difference between perceived stimulus positions in saccade trials and in non-adapted fixation trials from Experiment 2, averaged across stimulus positions. A value of 0 means no overall shift, negative values mean a shift in the direction of the fixation point. The light gray area indicates the times of saccade start and average saccade termination. The dashed part of the black curve indicates the epoch in which the peri-saccadic compression occurs.

shift, we aimed at eliminating the putative impact of the peri-saccadic shift. Therefore, in Experiment 3, we measured the isolated peri-saccadic shift in the same condition and with the same subjects as in Experiment 1 but without saccadic adaptation. The difference between these measurements in Experiment 1 and the measurements in Experiment 3 should reveal the time course of the thereby isolated adaptation-induced shift in more detail.

Therefore, we conducted an experiment without an intra-saccadic target displacement. The saccade target was presented at the location of T2 from Experiment 1. By this, we aimed at isolating the amount and time course of the peri-saccadic shift, unaffected by peri-saccadic compression and adaptation-induced shift—as there is no adaptation and no intra-saccadic target displacement in this experi-

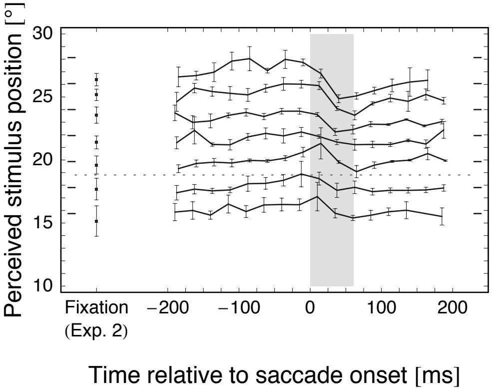

Figure 6.5: High luminance-contrast condition without previous adaptation procedure and without intra-saccadic target displacement in Experiment 3. The x-axis shows the presentation time of the stimulus relative to saccade onset. The y-axis shows the perceived horizontal position of the localization stimuli. Vertical tick marks indicate the real stimulus positions, the horizontal dotted line the position of the saccade target. The light gray area indicates the times of saccade start and average saccade termination (mean saccade duration 62 ms). All results are means across subjects (N=5). Error bars indicate standard errors. All subjects also participated in Experiments 1 and 2. The "Fixation" column shows results of non-adapted fixation from Experiment 2.

mental condition.

Figure 6.5 on the next page shows the results of this experiment. The data was divided and averaged in bins of 25 ms. Around the time of the saccade, there is a specific mislocalization noticeable. Immediately before saccade onset, subjects perceive the location of the stimuli slightly shifted in the direction of the saccade, while shortly after saccade onset, stimuli are perceived shifted in the opposite direction. This basically agrees with earlier results (Honda, 1991; Lappe et al., 2000). As specified for the adaptation-induced shift, the index of the mean peri-saccadic shift was calculated as the mean across stimulus positions of the differences between the localization in saccade trials and the localization in the non-adapted fixation condition in Experiment 2 (Fig. 6.6a).

Using this isolated peri-saccadic shift to subtract adaptation-independent mislocalization from the adaptation-induced shift obtained by Experiment 1, we were able to obtain the pure adaptation-induced shift around saccade onset (Fig. 6.6b). The adaptation-induced shift starts to diminish about 150 ms before saccade onset, reaching zero shortly after saccade onset. Fig. 6.6b indicates the way the characteristics of the time course change in comparison to the first experiment. Especially the slope of the decrease is less steep, with the maximum being reached later. Due to the time course of the peri-saccadic shift, it only affects the adaptation-induced shift in the epoch from about 100 ms before to about 100 ms after saccade onset.

6.4.3 Pre-saccadic temporal extent of the adaptation-induced shift

The adaptation-induced shift depends on the execution of a saccade and is not observed in—adapted or non-adapted—fixation trials. Moreover, it is present at least 300 ms preceding a saccade and disappearing before saccade onset (see Fig. 6.6b). To test whether the adaptation-induced shift is a transient effect, visible for a certain time before the planning and execution of an adapted saccade, or an effect arising from an error in the processing of positional information across saccades, being visible at any time before an adapted saccade, we conducted Experiment 4 with much earlier stimulus presentations. Thereby we were also able to rule out the possibility of the adaptation-induced shift continuously increasing with earlier pre-saccadic stimulus presentations, which could not be addressed in the previous experiments.

The results of Experiment 4 are shown in Fig. 6.7 on the facing page. Mean initial and adapted landing positions were 24.2 ° (SD

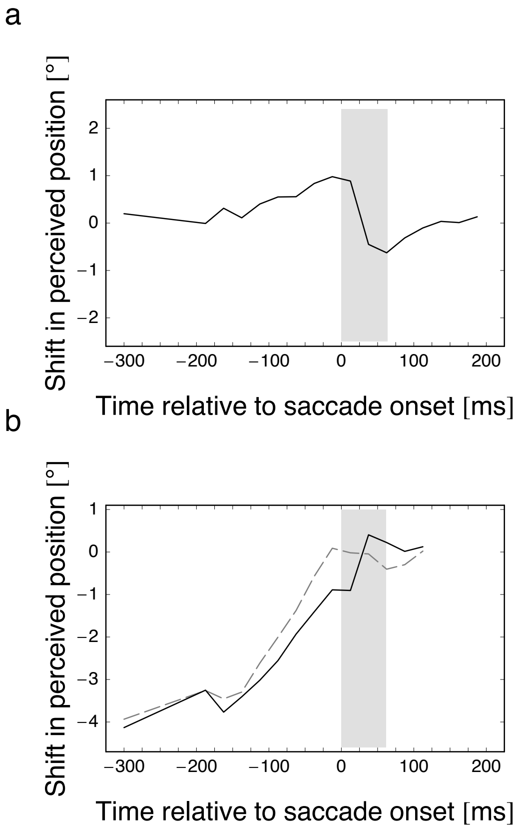

Figure 6.6: Time-courses of peri-saccadic and adaptation-induced shift. X-axes show the time of stimulus presentation relative to saccade onset. The light gray area indicates the times of saccade start and average saccade termination. All indices are based on mean results across identical subjects (N=5), computed as the difference between perceived stimulus positions in saccade trials and in non-adapted fixation trials from Experiment 2, averaged across stimulus positions. **(a)** Mean peri-saccadic shift from Experiment 3. Negative values indicate a shift in the direction of the fixation point, positive values in saccade direction. **(b)** Direct comparison of the pure adaptation-induced shift (solid black line), computed as the difference of the overall shift of Experiment 1 and the peri-saccadic shift from (a), and the overall shift from Fig. 6.4 on page 72 (dashed gray line).

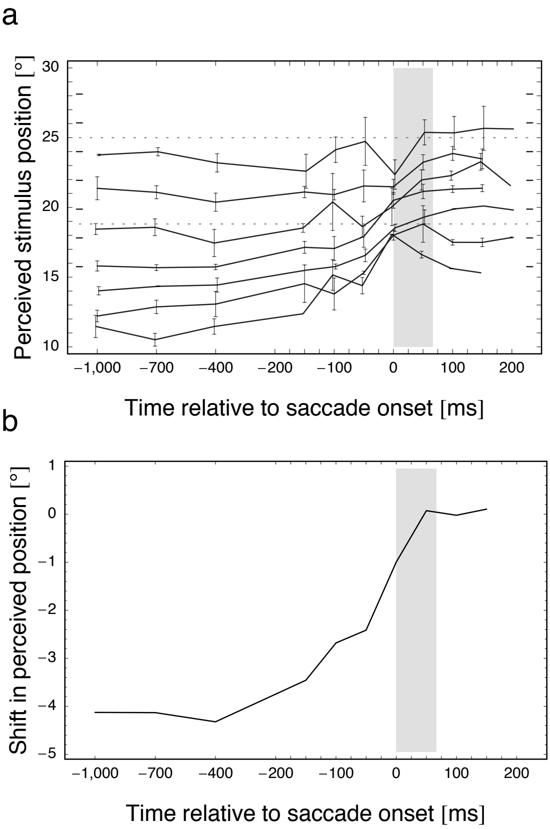

Figure 6.7: Results from Experiment 4 with early pre-saccadic stimulus presentation. **(a)** Peri-saccadic localization. **(b)** Adaptation-induced shift. The x-axis shows the presentation time of the stimulus relative to saccade onset, the y-axis the perceived horizontal position of the localization stimuli. Note that the x-axis is compressed for earlier pre-saccadic presentation times. The vertical tick marks indicate the real stimulus positions, the dotted lines the positions of T1 and T2. The light gray area indicates the times of saccade start and average saccade termination (mean saccade duration 67 ms). All results are means and standard errors across subjects (N=3).

1.8 °) and 19.1 ° (SD 0.8 °), respectively, the resulting amount of adaptation being 5.1 ° (SD 1.0 °). The adaptation-induced shift occurred similarly in all of the early pre-saccadic presentations (−400 to −1,000 ms) of the localization stimuli. If the stimuli were presented up to one second before saccade onset, there was still the qualitatively equal amount of shift. This adaptation-induced shift is not a transient effect of saccade execution or planning, only arising in a certain time window before the saccade. It rather is a stable effect that appears whenever a stimulus location is presented before an adapted saccade but the response is retrieved after saccade execution.

6.4.4 Validation of the adaptation procedure

In Experiment 5, a different stimulus procedure was utilized, not only in adaptation trials but throughout the experiment. We aimed at testing whether subjects show a comparable amount of adaptation-induced shift in this more variable experimental setup. Results are shown in Fig. 6.8 on the next page. Since the relative distances between the displayed items remained unchanged, graphic representation of the data is analogical to previous Figures. A 2 (pre-saccadic or post-saccadic presentation time) × 7 (stimulus position) repeated-measures ANOVA revealed significant differences for presentation time and stimulus position ($p < .01$ in both cases) and no significant interaction ($p > .8$). Pre- and post-saccadic stimulus presentation relates to each subject's earliest pre-saccadic and latest post-saccadic time bin, respectively. In Experiment 5, the adaptation-induced shift, i. e. the difference between pre-saccadic and post-saccadic localization, averages 2.8 ° (SD 1.1 °). The amount of saccadic adaptation, i. e. the difference between initial and adapted landing position, averages 4.6 ° (SD 1.0 °).

The results of Experiment 5 are in many aspects comparable to the results of previous Experiments. In particular, a pronounced amount of saccadic adaptation has been established and likewise adaptation-induced shift is visible. Thus, there is no evidence that our previous results are due to potential response strategies. Instead, the results are consistent with earlier findings that saccadic adaptation does not depend on eye position (Albano, 1996).

6.4.5 Emerging of the adaptation-induced shift during the acquirement of saccadic adaptation

In our previous experiments, subjects underwent 50 separate adaptation trials before the localization stimuli were presented. In Experiment 6, localization stimuli were presented throughout the experiment. In the first 50 trials, only T1 was visible, without an intra-saccadic target displacement. Landing position and localization performance during this period were used as a baseline and are referred to as pre-adaptation. In the next 100 trials, T1 was intra-saccadically replaced by T2. The first half of these trials (trials 51 to 100) are referred to as adaptation phase, the second half (trials 101 to 150) as post-adaptation. In trials 151 to 200, again only T1 was presented, referred to as de-adaptation phase. Dependent variables in each trial were the deviation of saccade landing position from T1 and the error in localization. Data from three of the ten subjects had to be discarded from further analysis due to their inability to systematically localize the stimuli (errors $> 5\,^\circ$). Since the amount of saccadic adaptation and of adaptation-induced shift varied across subjects, data was normalized to individual pre-adaptation and post-adaptation levels. In the pre-adaptation phase, landing positions show a considerable undershoot relative to T1 (average landing position across subjects $-2.5\,^\circ$, SD $1.6\,^\circ$), whereas localization is closer to veridical values (mean localization error $-1.6\,^\circ$, SD $1.7\,^\circ$; negative errors indicate mislocalization in the direction of fixation point and T2). This difference was also resolved by the normalization procedure.

Results of Experiment 6 are shown in Fig. 6.9 on page 82. Data was divided and averaged in bins of 10 trials. In the adaptation

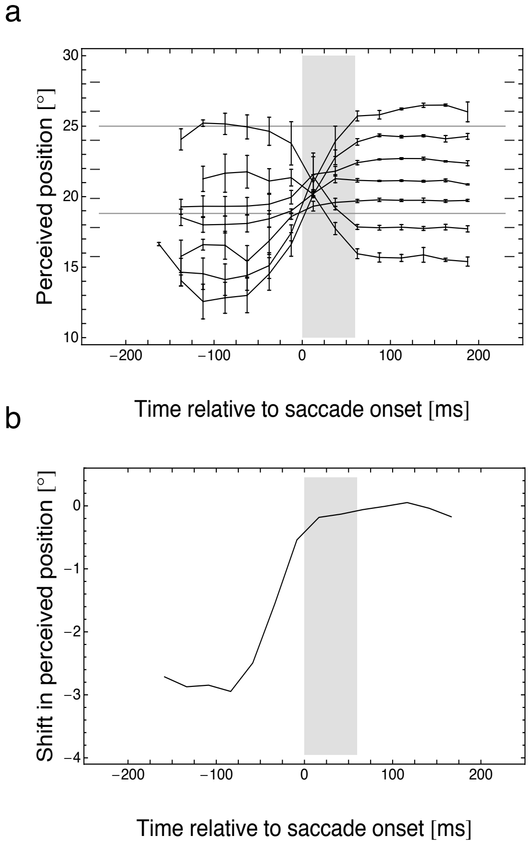

Figure 6.8: Results from Experiment 5 with alternative adaptation procedure. **(a)** Peri-saccadic localization. **(b)** Adaptation-induced shift. The x-axis shows the presentation time of the stimulus relative to saccade onset, the y-axis the perceived horizontal position of the localization stimuli. The vertical tick marks indicate the real stimulus positions, the horizontal gray lines the positions of T1 and T2. The light gray area indicates the times of saccade start and average saccade termination (mean saccade duration 60 ms). All results are means and standard errors across subjects (N=4).

phase (Fig. 6.9a), localization errors converge faster towards post-adapted level than deviations in landing position. More precisely, the transition of localization errors is abrupt, reaching values below 0.3 already in the first ten adaptation trials. In contrast, transition of landing positions is smooth, showing a roughly exponential time course. The de-adaptation phase (Fig. 6.9b) yields comparable but inversed results, even though not all subjects show complete de-adaptation of the landing position and variability is higher across subjects. These results are confirmed with a 2 (modality: landing position vs. localization error) × 5 (trial bins) ANOVA per experimental phase (adaptation and de-adaptation). For the adaptation phase, ANOVA revealed significant effects of modality and of trial number ($p < .04$ and $p < .01$, respectively), and no significant interaction ($p > .1$). For the de-adaptation phase, only modality reaches significance ($p < .01$).

We subsequently calculated paired t-tests across subjects for the first bin of trials, separately for each phase. In both adaptation and de-adaptation phase, differences between landing position and localization error are significant ($\alpha = .05$ and $\alpha = .01$, respectively). This means that landing position and localization error differ from each other in the first few trials of the adaptation and de-adaptation phase. In the adaptation phase, the normalized values for landing position and localization error drop from 1.0 to 0.84 and 0.27, respectively. Thus, localization error instantaneously and closely approaches post-adaptation level. However, it still differs significantly ($\alpha = .05$) from post-adaptation level. In de-adaptation phase, the difference between landing position and localization error becomes even more apparent. The normalized values increase from 0.0 to 0.03 and 0.74 for landing position and localization error, respectively. As before, localization error as well differs from pre-adaptation level ($\alpha = .05$).

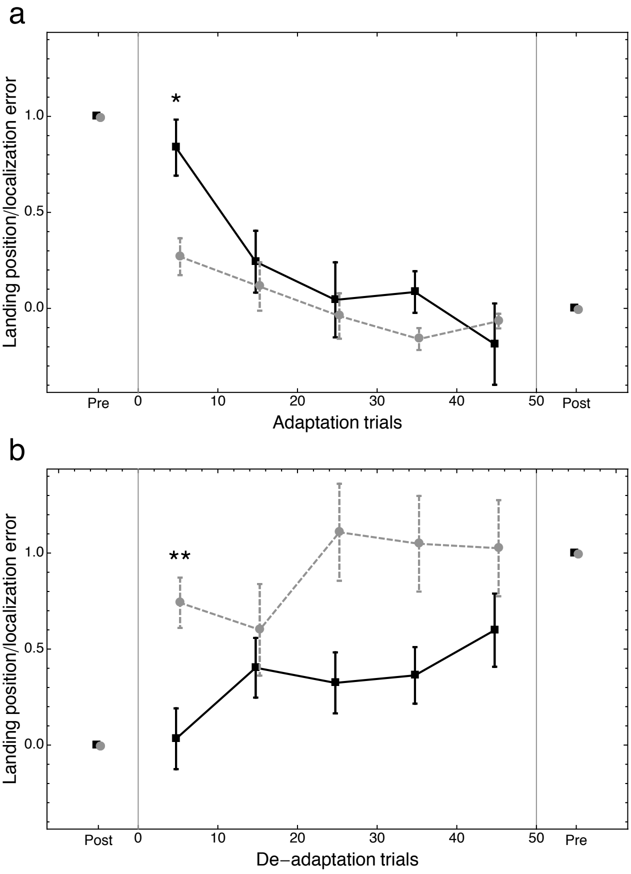

Figure 6.9: Results from Experiment 6. **(a)** Adaptation phase. **(b)** De-adaptation phase. The x-axis shows the trial number within the current phase (adaptation or de-adaptation), the y-axis the saccade landing position and the error in localization, respectively. "Pre" and "Post" columns indicate pre-adaptation and post-adaptation values, respectively. Pre-adaptation values are normalized to 1.0, post-adaptation values to 0.0. Black lines indicate saccade landing position, the dashed, gray lines indicate localization error. Subject's data have been normalized to individual subject's average landing position and localization error in pre-adaptation phase and post-adaptation phase, respectively. All results are means and standard errors across subjects (N=7). Asterisks indicate significant differences between graphs for the first bin of trials (paired *t*-test).

6.5 Discussion

In the first three experiments, we demonstrated that the adaptation-induced shift and the peri-saccadic compression are independent, whereby the two effects can be evoked separately and superimpose if occurring together. The adaptation-induced shift did not differ significantly in high and low luminance-contrast conditions, whereas peri-saccadic compression varied with luminance contrast. The focus of peri-saccadic compression, if occurring, was close to T2. This basically agrees with findings of Awater et al. (2005).

Having quantified the peri-saccadic shift under the same stimulus conditions as the adaptation-induced shift, but with non-adapted saccades, we were able to estimate the time course of the pure adaptation-induced shift by subtracting the data gained under non-adapted conditions from the data gained under adapted conditions, where both shifts occur together. By isolating the adaptation-induced shift in this way we were able to specify its time course in much detail. This revealed several findings. Firstly, the adaptation-induced shift begins to diminish about 100–150 ms before the onset of an adapted saccade. Consequently, pre-saccadic perceptual effects appear to be involved in the disappearance of this effect, since at this time the eyes had not started moving yet and the (adapted) saccade has not been executed. Note that the actual execution of an adapted saccade is nevertheless necessary, given that there was no adaptation-induced shift in adapted fixation trials. Secondly, the decrease of this effect is smooth and gradual and spans about 200 ms. Thirdly, it became obvious that the offset of the adaptation-induced shift occurs sometime during the saccade. This offset time is similar to the offset time of peri-saccadic compression and peri-saccadic shift. This suggests that there is a common time—late during the execution of the saccade—until which the spatial localization is derived from the processing of visual input together with eye movement signals and from which on exclusive retinal signals are used for localization. While the offset time of the adaptation induced shift and other peri-saccadic effects is similar, the time course before saccade start proved to be very different. While the adaptation-induced shift is visible long before an adapted saccade and actually begins to decrease 100 to 150 ms before its start, peri-saccadic compression, peri-saccadic shift, and peri-saccadic suppression all emerge temporally closer to saccade start. Consequently, the origin of the adaptation-induced shift is likely to be different from the origin of the peri-saccadic compression.

Isolating the time course of the pure adaptation-induced shift also enabled us to verify the post-saccadically visible target, T2, as the focus of peri-saccadic compression. Initially, this becomes apparent from Fig. 6.3a, corroborating findings from Awater et al. (2005). However, they had further hypothesized that subtracting the adaptation-induced shift from their data could reveal T1 as the real focus of compression. From our data, we can now exclude this possibility, since the adaptation-induced shift has already disappeared at the time of maximum compression (see Fig. 6.6b).

Awater and Lappe (2006) have suggested that the peri-saccadic compression can be understood as a combination of both: a pre-saccadic compression of the distance between the flashed object and the saccade target, and a post-saccadic localization procedure in which the saccade target is used as a reference, whereby the object location is estimated from its (compressed) distance to the saccade target. This trans-saccadic localization procedure becomes obsolete if the stimulus is presented late during the saccade, because it will still be visible after the saccade. In this case, pure retinal localization is sufficient. A similar trans-saccadic localization procedure may also underly in part the adaptation-induced shift. The localization of the stimulus may be encoded relative to the pre-saccadic target position and read-out after the saccade with respect to the post-saccadic target position. Since the target moved during the saccade, the localization of the stimulus shifts in the same direction as the target movement. This is also in line with T2 being the focus of compression in our experiments, since the occurrence of peri-saccadic compression depends on post-saccadic visual references (Lappe et al., 2000). Although there is strong evidence that peri-saccadic compression per se is not generated by post-saccadic references (Morrone et al., 2005a), post-saccadic references can still define its appearance by deciding whether the saccade target or the stimulus are mislocalized (Awater and Lappe, 2006). Compression towards T2 thus emphasizes the role of T2 as a post-saccadic reference and a potential anchor point for post-saccadic retrieval of positional information. However, the magnitude of the adaptation-induced shift is considerably smaller than the target displacement. The adaptation-induced shift in the amplitude-decreasing condition was only about 3–4 °, compared to the size of the target backstep during the saccade of 6.2 °, and the actual reduction of the saccade amplitude of about 4–5 °. Therefore, the adaptation-induced shift is not a simple one-to-one transformation of neither the target displacement nor the amplitude reduction. It is thus unlikely that the trans-saccadic localization procedure outlined above is the sole reason for the adaptation-induced shift, but it might at least partially be delivering the basis for spatial coding and decoding across an adapted saccade in general.

Experiment 4 with much earlier pre-saccadic stimulus presentations proved the adaptation-induced shift not to be a transient effect that is visible only for a certain time during the planning or execution of an adapted saccade. This applies at least for stimulus onsets up to about 1,000 ms before saccade onset. To our knowledge, there is no peri-saccadic effect that is operative that far pre-saccadically. Instead, the adaptation-induced shift can be expected to arise from a systematic error in the processing of positional information across adapted saccades, being visible for stimuli presented at any time before such a saccade, provided that the localization response is given post-saccadically. Moreover, results of Experiment 4 also limit the potential impact of memory loss on our data. If the adaptation-induced shift was generated by a loss of positional information over time, the adaptation-induced shift was expected to continuously evolve for more pre-saccadic presentation times. Given that there is a reliable positional reference available used for localization, a less reliable stimulus is biased towards this reference. The fixation point or one of the saccade targets could serve as this positional reference (Deubel et al., 1996, 1998; Müsseler et al., 1999;

Deubel, 2004). This bias is expected to increase with increasing reliability of the references and with decreasing reliability of the stimulus (Niemeier et al., 2003, 2007).

The adaptation-induced shift has also been found in trials in which the target was post-saccadically not available as a visual reference (Awater et al., 2005; Collins et al., 2007). We also conducted a control experiment with intra-saccadic target extinction that confirmed this findings (data not shown). If the adaptation-induced shift occurred without visual feedback of the target displacement, it must, at least in part, result from motor signals. Naturally, the actual availability of visual references is the crucial factor in these experiments. Since the experiments of Awater et al. (2005) and Collins et al. (2007) were both not conducted in complete darkness, the availability of external, visual references can not be ruled out.

Different possible origins of the adaptation-induced shift have been proposed, one of them the concept of perceptual remapping (Bahcall and Kowler, 1999). Short-term saccadic adaptation causes changes in saccade gain, i. e. the ratio between the intended and the executed saccade. After amplitude-decreasing adaptation—also referred to as gain-decreasing adaptation—this gain is smaller than 1. This gain change might cause errors, if the intended eye movement is used for converting pre-saccadic to post-saccadic positions, but the actual eye movement differs from that (see Bahcall and Kowler, 1999). In the absence of post-saccadic visual references, the location of a pre-saccadically presented object must be derived from trans-saccadic memory of the retinal location of the object and a motor estimate of the eye displacement, i. e. an efference copy signal (see Honda, 1989, 1991), or some measure of post-saccadic orbital position, such as proprioception of tonic rate of motoneuronal firing. Either of these would be adequate given that the pre-saccadic eye position was constant. Thus, in the case of saccadic adaptation changing the gain of the saccade but not the efference copy signal or the proprioceptive signal, the post-saccadic localization of the pre-saccadic object will be distorted. This model is implausible for several reasons. Firstly, if the altered gain of the eye movement drives the perceptual effects in this way, then the magnitude of the resulting error—the adaptation-induced shift—should equal the amount of saccadic adaptation. However, the observed adaptation-induced shift is somewhat smaller than the gain change of the saccade. Secondly, the localization error predicted from difference between intended and actual saccade is supposed to be mostly uniform across the visual field, which is clearly not the case (Awater et al., 2005; Collins et al., 2007; Bruno and Morrone, 2007). In our experiments, stimuli between T1 and T2 were also shifted significantly further in the direction of adaptation than stimuli before or beyond these targets.

A different approach was recently discussed by Collins et al. (2007). Initially, they established the characteristics of a human adaptation field, i. e. the spatial window around the adapted site in which adaptation transfers to saccades of differing vectors, analogue to the monkey adaptation field (Frens and van Opstal, 1994; Noto et al., 1999; Alahyane et al., 2007). Furthermore, they directly compared the human adaptation field with the pattern of adaptation-induced mislocalization. The stimulus was presented pre-saccadically but had to be localized after the saccade. In conditions with and without post-saccadically visible saccade target—and thus complete or reduced post-saccadic visual references—two distinct and potentially superimposing patterns of localization errors became identifiable. The authors attributed these different patterns to the use of two different sources of positional information: (1) When post-saccadic, exocentric information, i. e. the target T2, is available, it is used for localization; (2) when no or insufficient post-saccadic references are available, extraretinal information is used for localization. So far, this has been described in the reference object theory of Deubel and colleagues (Deubel et al., 1996, 1998, 2002; Deubel, 2004). Collins et al. (2007) applied this theory to the integration of positional information across adapted saccades. Available visual references induced a uniform shift in the direction of adaptation. This shift was larger around T1 and T2, decreasing with increasing distance. With reduced post-saccadic references, the pattern of mislocalization spatially was non-uniform, resembling the adaptation field previously established. The authors thus hypothesize that the metrics of a saccade required to acquire a certain position contribute to the localization at that position. The results of Bruno and Morrone (2007) also indicate that saccadic adaptation affects both the action map and the perception map. In their experiments, a spatially restricted shift in localization occurred for localization by verbal reports as well as for open-loop pointing movements.

Collins et al. (2007) gave evidence of the involvement of two independent mechanisms that may superimpose, interact, or alternate in generating adaptation-induced mislocalization. Following this approach, we aimed at estimating the weight of both sources of information—exocentric visual references, and egocentric extraretinal information—for localization in our experiments. In our experiments, the saccade target was always visible after the saccade. Therefore, visual references should be predominantly used for localization. The object reference theory also postulates that extraretinal information is of no importance when immediate post-saccadic visual references are available (Deubel et al., 1998). Hence, the impact of extraretinal information remains unclear from our Experiments 1 to 5. Moreover, subjects were completely adapted in these experiments. Thus, any observed effects cannot unambiguously be attributed to the use of either visual references or extraretinal signals.

However, Experiment 6 allows for disentangling, at least to some extent, the potential impact of these different sources of information that are potentially used for the retrieval of positional information across adapted saccades. Although usually unnoticed, the pre-saccadic target T1 and the post-saccadic target T2 are not identical. If a stimulus position is pre-saccadically encoded relative to T1 and post-saccadically decoded relative to T2, a constant error of the size of the target displacement (6.2 °) is introduced. Nevertheless, the expected size of the localization error resulting from this landmark effect is smaller than the size of the target displacement (Deubel, 2004). The target is displaced by the same amount in each adaptation trial. In contrast, saccadic adaptation is a gradual process and can be described with an exponential decay curve. Especially in the early trials of the adaptation phase, there is still a considerable mismatch between the actual landing position and the post-saccadic target position. Thus, there is also a considerable mismatch between extraretinal information and post-saccadic visual references. In Experiment 6, the localization error predominantly follows the displacement of the post-saccadic visual reference (see Fig. 6.9 on page 82). From trials with a continuously visible target to trials in which it is displaced during the saccade, the transition of the localization error is quite abrupt, compared to the more gradual adaptation of the saccade amplitude. Consequently, a large part of the localization error is likely to rely on visual references or "landmarks" (Deubel, 2004).

A landmark effect forming the basis of the observed mislocalization is also in line with the notion of the adaptation-induced shift as a non-transient effect, being detectable as long as 1,000 ms before the execution of an adapted saccade. If the position of a stimulus is encoded before but decoded after an adapted saccade, the subsequent localization is affected no matter how long before the saccade the stimulus was actually presented—given that the position is still stored in memory. In our results, there is no evidence for a noticeable memory loss, neither localization judgments nor variability systematically change for stimulus presentations between 400 and 1,000 ms before the saccade. This could be explained by the relatively simple and reduced experimental setup, containing only few potentially competing visual stimuli. Note that before the saccade, stimulus position is not necessarily encoded directly relative to T1. For early pre-saccadic presentation times only the fixation point is visible. Rather, the whole reference system has to be realigned to the post-saccadic reference.

With regard to the use of pre- and post-saccadic visual references, also the time course of the adaptation-induced shift relative to saccade onset has to be reassessed. The adaptation-induced shift gradually decreases between about 150 ms before and 50 ms after saccade onset. This decrease might well reflect the changeover between the pre-saccadic and the post-saccadic reference, relative to which positional information is encoded. Due to latencies and filtering operations in the visual system (see Pola, 2004), stimuli presented shortly before saccade onset might interact with post-saccadic available references. And if a stimulus position is already encoded relative to the displaced, post-saccadically visible target, no adaptation-induced shift becomes apparent. Moreover, the time at which the adaptation-induced shift had completely disappeared, about two-thirds through the saccade, is almost exactly the time at which T1 is replaced by T2.

Visual references are not the only source of information used for the integration of positional information across adapted saccades. From Experiment 6 it becomes apparent that additionally a smaller component is involved that develops slower, potentially along with the motor adaptation. However, our methods utilized here are not sensitive enough to further specify the characteristics of this component in more detail. In particular, we could not distinguish between a perceptual remapping as proposed by Bahcall and Kowler (1999) or the re-structuring of perceptual space as proposed by Collins et al. (2007). More specialized experiments are necessary to clarify this.

Chapter 7

Peri-saccadic representation of object features

Contents

7.1 Abstract

Around the onset of a saccadic eye movement perception is suppressed. This effect is called peri-saccadic suppression. Nevertheless, highly salient stimuli are yet perceived. Stimuli presented briefly around the onset of a saccade are perceived as compressed towards the saccade target. This effect is called peri-saccadic compression. Despite these perceptual deficiencies, object identity is usually retained across saccades. If multiple objects are simultaneously presented and perceptually shifted onto a single location due to peri-saccadic compression, the number of presented objects is underestimated. However, different object features are potentially retained and compete for access to conscious perception irrespective of the corresponding objects being explicitly perceived. This has been demonstrated for the object features *form* and *color*. In our experiments we simultaneously presented stimuli with different motion directions. We show that an object's motion is not retained in the same way as its form or its color. We relate this findings to the dorsal stream—which processes both positional and motion information—being affected by peri-saccadic suppression and peri-saccadic compression. This is not the case for the ventral stream, processing object features as *form* and *color*. In contrast to *form* and *color*, *motion* is not retained independently of other object features and independently of peri-saccadic mislocalization.

7.2 Introduction

Between successive fixations the gaze is rapidly being shifted across the visual scene. Information about the visual world is almost exclusively gathered during fixations. Nevertheless, eye movements are necessary because during each fixation only the small region of the visual scene that falls on the fovea is thoroughly perceived. The rapid, ballistic eye movements between fixations are called saccades.

7.2.1 Peri-saccadic suppression

In the temporal vicinity of saccades visual perception is suppressed. This effect is called *peri-saccadic suppression*. It selectively affects the magnocellular pathway in visual processing (Burr et al., 1994). Therefore, particularly the perception of motion and of low spatial frequencies is impaired, and especially luminance-modulated stimuli contrary to color-modulated stimuli are suppressed (Burr et al., 1994). Peri-saccadic suppression arises about 50 ms before a saccade, peaks around saccade onset, and diminishes within 50 ms after saccade onset (Burr et al., 1994; Diamond et al., 2000; Michels and Lappe, 2004).

Under most conditions peri-saccadic suppression presupposes the execution of a saccade (Diamond et al., 2000) but is independent of the speed, the duration, and the direction of this eye movement (Ilg and Hoffmann, 1993). In contrast, under certain conditions image motion alone—without an actual eye movement—is sufficient to give rise to a suppression of contrast sensitivity that is in many aspects similar to peri-saccadic suppression (Diamond et al., 2000; see also Ross et al., 2001a, for a review). But also with eye movements, peri-saccadic suppression depends on low-level visual features such as background contrast (Diamond et al., 2000) and stimulus contrast (Michels and Lappe, 2004).

However, Castet and Masson (2000) challenged this concept of peri-saccadic suppression. In their experiments they briefly presented moving gratings during saccades. These gratings were spatio-temporally optimized for the characteristics of the magnocellular pathway—i. e. low spatial frequency and luminance modulation—and their motion was adapted to the speed of the eye movement. When the gratings rapidly moved in the direction of the saccade but slightly slower than the velocity of the eye movement at that time, subjects clearly perceived motion opposite to saccade direction (Castet and Masson, 2000). The authors therefore argued that peri-saccadic suppression was due to changing eye velocities during saccades in combination with masking effects of pre- and post-saccadically presented stimuli, rather than a central, extra-retinal mechanism (Castet and Masson, 2000; Castet et al., 2002). But this notion also is debatable, since—under certain conditions, see above—image motion does not generate suppression while eye movements do (Castet et al., 2001; Ross et al., 2001b). Possibly, it is common ground that a central, peri-saccadic compression, driven by extra-retinal signals, “attenuates visual motion but does not eliminate it” (Ross et al., 2001a, page 116).

7.2.2 Peri-saccadic compression

Despite peri-saccadic suppression, particular salient stimuli are still perceived. But the localization of stimuli briefly presented immediately before, during, or after a saccade is systematically distorted towards the saccade target. This effect has been termed *peri-saccadic compression* (Ross et al., 1997). Mostly parallel to the above-mentioned peri-saccadic suppression, it arises about 50 ms before saccade onset, peaks around saccade onset, and elapses within about 50 ms after saccade onset (Ross et al., 1997, 2001a). The error in perceived position is directed towards the saccade target, i. e. in the direction of the saccade for stimuli presented before the saccade target, and against saccade direction for stimuli presented beyond saccade target. This similarly applies to stimuli presented above or below the saccade target on a two-dimensional plane (Kaiser and Lappe, 2004). Peri-saccadic compression depends on stimulus contrast (Michels and Lappe, 2004), and on the availability and usage of post-saccadic visual references (Lappe et al., 2000). Awater and Lappe (2006) developed a multiple-stage model of peri-saccadic compression. It is based on the stimulus position being pre-saccadically encoded relative to the saccade target. According to this, compression occurs as a decrease of this relative distance. For post-saccadic decoding of the positional information, either target or stimulus position serve as absolute reference, depending on respective availability and saliency. Thus, peri-saccadic compression emerges during the retrieval of positional information after the saccade, and manifests as a shift of either perceived stimulus position towards saccade target position or vice versa (Awater and Lappe, 2006). This is in line with a model of Niemeier et al., which implements peri-saccadic compression by optimal inference of information with sub-optimal reliabilities (Niemeier et al., 2003, 2007). The peri-saccadic compression has already been addressed in Chapter 6 on page 53 and the following.

Peri-saccadic compression not only impairs stimulus localization but might also—under certain conditions—improve performance in tasks other than localization. For glass patterns with relatively large displacements in the direction of the saccade, detection performance increases around saccade onset (Santoro et al., 2002). Theoretically, this might be due to peri-saccadic compression scaling down the displacement between the individual pairs of dots. For displacements orthogonal to saccade direction, detection performance decreases (Santoro et al., 2002).

7.2.3 Eye movements and object identity

Both the peri-saccadic compression and the peri-saccadic suppression might yet have further implications for the recognition of objects. Due to peri-saccadic suppression and fast image motion, object perception is likely to be seriously impaired during saccades. Moreover, the pre- and the post-saccadic positions of each object in the visual scene are different. To retain object identity across saccades, objects recognized pre- and post-saccadically have to be linked. As a matter of fact, the visual system preferentially retains object identity across saccades—potentially at the expense of disregarding positional information. This is the case in experiments involving an intra-saccadic stimulus displacement. In these experiments a stimulus, often—but not necessarily—the saccade target, is intra-saccadically removed and replaced at a different position. Nevertheless, subjects predominantly judge the object as being stable, provided that no other visual references are available. Thereby, they disregard the positional offset of the stimulus. This effect has been named the *saccadic suppression of displacement* (SSD). Only if the displacement is too large, or the stimulus has not reappeared by saccade offset, the SSD does not become apparent (Deubel et al., 1996, 1998, 2002; Matsumiya and Uchikawa, 2003).

This is in line with findings of Irwin and Brockmole (2004). In experiments involving an object/non-object discrimination task, saccades did interfere with the recognition of object orientation whereas saccades did not interfere with object recognition. The authors thus conclude that stimulus processing along the so-called *dorsal stream* is selectively suppressed around the time of saccades while this is not the case for the *ventral stream*. These two pathways, although significantly interacting with each other, are functionally dissociable. Areas of the dorsal stream—amongst others MT/V5, MST/V5a, and STS—are specialized for motion processing and spatial localization. Areas of the ventral stream—V4, TE, and TEO—are specialized for object recognition and the processing of object features as depth, color and contours (for reviews, see Haxby et al., 1991; Hoffmann and Wehrhahn, 1996). A simplified illustration of these two visual streams of the visual system can be found in Figure 7.1.

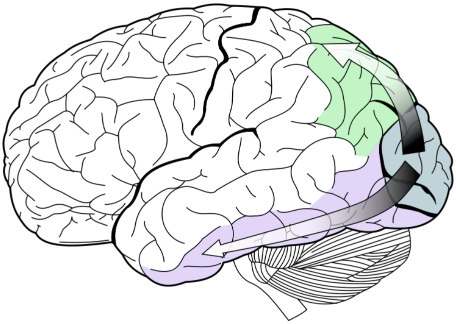

Figure 7.1: Simplified illustration of the dorsal and the ventral stream, represented by the green and purple areas, respectively. Both visual streams originate from a common source in early visual cortex. This picture is published under the terms of the GNU Free Documentation License, Version 1.2 (Free Software Foundation, Inc., 2002).

7.2.4 Peri-saccadic compression and perceived form

With regard to peri-saccadic compression, the perceived position of a briefly presented object is shifted as a function of the presentation time relative to saccade onset, and of the presented position relative to the saccade target. The questions remain whether the form of individual objects is affected by peri-saccadic compression, and whether the post-saccadic retrieval of object features other than position is likewise impaired.

First of all, object identity is also retained under conditions of peri-saccadic compression. Matsumiya and Uchikawa (2001) conducted experiments with the simultaneous presentations of multiple objects around the time of saccade onset. Four vertical bars, arranged side by side, were briefly presented around the saccade target. Subjects were asked to judge the perceived width of this array of four bars. For comparison, a single, solid rectangle of the same width was presented under similar conditions. At the time of saccade onset the perceived width of the four parallel bars was reduced to a much higher extent than the width of the single rectangle. Together with the perceived width, also the total number of perceived bars was considerable reduced. Note that in no case subjects reported perceiving anything like a broader bar, originated from the perceptual merging of several bars (Matsumiya and Uchikawa, 2001). This means that the object feature *form* was unaffected by peri-saccadic compression while the individual object's perceived position was highly distorted.

In contrast, Sogo and Osaka (2007) conducted an experiment in which the form of briefly presented objects was indeed affected by peri-saccadic compression. In their experiments the apparent shape of triangles was distorted in the direction opposite to the saccade. But for one thing this was only a minor ($< .2\,^\circ$) effect, compared to the effect size exceeding $4\,^\circ$ as reported by Matsumiya and Uchikawa (2001), for another object identity—a triangle of a certain size—was nevertheless retained.

However, the form of objects with only illusionary contours is not protected against peri-saccadic compression. Sogo and Osaka (2005) conducted experiments involving the peri-saccadic presentation of Kanizsa rectangles, consisting of single, so-called inducers. These inducers were subject to peri-saccadic compression regardless of their forming an illusionary object. The authors thus conclude that saccadic compression occurs at an earlier level of visual processing than the interpolation process of illusionary contours. In further experiments they increased the number of inducers defining an object. This resulted in a continuum from illusionary figures to “solid” contours. Similarly, the amount of peri-saccadic compression showed a gradual decrease from high values with only four inducers to only little compression with near-solid contours (Sogo and Osaka, 2005).

7.2.5 Object features

More recently, Lappe et al. (2006) extended these findings by investigating the impact of peri-saccadic compression on the object feature *color* in addition to *form*. Their experiments involved—among other things—the presentation of multiple objects of different colors under conditions of peri-saccadic compression. Being compressed onto a single position, their color attributes not only remain distinguishable but further on compete for access to visual awareness. In their experiments, *form* and *color* were retained independently of each other and independently of peri-saccadic mislocalization, i. e. independently of the object’s *position*. Frequently, subjects perceived more different colors than they perceived different bars. The authors thus concluded that peri-saccadic mislocalization affects the position of objects but retains other object features.

7.2.6 Experimental approach

Instead of using *form* and *color* attributes we investigated the peri-saccadic representation of *motion*. We aimed at testing whether *motion* is peri-saccadically retained as this is the case for the aforementioned object features.

Motion information is processed in the magnocellular pathway, and in higher visual areas of the dorsal stream. The magnocellular pathway is selectively suppressed around the time of saccades (Burr et al., 1994). Therefore, also in our experiments motion perception around the time of saccades might be severely impaired. Hypothetically, subjects might be unable to discriminate the presented motion stimuli or the subject's performance might be biased towards some certain motion percept. However, under certain conditions a veridical motion perception is possible around the time of saccades (see Section 7.2.1 on page 93). We designed our stimuli with regard to high saliency and maximum motion strength. Furthermore, in our experiments the motion direction of the presented stimuli was orthogonal to saccade direction to minimize possible effects of eye movement and image motion.

Besides motion information, the dorsal stream also processes positional information, which is known as being highly affected by peri-saccadic compression (see Section 7.2.2 on page 94). This influence on positional information brings about the question of how a different object feature—*motion*—likewise being processed in the dorsal stream, might also be retained. Hypothetically, *motion* could not be retained the same way as object features processed in the ventral stream which is apparently not impaired peri-saccadically.

A new problem arises with regarding *motion* as an object's feature: *Motion* might not be a self-contained attribute of an object. Mathematically, velocity is the derivative of position with respect to time. This means that *motion* could already be extracted from the development of positional information over time. Theoretically, a representation of *position* would be sufficient for keeping track of an object's motion. However, this notion would be highly implausible given that in the human visual system there are at least three systems, working in parallel, explicitly dedicated to the perception of motion (see, for example, Lu and Sperling, 1995). Thus, qualitative and quantitative motion information is effectively being available to the visual system.

In our experiments we used a "pure" motion signal. This means that the stimulus objects—vertical bars—did not move themselves. Their form, i. e. the outline, remained unchanged and stationary on the screen throughout stimulus presentation. Instead, only the bar's surface showed apparent motion. The surface of the bars was a luminance-modulated, sinusoidal grating. The complete motion stimulus was presented for two monitor frames only. The sinusoidal grating moved exactly once from the first to the second monitor frame. By this means we aimed at decoupling the representation of the object's *form* from the mere *motion* signal. We were interested in finding out whether *motion* might be represented as an object's feature independently of its position.

We presented motion stimuli under conditions of peri-saccadic compression. Early before or late after the saccade both bars are perceived side by side near their veridical positions. Around saccade onset both bars are perceptually shifted onto the same position. Hence, subjects perceive only one bar. Trials in which—around saccade onset—only one stimulus is perceived due to peri-saccadic compression constitute the critical condition in this experiment. If *motion* as a stimulus feature is retained independently of *form* or *position*, the motion information of both bars might interact with each other when these bars are shifted onto each other. Hypothetically, compression could improve performance if motion signals were additively (see Santoro et al., 2002). On the other hand, inversely oriented motion signals can as well extinguish each other if something like transparent motion is perceived. Trials with only one stimulus being presented serve as an adequate baseline condition for measuring performance under largely similar conditions. Different assumptions can be made concerning how motion information is represented peri-saccadically. Predictions of the experimental outcomes depend on these assumptions:

(1) *Motion* as an object feature is retained analog to *form* and *color*, and independently of other object features. Hence, in some trials—when two stimuli with opposite motion direction are perceptually shifted onto the same location—single bars with more than just one motion direction are perceived. Potentially, different fea-

ture characteristics, i. e. different motion directions, are perceived as different patches of the stimulus, as reported for perceptual rivalry under conditions of binocular rivalry (Kovacs et al., 1996; Lee and Blake, 2004) and peri-saccadic compression (Lappe et al., 2006). This might as well result in perceiving some kind of transparent motion.

(2) *Motion* as an object feature is retained peri-saccadically, but is not independent of *position*. Thus, in trials with different bars being perceptually shifted onto the same position, representations of *motion* interact with each other in some way. For example, different feature characteristics might mix or superimpose. In contrast to (1), identical motion directions might be preferentially discriminated while opposite motion directions might rather extinguish each other.

(3) *Motion* as an object feature is not retained peri-saccadically. At least, it is not retained independently of *position*. When two stimuli are perceptually shifted onto one identical position, only one feature characteristic of *motion* is perceived. The different motion stimuli—as opposed to their object feature *motion*—compete for access to visual awareness in a "winner takes all" manner. Therefore, no difference between identical and opposite motion directions should become apparent.

7.3 Methods

7.3.1 Subjects

A total of sixteen subjects, twelve female and four male, participated in the experiments described below. Of those, fifteen were naïve to the aims of the experiment, ten actually being completely unexperienced in eye movement experiments, and one an author. Their age ranged between 21 and 38 years. For more information see Section 4.4 on page 27.

Data of four subjects had to be discarded due to a lack of valid trials in the critical condition, as described in the Data analysis section (see Section 7.3.4 on page 106).

7.3.2 Apparatus

Two personal computers were running the experiments: a Windows PC housing the eye tracking system, thus sampling gaze position throughout the experiments, and a Macintosh PC for stimulus presentation. The two computers were synchronized and connected to each other via a dedicated ethernet connection. The *EyeLink II* system (*SR Research, Inc.*, Canada) was used, sampling eye position at a frequency of 500 Hz. For more information see Section 4.1 on page 24.

The presentation monitor was a 22 " (20 " visible screen diagonal) *iiyama Vision Master Pro 514*, running with a vertical frequency of 200 Hz at a resolution of 800×600 pixels. Stimulus events (onset and offset times of presented items, synced to actual monitor refreshes) were sent from the Macintosh PC to the Windows PC. Stimulus events were stored together with the eye movement events for offline analysis. Subjects were seated in a dimly lit room. Their head was supported by a chin rest, about 45 cm distant from the center of the stimulus screen.

7.3.3 Experimental conditions

Main experiment

All 16 subjects participated in the main experiment. Before beginning the first experimental block, each subject received detailed instructions by the investigator and was allowed to perform some trials to familiarize with the task. At the beginning of each experimental block the eye-tracking system was adjusted, calibrated and validated. An experimental block comprised of 100 trials, and each subject participated in between four and ten experimental blocks (on average 5.5 blocks, corresponding to 550 trials).

The background of the monitor screen was medium gray throughout the experiment. In the beginning of each trial the subject fixated a fixation mark (a yellow square of $1.25\,^\circ \times 1.25\,^\circ$ visual angle) that was presented $12.5\,^\circ$ to the left of the center of the screen and vertically centered. The luminance of the background and the fixation mark was 6.2 cd/m^2 and 47.5 cd/m^2, respectively, resulting in a Michelson contrast (C_M) of 0.77. After a random interval between 700 ms and 1,300 ms the fixation mark disappeared and at the same time the saccade target appeared 25 ° to the right of the fixation mark. Subjects were instructed to execute a saccade towards the target as fast as possible after its presentation. At some pseudo-randomized time between about 80 ms before (referred to as −80 ms) and about 80 ms after saccade onset one or two motion stimuli were presented. The time of stimulus presentation was estimated *a priori* from subject's latency if available. 500 ms after presentation of the motion stimuli a response mask appeared. Subjects were required to indicate the number of perceived bars (from 0 to 2 bars). Independently for each perceived bar subjects also indicated perceived motion directions: either upward, downward, both, or none. That way, two tasks were performed independently: a *stimulus detection* task (indicating the number of bars), and a *motion discrimination* task. After completion of both tasks, the next trial started. A simplified diagram of the sequence of events in a single trial can be found in Figure 7.2.

The motion stimuli consisted of vertical bars of 0.75 ° × 31.25 °. The luminance of these bars was sinusoidally modulated along their vertical length with a spatial frequency of 0.5 cycles per degree (CPD). Peri-saccadic compression has been demonstrated to occur only moderately for stimuli of this spatial frequency (Burr et al., 1994). The luminance of the gratings was sinusoidally modulated between minimum and maximum gamma-corrected values of 3.0 cd/m^2 and 119.9 cd/m^2, respectively, resulting in a contrast C_M of 0.95. The motion stimuli were each presented for 10 ms, i. e. two monitor frames. From the first to the second frame the phase of the grating was shifted by 0.625 °, corresponding to 0.31 cycles. This single step between two monitor frames is the minimal prerequisite for inducing apparent motion. The velocity of this apparent motion theoretically adds up to 125 °/s, corresponding to 62.5 cycles per second (Hz).

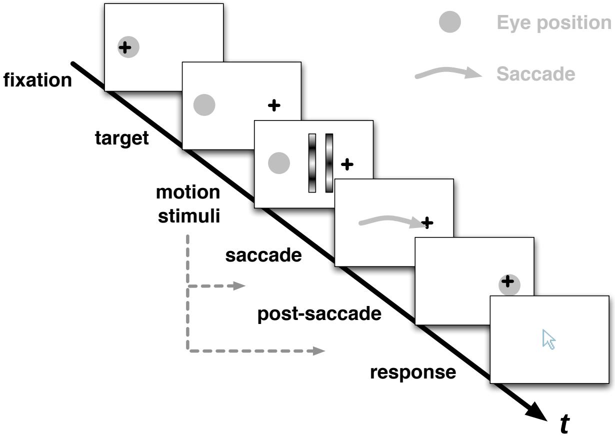

Figure 7.2: Diagram of the sequence of events in the main experiment. In the beginning of each trial subjects fixated a fixation mark. After 700–1,300 ms the fixation mark disappeared and the saccade target appeared 25 ° to the right. At some random time before, during, or after the saccade (indicated by dashed, gray arrows) one or two motion stimuli were presented for 10 ms (see Fig. 7.3). 500 ms after appearance of the saccade target, a response mask and a mouse pointer appeared. Subjects indicated the number of perceived bars and the perceived motion direction of each bar.

Both step size (Δx) and motion velocity were adjusted to maximize the subjective motion percept. Moreover, parameters were chosen to be as close as possible to parameters that yielded reliable activation of motion selective neurons in areas V1 and MT in macaque monkeys (Mikami et al., 1986a,b), and that have already been tested psychophysically (Newsome et al., 1986).

In 33 % of trials, pseudo-randomly selected, only one stimulus was presented. In the remaining 67 % of trials two stimuli were presented simultaneously. Stimulus positions were 22.5 ° and 23.75 ° to the right of the fixation mark, corresponding to 2.5 ° and 1.25 ° to the left of the saccade target, respectively. In trials with only one stimulus being presented, stimulus position was pseudo-randomly selected from one of the two possible positions. The direction of motion (upwards or downwards) was also pseudo-randomly selected for each motion stimulus independently. The hence resulting combinations of stimulus positions and motion directions are shown in Figure 7.3 on the facing page.

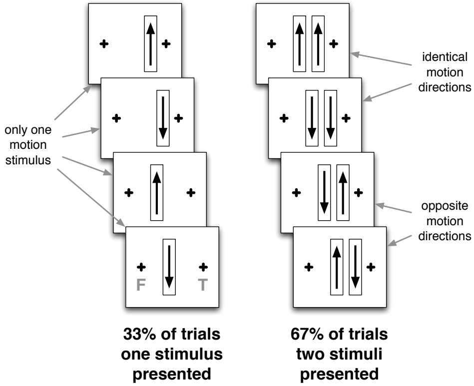

Figure 7.3: Possible combinations of motion stimuli. In 33 % of trials only one motion stimulus was presented. The stimulus appeared at one of two positions; motion direction was either up- or downwards. In 67 % of trials two motion stimuli were presented simultaneously. Motion direction of each stimulus was either up- or downwards, randomized independently.

Localization experiment

The main experiment, as described above, presupposes the occurrence of peri-saccadic compression. It is assumed that under the given conditions two motion stimuli are perceptually shifted onto a single position in certain trials. In the localization experiment this is exemplarily verified for a narrowed group of subjects.

Only four of the subjects from the main experiment, two male and two female, and one the author of this thesis, also participated in the localization experiment. Subjects were arbitrarily chosen according to their availability for further experiments. The localization experiment was conducted after completion of the main experiment. An experimental block consisted of 150 trials, and each subject participated in two experimental blocks.

The experimental setup was identical in many respects to the main experiment. The two experiments only differed in the number of presented stimuli per trial and in the response procedure. In the localization experiment only one motion stimulus was presented in each trial. Stimulus position and appearance remained unchanged. Furthermore, subjects only indicated the perceived position of the stimulus by means of the mouse pointer. Neither the number of perceived bars nor the direction of motion had to be answered.

Control experiments

We conducted control experiments in two conditions with modified stimulus parameters. Thereby, we aimed at testing whether different spatial and temporal frequencies might yield stronger motion percepts.

Three subjects, one female and two male, one of which the author of this thesis, participated in the control experiments. Two subjects took part in each of the two experimental conditions. All subjects had also participated in the main experiment. The control experiment was conducted after completion of the main experiment. An experimental block comprised 100 trials, and each subject participated in between two and four blocks.

The experimental setup was in all respects identical to the main experiment, except some parameters of the moving sinusoidal grating. In one condition motion velocity was increased, in the other condition it was decreased. In the *increased motion condition* the spatial frequency of of the grating was lower, while the displacement of the grating (Δx) was increased, resulting in a higher overall motion velocity. Spatial frequency of the grating was 0.18 CPD, Δx was 1.375 ° (corresponding to 0.25 cycles), and velocity was 275 °/s (corresponding to 50 Hz). In the *decreased motion condition* spatial frequency was not changed. Instead, the displacement of the grating was decreased, resulting in a lower overall velocity. Spatial frequency was 0.5 CPD, Δx was 0.25 ° (0.125 cycles), and velocity was 50 °/s

(25 Hz).

Experiments with the motion stimuli being presented for more than two stimulus frames had been discarded in early stages of realization. Such an experimental setup turned out to be problematic because subjects frequently reported perceiving far more than two bars.

7.3.4 Data analysis

Data analysis was accomplished in *Mathematica 6.0* (*Wolfram Research, Inc.*). Single trials were discarded when the saccade latency was higher than 500 ms, the saccade target was missed by more than 5 °, or subjects responded they had not seen a stimulus.

To test the introduced hypotheses (see Section 7.2.6 on page 98) the critical condition comprised trials with stimulus presentations in a time window 50 ms around saccade onset, in which two motion stimuli were presented but only one stimulus was perceived. In this time interval, peri-saccadic compression occurs. The underestimation of the number of presented bars in this epoch is due to the perceptual shifting of two stimuli onto one identical location. The amount of this peri-saccadic compression varies across subjects. Thus, the number of trials in the critical condition likewise varied across subjects in our experiment. For analysis the probability for perceiving motion in different conditions was calculated. A minimum number of trials is necessary to allow for meaningful calculations. Thus, subjects of which less than 25 valid trials in the critical condition were achieved were discarded from further analysis.

7.4 Results

7.4.1 Main experiment

Data were analyzed separately for trials with one or two motion stimuli being presented, respectively.

Results of trials in which only one motion stimulus was presented are shown in Figure 7.4 on the following page. Subjects indicated perceiving one stimulus in most trials—in the *stimulus detection* part of the task—given that the stimulus was presented either before saccade onset or after saccade end. Only just around saccade onset a slight dip is visible, potentially due to peri-saccadic suppression. Thus, stimuli are correctly perceived in a vast majority of trials. In contrast, when presented during saccades, subjects more frequently perceived two bars where only one was presented. Due to the velocity of the eyes, the images of the single bar in two successive monitor frames probably deviated as much, so that they were interpreted as two separate bars. Only between 30 ms and 50 ms after saccade onset the results in the stimulus detection task differ significantly from 1 (t-test; $\alpha = 5\%$, Bonferroni-corrected) across subjects. Performance in the *motion discrimination* task differed from stimulus detection. If a stimulus was presented more than about 30 ms before saccade onset or after saccade end, subjects most likely perceived the motion of the stimulus. Around saccade onset subjects more frequently responded perceiving no motion. The minimum in performance is reached at saccade onset. At this time, averaged across subjects, in only about 25 % of the trials the motion of the stimulus was perceived. Results significantly (t-test; $\alpha = 5\%$, Bonferroni-corrected) differ from 1 between −20 ms and 20 ms relative to saccade onset.

Results of trials in which two motion stimuli were presented can be found in Figure 7.5 on page 110. In the *stimulus detection* task, the average number of perceived bars dropped from slightly less than 2 to about 1 around saccade onset. Before saccade end, ratings already recovered to a value of about 2. Results differed significantly (t-test; $\alpha = 5\%$, Bonferroni-corrected) from 2 between −20 ms and 40 ms relative to saccade onset. This decrease is probably due to a combination of both peri-saccadic suppression and peri-saccadic compression. Peri-saccadic suppression alone is not sufficiently strong, as estimated from the condition with only one stimulus being presented (see Figure 7.4). Peri-saccadic compression shifts the perceived po-

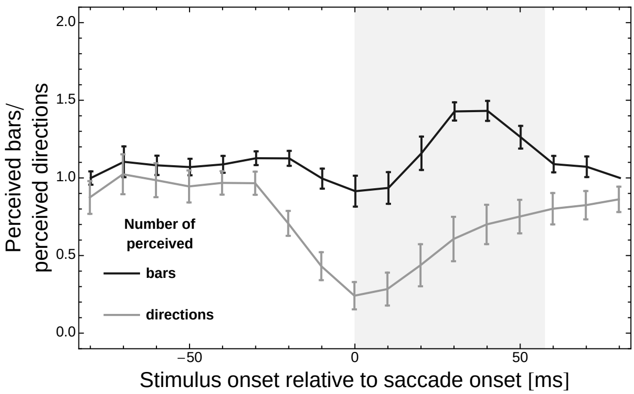

Figure 7.4: Number of peri-saccadically perceived bars and directions when only one bar was presented. All results are means across subjects (N=12); error bars indicate standard errors. The black and the gray line represent the number of perceived bars and motion directions, respectively. The light gray area indicates the time of saccade start and average saccade termination.

sition of the two stimuli towards saccade target. If both stimuli are shifted onto one identical position, i. e. the saccade target, subjects underestimate the number of presented stimuli (see Matsumiya and Uchikawa, 2001). Our localization experiment (see Section 7.2.2 on page 94) addresses this issue, measuring the actual amount of perisaccadic compression under similar experimental conditions. In the *motion discrimination* task early before saccade start and after saccade termination on average about 1.5 motion directions were perceived, i. e. subjects responded the motion of about 75 % of the presented bars. Around saccade onset the number of perceived motion direction drops to values below 0.5 around the time of saccade onset. This corresponds to less than 25 % of motion stimuli being discriminated as moving, thus comparable to the results of trials with only one stimulus being presented. Results differed significantly (t-test; $\alpha = 5\%$, Bonferroni-corrected) from 2 between -60 ms and 70 ms

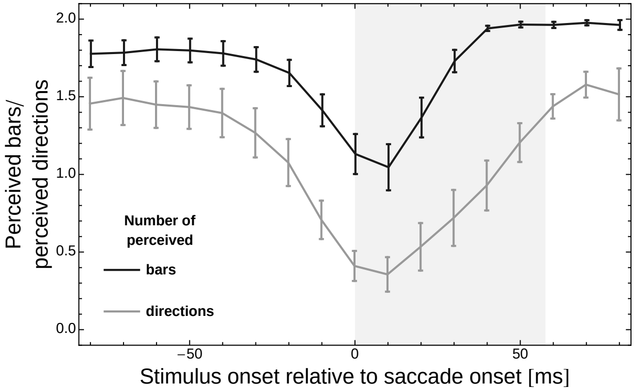

Figure 7.5: Number of peri-saccadically perceived bars and directions when two bars were presented. All results are means across subjects (N=12); error bars indicate standard errors. The black and the gray line represent the number of perceived bars and motion directions, respectively. The light gray area indicates the time of saccade start and average saccade termination.

relative to saccade onset. Note that the number of perceived motion directions was lower than the number of perceived bars. This is in contrast to experiments with bars of different colors (Lappe et al., 2006), in which subjects reported perceiving more different colors than bars around saccade onset.

So far, we did not differentiate between trials with opposite and identical motion directions for trials in which two stimuli were presented. However, if we hypothesize that the representations of the object feature *motion* of stimuli perceptually shifted onto the same location might interact with each other, data has to be broken down by motion directions. The *critical condition* exclusively comprises trials with two stimuli being presented but only one stimulus being perceived. To increase probability that this underestimation of stimulus number is actually due to peri-saccadic compression only trials were included with stimulus presentation times between −50 ms and

50 ms relative to saccade onset. In a first step, we calculated the total number of trials in this critical condition for each subject independently. Trials with identical and opposite motion directions were analyzed separately. In a second step, we calculated from these trials the proportion of *perceived* bars to which subjects assigned a motion percept. Note that this is done for each bar independently, and only for perceived bars, i. e. successfully detected stimuli. Theoretically, individual bars to which subjects assigned two motion directions at the same time are included in analysis with twice the weight of bars to which only one motion is assigned. However, this was rarely the case. Note that there is no consideration of whether a motion discrimination is *correct* or not. This is inevitable since in trials with two stimuli being presented and only one stimulus being perceived there is no “correct” answer, given that the stimuli move in opposite directions. In this case both motion directions are actually presented. Analog calculations were carried out for trials with only one stimulus being presented—serving as a baseline without potential interaction between different object features—and for trials with two stimuli being presented and both of them being perceived. In these trials stimulus presentation times were likewise restricted to a time window of 50 ms around saccade onset. By doing so, discrimination performance in these three different conditions became quantitatively comparable.

Results of these analyses are shown in Figure 7.6. In trials with only one stimulus being presented—the baseline condition—subjects were able to discriminate motion direction in about 50 % of all stimuli that were perceived at all. This proportion was slightly smaller in trials with two stimuli being presented but only one stimulus being perceived. In trials with two stimuli presented and two stimuli perceived, the proportion of perceived bars with a perceived motion was comparable to baseline condition. Furthermore, in the critical condition the proportion of bars with a perceived direction, i. e. the conditional probability of perceiving motion when perceiving a bar, was lower for opposite compared to identical motion directions. The

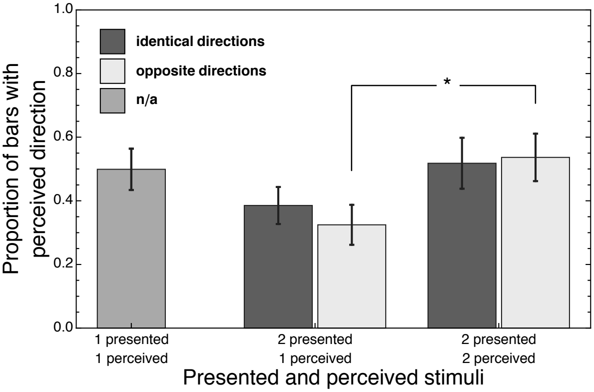

Figure 7.6: Probability of perceiving the direction of motion of perceived bars. Results are means across subjects (N=12); error bars indicate standard errors. The three conditions are different combinations of actually presented and subjectively perceived bars in each trial. Bar colors indicate identical (dark gray) and opposite (light gray) motion directions, respectively. This is not applicable to trials with only one stimulus being presented. The asterisk indicates significant (t-test, $\alpha = .05$) differences between conditions.

opposite is true in the condition with two stimuli presented and both of them perceived. Only for opposite motion directions the difference between these two conditions were statistically significant (dependent t-test, $\alpha = .05$). All other differences did not reach significance.

7.4.2 Localization experiment

The results of the localization task are represented in Figure 7.7 on the facing page. Results for the two different stimulus locations were analyzed separately. Stimulus locations were identical to the main experiment. Localization was erroneous for stimuli presented at either location and for a wide range of presentation times relative to saccade onset. Only after saccade termination localization was nearly veridical. Early before saccade onset ($< -50\,\text{ms}$) localization judg-

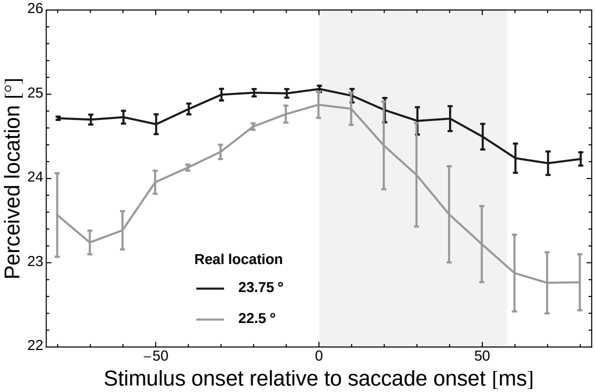

Figure 7.7: Localization of peri-saccadically presented bars. All results are means across subjects (N=4); error bars indicate standard errors. The black and the gray line represent different stimulus locations. The light gray area indicates the time of saccade start and average saccade termination.

ments were biased towards saccade target. Nevertheless, localization judgments were clearly different from each other for different stimulus positions. Between about 50 ms before saccade onset and saccade offset both graphs converge towards saccade target. In this epoch localization is affected by peri-saccadic compression. This effect is maximal around saccade onset. At this time perceived location of stimuli presented at different positions are nearly congruent. Localization results of both stimulus locations are no longer significantly (t-test; $\alpha = 5\%$, Bonferroni-corrected) different between -10 ms and 40 ms relative to saccade onset. Note that the graphs only represent the mean position of the stimuli. Individual motion stimuli are 0.75 ° wide. Therefore, stimuli would be overlapping if their mean positions were separated by less than 0.75 °. Naturally, in these trials only one stimulus was presented at a time.

7.4.3 Control experiments: Variation of stimulus parameters

Results of the control experiments are not shown here. Subjects performance was not better in one of the tasks, neither *stimulus detection* nor *motion discrimination*, compared to the main experiment. Furthermore, in the critical condition, differences between stimuli with opposite or identical motion directions were comparable to the main experiment. Thus, no qualitatively new findings could be obtained from these experiments.

7.5 Discussion

The experiments described in this chapter were designed to investigate the peri-saccadic representation of motion information, and of the object feature *motion* in particular. The object features *form* and *color* are known to be represented independently of an object's *position*, and to be—at least partially—retained under conditions of peri-saccadic compression, when multiple objects are perceptually shifted onto one single position. In this case, individual object features compete for access to visual awareness. The peri-saccadic perception of the respective objects reflects this competition. For example, the form of compressed objects is protected (Matsumiya and Uchikawa, 2001), subjects frequently perceive a single bar with different colors at the same time, and the contour of an object is perceived on a background of identical color and luminance (Lappe et al., 2006).

We aimed at testing whether *motion* is also an object feature that is preferentially being processed, and represented independently of other object features under conditions of peri-saccadic compression. An argument in favor of this assumption is that motion information is indeed extensively processed by specialized structures of the visual system. This ranges from direction selective cells in V1 to higher visual areas dedicated to the analysis of complex motion patterns.

An argument against this is that motion information is processed in brain areas along the magnocellular pathway and the dorsal stream, which are supposed to be suppressed around the time of saccades (Burr et al., 1994). The object features *form* and *color* are both processed along the ventral pathway, which is not suppressed in the temporal vicinity of saccades.

We put forward different hypotheses that predict different experimental outcomes. (1) *Motion* is retained the same way as the object features *form* and *color*. Independently of an object's *position* and independently of the number of perceived objects their motion directions remain—at least to some extent—distinguishable. Under conditions of peri-saccadic compression subjects potentially perceive more different motion directions than different objects. (2) *Motion* as an object feature is peri-saccadically retained, but not independently of *position*. If two objects are perceptually shifted onto the same position their feature characteristics might interact with each other. In the case of identical motion directions the motion percept at the position of the single, perceived object might even be increased. In the case of opposite motion directions both feature characteristics might extinguish each other. (3) *Motion* as an object feature is not retained peri-saccadically—at least not independently of the object itself, i. e. the object's *identity*. If two objects are perceptually shifted onto the same position the feature characteristic of either the one or the other object is perceived, without interaction. In this case motion discrimination is independent of the relative motion direction of the two stimuli. See also Section 7.2.6 on page 98 in the Introduction of this chapter.

In the main experiment (see Section 7.4.1 on page 107) subjects were required to attend to two tasks at the same time: to *detect* briefly presented stimuli and to *discriminate* their motion direction. The combination of both tasks should allow for assessing the representations of objects and of this object's features, i. e. its motion direction, independently. Thereby, the afore-mentioned hypotheses could be tested. The main experiment revealed several findings. Firstly, peri-saccadic suppression affects the motion discrimination task to a higher extent than the stimulus detection task (see Figure 7.4 on page 108). This corroborates what was already known of peri-saccadic suppression selectively affecting the magnocellular pathway (Burr et al., 1994). Secondly, subjects did not perceive more different motion directions than they perceived different stimuli (see Figure 7.5 on page 110). This is unlike experiments with *form* and *color* (Matsumiya and Uchikawa, 2001; Lappe et al., 2006), and already renders the first hypothesis improbable. However, the relative motion directions of the stimuli—either identical or opposite—and the number of perceived stimuli in each trial have to be taken into account to allow definite conclusions to be drawn about the representation, retaining, and independence of *motion*.

The probability of perceiving the motion direction of a perceived bar was slightly lower in the *critical condition*—i. e. two stimuli being presented but only one stimulus being perceived—compared to only one stimulus being presented (see Figure 7.6 on page 111). Naturally, not all missed stimuli are subject to “complete” peri-saccadic compression, i. e. two stimuli being perceptually shifted onto each other, although the occurrence of peri-saccadic compression was confirmed in the localization experiment (see Section 7.4.2 on page 112). Some misses could also be caused by peri-saccadic suppression. But peri-saccadic suppression also affects trials in which only one stimulus is presented. Moreover, peri-saccadic suppression would affect perception independently of motion direction. Potential differences between stimuli with identical and opposite motion directions cannot be due to peri-saccadic suppression. But in the critical condition the probability of perceiving motion is indeed lower for opposite than for identical motion directions. Although this difference is only minor and falls short of reaching significance, it is further evidence of *motion* not being retained independently of other object features. Thus, the first hypothesis could be disproved with some probability as it predicts the exact opposite.

In the case of two stimuli being presented and both being perceived, the overall probability of perceiving motion was higher compared to the critical condition. It approximately equals the probability in the baseline condition with only one stimulus being presented. Moreover, the effect of motion direction reversed compared to the critical condition. Here, the probability of perceiving motion was higher for opposite compared to identical motion directions. As in the critical condition, this effect was rather small and did not reach significance. Nevertheless, results for trials with opposite motion directions differed significantly across conditions. This was not the case for identical motion directions.

Both effects—a lower overall probability of perceiving motion in the critical condition and the apparent interaction of relative motion direction with the probability of perceiving motion—give evidence of *motion* not being retained independently of an object's *position.* This is in line with the second hypothesis. Furthermore, this interaction of the perception of *motion* with the relative motion direction of the stimuli is in conflict with the third hypothesis, which postulates the independence of motion perception and relative motion direction. We therefore conclude that, firstly, *motion* as an object feature is peri-saccadically retained independently of object *identity. Motion* attributes of objects perceptually shifted onto the same location are able to interact with each other, irrespective of the corresponding object being perceived. Secondly, in contrast to object properties as *form* and *color*, *motion* is not represented independently of *position. Motion* attributes of objects perceptually shifted onto the same location are not able to independently compete for access to visual awareness. Neither only one *motion* attribute is perceived independently of the other, nor is more than one attribute perceived at the same time and at the same location. Instead, different *motion* attributes perceptually shifted onto the same position interfere with each other, resulting in a motion discrimination performance inferior to performance with only one *motion* attribute being processed.

Motion information, as well as positional information, is processed along the dorsal stream. Peri-saccadic compression is reflected in highly distorted positional information. The partial interference of *motion* and *position* found in our experiments is best explained by assuming parallel processing of both object features. During object recognition motion representations are generated from each of the two stimuli independently. Before completion of these representations, identical positions are assigned to these stimuli during feature binding, and thus interfere with each other. This is unique for the object feature *motion*, due to its appertaining to the dorsal stream. Object features other than *motion*, such as *color* and *form*, are processed in the ventral stream, and representations are completed before entering the level of feature binding. However, feature binding itself, i. e. the mechanism of creating a unified conscious perception from distributed and parallel neuronal representations, is far from being understood. Peri-saccadic perception, by means of bringing individual object features into conflict with each other, might be a tool for further exploring the mechanisms underlying feature binding.

Chapter 8

Affective saccade targets[1]

Contents

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[1] The experiments described in this chapter have been designed and conducted in collaboration with Ms. Claudia Fontaine, University of Münster

8.1 Abstract

The selective orienting of spatial attention is a key factor for the exploration and analysis of the visual world. Spatial attention enhances and accelerates processing of information from spatially confined areas in the visual field. Emotionally relevant stimuli attract attention with high probability. Attention also plays a crucial role for the preparation of saccadic eye movements. We conducted experiments combining both the presentation of affective pictures and the execution of a saccade. Pictures were selected from the *International Affective Picture System* (IAPS; see Lang et al., 2005), and subdivided into three groups with negative, neutral, and positive affective valences, respectively. Single pictures served as saccade targets and were presented for 100 ms. At a random time before, during or after the saccade a localization stimulus was briefly presented. We examined influences of the affective valence of the saccade target on saccade execution and peri-saccadic localization. We found a trend towards shorter saccade latencies in trials with affective, i. e. negative and positive, compared to neutral saccade targets. Furthermore, the amount of peri-saccadic suppression was higher for negative affective valences.

8.2 Introduction

Exploring the visual world is a vital skill for humans. On the retina only the fovea has the characteristics necessary to provide the visual system with the desirable degree of detail, for instance, high spatial resolution, high contrast sensitivity, the ability to process color. Therefore, eye movements are necessary for rapidly shifting the fovea across the visual scene. These fast, exploratory eye movements are called saccades.

Salient visual features, and especially abruptly appearing stimuli, are likely to capture spatial attention (Yantis and Jonides, 1984; Remington et al., 1992; Schreij et al., 2008). Independently of eye movements, attention enhances visual processing in terms of accuracy (Cameron et al., 2002; Carrasco et al., 2004b) and processing speed (Handy et al., 1996; Carrasco and McElree, 2001; Carrasco et al., 2003, 2004a, 2006). Spatial attention is shifted to potential targets of future eye movements (Deubel and Schneider, 1996; Hunt et al., 2007b; Baldauf and Deubel, 2008). Often—but not indispensably—the eyes follow this shift of attention. While attention can be shifted covertly without preparing a saccade (Juan et al., 2004), saccades cannot be elicited without previously shifting the attention (Hoffman and Subramaniam, 1995; Kowler et al., 1995). Moreover, saccade preparation and the orienting of spatial attention share common neural networks, particularly FEF (van der Lubbe et al., 2006; Neggers et al., 2007). In Chapter 5 on page 29 we already emphasized the close connection between eye movements and spatial attention. Emotionally relevant stimuli are also likely to capture attention (Öhman et al., 2001; Phelps and LeDoux, 2005; Bradley et al., 2006). This makes sense given that many emotional stimuli are also behaviorally relevant, for instance social interactions or threat signals. Therefore, these stimuli receive preferential processing to facilitate potential reactions.

The amygdala is a brain region in the medial temporal lobes that is involved in the fast processing of emotionally relevant information (Anderson and Phelps, 2001; Anderson et al., 2003; Vuilleumier et al., 2004). In some contexts the amygdala is more specifically described as a “danger detector”, tuned especially to threat signals (Amaral, 2003; Anderson et al., 2003). The amygdala enhances perceptual and attentional processes subsequent to such relevant stimuli. This can be accomplished even without conscious perception of the respective stimulus (Whalen et al., 1998; Williams et al., 2004; Phelps and LeDoux, 2005). Furthermore, during fear conditioning the amygdala is active parallel to the sensory cortex (Morris et al., 2001). The amygdala receives sensory input via two pathways, the so-called “high route” and “low route” (see LeDoux, 1998; Pessoa, 2008). Firstly, the low route leads from the thalamus directly to the amygdala. This direct projection lacks most processing stages of the visual system but is fast enough to realize very short reaction times to potentially aversive stimuli. For instance, the amygdala stimulates the sympathic nervous system via the lateral hypothalamus, and the release of ACTH via the paraventricular nucleus of the hypothalamus. These are preparations for typical, so-called “fight or flight” reactions. Secondly, via the high route, visual information from the thalamus is processed in striate and extrastriate visual cortices, and further on by areas of the ventral stream, before being relayed to the amygdala. The ventral stream comprises areas involved in different levels of object recognition. The high route is slower compared to the low route, but it provides more detailed and highly processed information (Phelps and LeDoux, 2005; Pessoa, 2008). Furthermore, there are differences in spatial frequency selectivity between both routes (Vuilleumier et al., 2003).

Emotion and attention interact in various ways relating to visual perception. (1) Emotional stimuli most likely attract attention. Information from ventral areas—i. e., via the high route—reaches the amygdala, which projects to attentional areas, like the lateral prefrontal cortex (LPFC). Connections of the amygdala with selected visual and attentional areas are shown in Figure 8.1 on the facing page. (2) Stimuli of only potential emotional relevance might also attract attention. Information from the thalamus is passed directly to the amygdala—i. e., via the low route—which then projects to attentional areas. No object recognition occurs along this pathway. Thus, the potential relevance of information is based on rather low-level visual information, such as luminance, color, and spatial frequencies (see Pessoa, 2008). (3) Emotionally relevant—or at least potentially relevant—stimuli are processed preferentially. The amygdala projects to different visual areas, presumably enhancing the processing of information from spatially confined retinal positions independent of spatial attention. This has been demonstrated with facial expressions in humans (Schupp et al., 2004). Furthermore, emotion enhances contrast sensitivity irrespective of attention *and* potentiates the effect of attention on contrast sensitivity (Phelps et al., 2006; Schupp et al., 2007b). This is consistent with findings that in

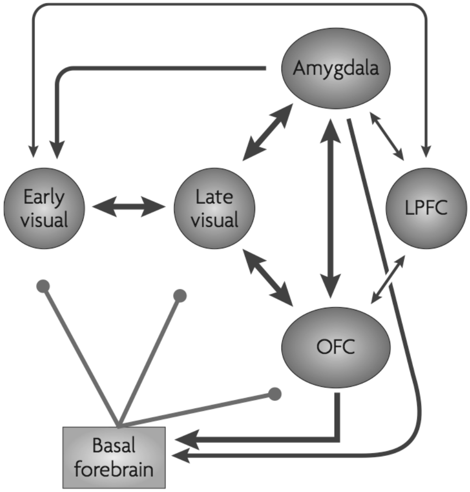

Figure 8.1: Simplified connectivity of the amygdala with selected visual and attentional brain areas. Line thickness gives an idea of approximate connection strength. The basal forebrain exerts diffuse, modulatory effects. LPFC, lateral prefrontal cortex. OFC, orbitofrontal cortex. From Pessoa (2008).

macaque monkeys projections from the amygdala to visual areas V1 and TE are organized topographically (Amaral et al., 2003; Freese and Amaral, 2005). (4) Moreover, emotion might interfere with explicit, feature-based attention under conditions of highly demanding tasks (Schupp et al., 2007a).

Amygdala activation in response to the presentation of emotional pictures has been directly verified by means of fMRI (Anderson et al., 2003; Williams et al., 2004; Junghöfer et al., 2006). Besides the measuring of brain activity, several physiological and behavioral parameters have been utilized to indirectly estimate the impact of affective stimuli processing. Bradley et al. (2001a,b, 2006) used measurements of skin conductance, heart rate, and the startle reflex while presenting pictures from the *International Affective Picture System* (IAPS). Thereby, brief presentations of emotional pictures are sufficient to elicit the respective reactions. With unmasked stimuli, Codispoti et al. (2001) observed physiological reactions—i. e., heart rate, skin conductance, and corrugator EMG—persisting several seconds after a brief (500 ms) presentation of emotional pictures. Larson et al. (2005) found a modulation of the blink reflex after a presentation of emotional pictures for only 300 ms. Even shorter presentation durations were used by Junghöfer et al. (2006) in a rapid serial presentation with rates of up to 6 Hz. Nevertheless, fMRI revealed emotion-sensitive activation in different attentional and visual brain areas. The possibility of presenting stimulus pictures very briefly is of particular importance for our experiments, as described below.

As described above, attention and saccadic eye movements are closely coupled, as well as attention and emotion interact on different levels. In our experiments, we combined the presentation of affective pictures with eye movements in a novel approach. To our knowledge, the potential impact of affective pictures on saccade planning and execution, and on peri-saccadic perception has not been studied yet. We used pictures taken from the IAPS, and presented them as saccade targets. Additionally, a localization stimulus was briefly presented around the time of saccade onset. Subjects were instructed to indicate the perceived position of this stimulus after each trial. Although this is in parts an exploratory study, we nevertheless aimed at testing several hypotheses and predictions.

(1) Does the affective valence of the saccade target influence subject's reaction time, i. e. saccade latency? Prior to a saccade, attention is mandatorily shifting to the saccade target. Furthermore, affective pictures are able to attract attention. The question remains whether both attentional effects interact and whether this interaction affects saccade planning and execution.

(2) Does the affective valence of the saccade target interfere with the perception of the localization stimulus? Anyway, perception is in parts suppressed around the time of saccade onset. This effect is called *peri-saccadic suppression*, and has already been introduced in previous Chapters 5, 6, and 7. There is no evidence of peri-saccadic suppression being an attentional effect. Nevertheless, an attraction of spatial attention to the affective target pictures might additionally

impair stimulus perception.

(3) Does the affective valence of the saccade target influence the peri-saccadic localization of the stimulus? Around the time of saccade onset *peri-saccadic compression* occurs. This is a specific localization error resulting in briefly presented stimuli being perceived as shifted towards the saccade target. This is described in more detail in previous Chapters 6 and 7. If saccade latency was influenced by the affective valence of the target pictures (see above), then the time course of peri-saccadic compression might also be influenced. Peri-saccadic compression arises during saccade planning previous to saccade onset. If saccade latency by some means reflects the duration of saccade preparation, it could be correlated with the time course of peri-saccadic compression. Furthermore, there is recent but unsystematic evidence that saccade preparation alone might be sufficient to generate peri-saccadic compression (Georg et al., unpublished data).

We conducted a total of three experiments. In Experiment 1, the impact of affective targets was investigated by measuring several dependent variables relating to saccade execution and peri-saccadic localization. In Experiment 2, subjects—instead of indicating the position of the localization stimulus—were required to judge the affective valence of the target picture. These judgments were used to validate the accessibility of the depicted affective material. In Experiment 3, the target pictures were inverted, i. e. rotated by 180 °, to exclude effects of low-level picture attributes on the observed variables. In all three experiments we expected the most pronounced differences to appear between negative and neutral, and between negative and positive valences, found similarly in previous experiments (Codispoti et al., 2001; Phelps et al., 2006).

8.3 Methods

8.3.1 Subjects

Ten subjects, six male and four female, participated in this experiment. Their age ranged between 20 and 38 years. All of them were students at the Department of Psychology and had normal or corrected-to-normal vision. Two of them were the investigators conducting this study, the others were naïve to the aims of the experiments. All subjects gave informed consent.

Data of three of the ten subjects had to be discarded during data analysis (see Section 8.3.5 on page 132). The remaining seven subjects participated in all three experiments described below.

8.3.2 Apparatus

Two personal computers were running the experiments: a Windows PC containing the eye tracking system and a Macintosh PC for stimulus presentation. The two computers were connected to each other via a dedicated ethernet connection The *EyeLink II* system (*SR Research, Ltd.*, Canada) was used to record eye movements. Gaze position was sampled and stored with a frequency of 500 Hz. Eye movement events, i. e. saccades, fixations, and blinks, were detected and stored online. For more information see Section 4.1 on page 24.

The presentation monitor was a 22 " (20 " visible screen diagonal) *iiyama Vision Master Pro 514*, running with a vertical frequency of 120 Hz at a resolution of 1280 × 1024 pixels. Subjects were seated in a dimly lit room. Their head was supported by a chin rest, about 45 cm distant from the stimulus screen.

8.3.3 Affective pictures

The pictures that served as saccade targets have been taken from the *International Affective Picture System* (IAPS; see Lang et al., 2005). The IAPS is a collection of color photographs, especially compiled to provide a comprehensive set of affectively potent pictures for scientific studies. Over several decades, this collection of pictures has been analyzed and continually enhanced to improve validity and generalizability across subjects of different age, gender or cultural background.

In earlier studies, the pictures of the IAPS have been rated by several hundred subjects (Lang et al., 2005). Ratings have been conducted on three different scales, *pleasure*, *arousal*, and *dominance*, the latter being disregarded here due to methodical concerns. *Dominance* accounts for only relatively little unique variance in picture perception (Lang et al., 1997). Possible values on each scale ranged from one (least) to nine (highest). *Pleasure* is the affective valence, describing how pleasant the pictures were rated. The *arousal* scale describes how exciting the pictures were rated.

For our experiments, only 202 from a total of 704 pictures were selected in order to form three distinct groups with respect to the picture's individual *pleasure* and *arousal* ratings. Moreover, the contextual unambiguousness of the pictures, the size of the depicted items, and the perceptibility during brief presentations was taken into consideration by visual inspection. Each of the three groups exclusively contained pictures with low, medium, or high *pleasure* ratings, respectively. Thus, pictures in the respective groups are referred to as possessing a *negative*, *neutral*, or *positive* affective valence, respectively. Furthermore, the choice of pictures was based on *arousal*. In the groups with negative and positive affective valences, *arousal* ratings were to be as high as possible, whereas in the neutral group, the respective ratings were to be as low as possible. Table 8.1 shows the average *pleasure* and *arousal* ratings of the three groups for the totality of pictures taken from the IAPS.

The *pleasure* and *arousal* ratings of all individual pictures are represented in Figure 8.2 on the following page. The three groups—with positive, neutral, and negative valence, respectively—form distinct, almost non-overlapping clusters on an *arousal*-*pleasure*-plane.

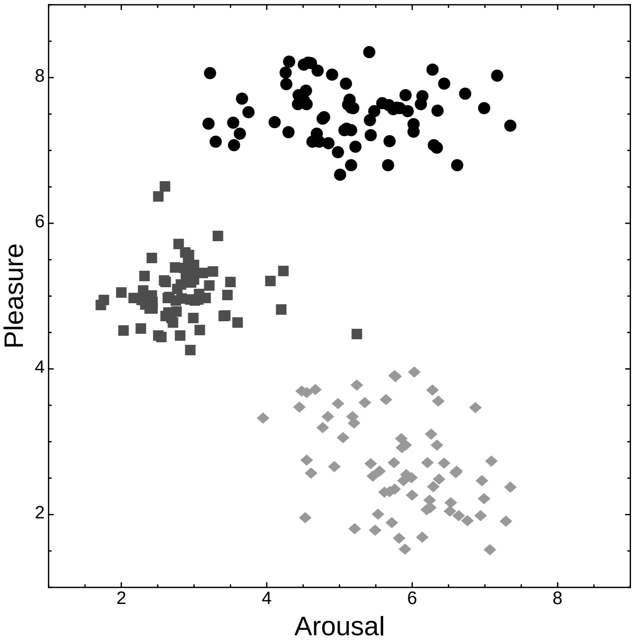

Figure 8.2: Pleasure and arousal ratings of the 202 target pictures selected from the IAPS. Both scales span a range from 1 (lowest) to 9 (highest) in arbitrary units. We subdivided the sample pictures into three distinct categories: negative valence (light gray diamonds), neutral valence (medium gray boxes), and positive valence (black disks).

Table 8.1: Average *pleasure* and *arousal* ratings of the target pictures from the IAPS. 202 pictures have been selected with respect to *pleasure* and *arousal* ratings, contextual unambiguousness, and perceptibility during brief presentations. The selected pictures have been subdivided into three groups.

Valence	**Number**	**Pleasure rating**	**Arousal rating**
		Mean ± SD	Mean ± SD
negative	67	2.69 ± .67	5.83 ± .78
neutral	67	5.05 ± .41	2.85 ± .57
positive	68	7.52 ± .39	5.13 ± .96

Pictures were clipped to match an aspect ration of 1, and were subsequently resized to 300×300 pixels, corresponding to $12\,^\circ \times 12\,^\circ$ of visual angle. Identical pictures were used for all experiments described in this chapter, although in Experiment 3 the target pictures were rotated by $180\,^\circ$. Minimized versions of the selected and clipped pictures can be found in Appendix A on page 171.

8.3.4 Experiments

Experiment 1: Impact of affective saccade targets

Experiment 1 was designed to investigate the potential impact of affective saccade targets on saccade parameters and peri-saccadic localization. Before beginning the first experimental block, each subject received detailed instruction by the investigator. At the beginning of each experimental block, the eye-tracking system was calibrated and validated. A single block comprised 202 trials.

In each trial, initially, only a fixation point was visible vertically centered and horizontally $6\,^\circ$ left of the center of the screen. The fixation point was a small ($0.4\,^\circ \times 0.4\,^\circ$) bright yellow square on an otherwise uniform gray background. Luminance of the background and the fixation point was $6.2\,\mathrm{cd/m^2}$ and $47.5\,\mathrm{cd/m^2}$, respectively, the resulting Michelson contrast (C_M) being 0.77. The fixation point was visible for a random time interval between 1,000 ms and 1,600 ms. After this time interval, the fixation point disappeared and at the same time the saccade target was presented. Pictures from the IAPS (see Section 8.3.3 on page 126) served as saccade targets, presented at a size of 12 ° × 12 °, and centered 10 ° to the right of the fixation points. In each trial, only one affective picture was presented. Each picture was presented once per experimental block, the order being pseudo-randomized independently in each block. Subjects were instructed to elicit a saccade into the picture as fast as possible. Since the saccade targets had such a considerable spatial extent, saccades with horizontal components between 4 ° and 16 ° could end within the boundaries set by the target picture. The saccade target was visible for 100 ms. Due to saccadic latency, although varying across subjects, the picture had already disappeared before actual saccade onset. At a random time before, during or after saccade onset a localization stimulus was presented briefly. Presentation time was estimated *a priori* from subject's latencies—if available—but not before target offset. The localization stimulus was a light gray, vertical bar (0.4 ° × 16 °, 7.8 cd/m^2, contrast to background C$_M$ = 0.11), presented for about 8 ms. The localization stimulus was presented at one of four horizontal positions—1 °, 5 °, 15 °, and 19 ° to the right of the fixation point—pseudo-randomly intermixed independently in each trial. Subjects were required to indicate the perceived horizontal position of the localization stimulus by means of a mouse pointer, appearing 500 ms after the disappearance of the localization stimulus. If the stimulus was not noticed at all, the subject was instructed to indicate this by clicking a black rectangle in the lower left corner of the screen. The response started the next trial. The temporal scheme of a single trial is diagramed in Figure 8.3.

One experimental block took about ten minutes. Each subject completed between three and seven blocks. Between different blocks, subjects had at least a 15 minute's break under normal lighting conditions. In a previous study it had been demonstrated that cortical

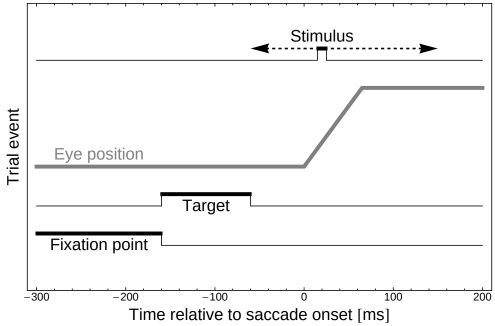

Figure 8.3: Temporal scheme of events during a single trial. Initially, only the fixation point was visible and the subject fixated it. After a random time period of 1,000–1,600 ms the fixation point disappeared. At the same time a target picture was presented, and the subject conducted a saccade into the picture. At some time before, during or after the saccade (from about 100 ms before to 200 ms after saccade start) a stimulus was presented briefly (8.3 ms). The next trial started after the subject had indicated the perceived position of the flashed stimulus by means of a mouse pointer that appeared 500 ms later.

responses to affective pictures remain relatively constant even during repetitive presentation of identical pictures (Codispoti et al., 2006). This might be of relevance because identical pictures were used in successive experimental blocks.

Experiment 2: Validation of affective valence and perceptibility

Experiment 2 was conducted to assess whether subjects were able to accurately identify the affective valence of the used target pictures under the given conditions. Although the IAPS was extensively tested and validated (see Lang et al., 2005), there is little empirical data concerning presentation duration or size of the individual pictures. Usually, reactions to emotionally relevant pictures are investigated in active viewing conditions during sustained presentation of the respective picture for several seconds (e.g. Bradley et al., 2001a,b). For shorter presentation durations of only 500 ms, Codispoti et al. (2001) confirmed differences in physiological parameters, i. e. heart rate, skin conductance, EMG responses, and startle reflex, when affective relevant—pleasant or unpleasant—compared to neutral pictures were presented. They also proved the epoch of the differential reflex modulation to exceed the absolute presentation time of the affective relevant picture. To our knowledge, presentation durations in the range of about 100 ms had not been tested before. Sanchez-Navarro et al. (2006) found an effect of the affective content of pictures from the IAPS on similar physiological parameters and on emotional ratings, but no effect of the size the respective pictures. However, they only used two different picture sizes, both considerably larger than in our experiments.

Subject's responses were to be compared to the rating scales from the IAPS. All subjects from Experiment 1 also participated in Experiment 2. Each subject participated in only one experimental block of 202 trials. Experiment 2 was conducted either before the first, after the second or after the last block of Experiment 1.

The setup in Experiment 2 very much resembled that in Experiment 1. Single trials in Experiment 2 were identical to trials in Experiment 1 except for the response procedure. In Experiment 2, 500 ms after extinction of the localization stimulus, a response mask appeared. This response mask consisted of three squares of $5^\circ \times 5^\circ$ each, arranged in a horizontal row across the screen. Each square depicted a stylized face ("smiley"), one with a happy, one with a neutral, and one with a sad expression. Subjects were instructed to indicate the affective valence of the target picture by clicking at the respective icon in a three-alternative forced choice (3AFC).

Experiment 3: Influence of low-level picture attributes

Experiment 3 was conducted to provide support for the results of the previous experiments. Differences between categories of pictures with different affective valences might be in part arise from differences in low-level picture attributes, such as contrast, brightness, color, and spatial frequencies. Delplanque et al. (2007) found differential amounts of energy in certain spatial frequencies for selected subsets of pictures from the IAPS after discrete wavelet transform. Experiment 3 was designed to control for these low-level image properties by using identical, but inverted target pictures. Inversion is a common method of making the emotional content of stimuli inaccessible while preserving many of their physical properties (e.g. Phelps et al., 2006).

All subjects from Experiment 1 and Experiment 2 also participated in Experiment 3. Subjects conducted between two and three experimental blocks. Experiment 3 was performed after completion of the previous experiments. Setup and procedure in Experiment 3 were identical to Experiment 1 except the target pictures being rotated by 180 °.

8.3.5 Data analysis

In Experiment 1 and Experiment 3, single trials were discarded when the target picture was was missed by more than 2 ° in any direction, or when saccadic latency was outside the range from 100 ms to 300 ms. Valid trials were analyzed separately according to affective valence. In contrast, in Experiment 2 no trials were discarded.

Data of three subjects had to be discarded due to unusually high saccade latencies systematically exceeding 300 ms. This might be based on subject's cognitive strategies in response to the particular task. The three subjects probably delayed their saccades until the localization stimulus had been presented, thereby making the localization task easier. Since saccadic latency itself is used as a dependent variable, subjects whose latencies do not depend on stimulus properties might otherwise obscure potential differences across conditions.

Of the remaining subjects, calculated saccade parameters were the median latency and the median landing position for each affective valence separately. Only the first saccade after presentation of the target picture was considered. Calculated perceptual parameters were the maximum amount of peri-saccadic compression, the point in time relative to saccade onset when this maximum is reached, and the amount of peri-saccadic suppression.

Perceived stimulus positions were analyzed by plotting the localization responses against the corresponding presentation time relative to saccade onset for each stimulus position separately. Data was fitted with a gaussian-weighted moving average with a standard deviation of 15 ms. A time-resolved index of peri-saccadic compression—referred to as *compression index* (CI)—was calculated from the fitted curves as per formula below:

$$CI(t) = 1 - \frac{SD(perceived_t)}{SD(actual)},$$

with *actual* representing the actual stimulus positions, and *perceived* representing the perceived stimulus positions at a certain time relative to saccade onset. An example of perceived stimulus positions and the corresponding CI is shown in Figure 8.4 on page 135.

Trials in which subjects responded that they had not seen a localization stimulus were used only for calculating the proportion of suppressed trials. Only trials with stimulus presentations between 50 ms before to 50 ms after saccade onset were taken into account since the peri-saccadic suppression is predominantly effective in this epoch (Burr et al., 1994; Diamond et al., 2000; Ross et al., 2001a).

8.4 Results

8.4.1 Experiment 1: Impact of affective saccade targets on saccade parameters and peri-saccadic localization

Saccade parameters

Saccadic latencies and saccade metrics were analyzed separately for each affective valence to assess the potential impact of affective tar-

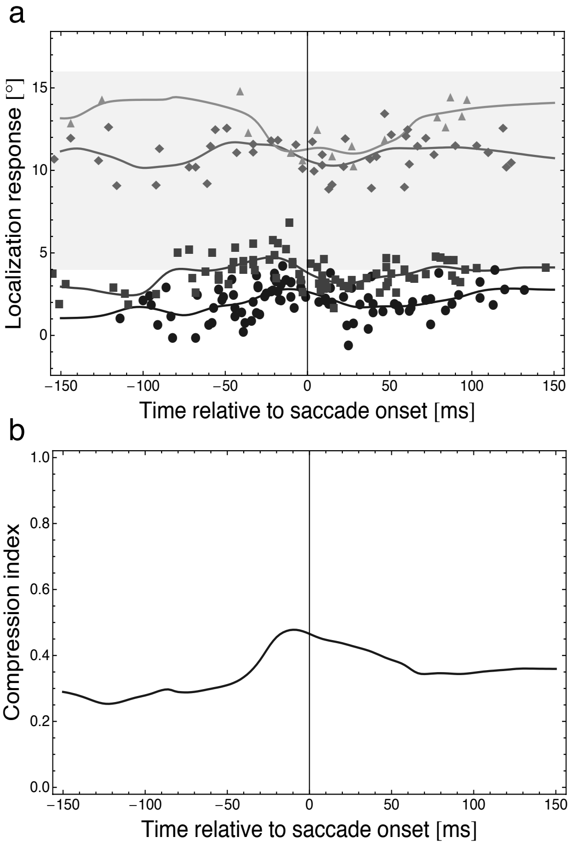

Figure 8.4: Results of Experiment 1 for subject CF. **(a)** Localization responses. X-axis shows the time of stimulus presentation relative to saccade onset. Negative times indicate pre-saccadic presentation. The light grey area indicates the horizontal dimensions of the target picture. Symbols represent individual localization judgments, solid lines represent gaussian-weighted moving averages. Different symbols and gray scales represent different veridical stimulus positions. **(b)** Compression index, calculated from (a). For calculation of the compression index see Section 8.3.5 on page 132. A value of 0 means no compression, a value of 1 means complete compression onto one single position.

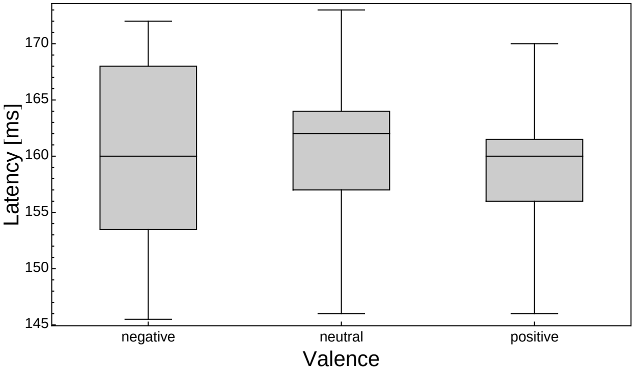

Figure 8.5: Saccade latencies in Experiment 1. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

gets on saccade parameters.

Latency Results for saccadic latencies are shown in Figure 8.5 on page 136. A non-parametric, one-factorial analysis of variance, the Friedman test, did not reveal a significant influence of affective valence on saccade latency ($p = .0886$), although a minor trend towards higher latencies for neutral compared to negative and positive affective targets might be existent. However, the effect size of only 2 ms is relatively small.

Saccade metrics Saccade metrics are derived from the post-saccadic landing position relative to the previous fixation position. Only the horizontal component of the saccades were analyzed. Results are shown in Figure 8.6 on page 136. The horizontal component of saccade amplitude did not depend on affective valence of the target

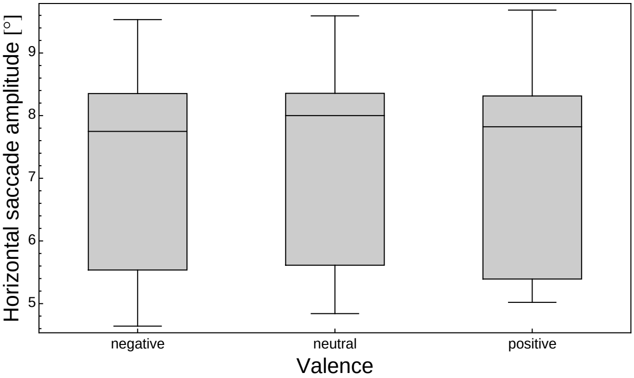

Figure 8.6: Horizontal component of saccades in Experiment 1. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

picture, as revealed by the Friedman test ($p > .6$).

Peri-saccadic perception

Peri-saccadic compression and peri-saccadic suppression were analyzed to assess the potential impact of affective targets on peri-saccadic perception and localization.

Peri-saccadic compression Peri-saccadic localization was analyzed for each subject independently. For all subjects, peri-saccadic compression occured. To quantify the characteristics of this peri-saccadic compression, a compression index (CI) was calculated for each individual subject (see Section 8.3.5 on page 132). From this CI, the local maximum between 50 ms before and 50 ms after saccade onset is determined. The local maximum was confined to 50 ms around saccade onset since from previous experiments (Ross et al., 1997; Lappe et al., 2000; Ross et al., 2001a; Michels and Lappe, 2004) peri-saccadic compression is known to predominantly occur in this epoch.

Both the amount and the time relative to saccade onset of this maximum CI varied considerably across subjects. Results are shown in Figure 8.7 on the following page and in Figure 8.8 on the next page. The Friedman test revealed no significant influence of affective valence on neither the amount of peri-saccadic compression ($p > .3$) nor the time of maximum peri-saccadic compression ($p > .1$).

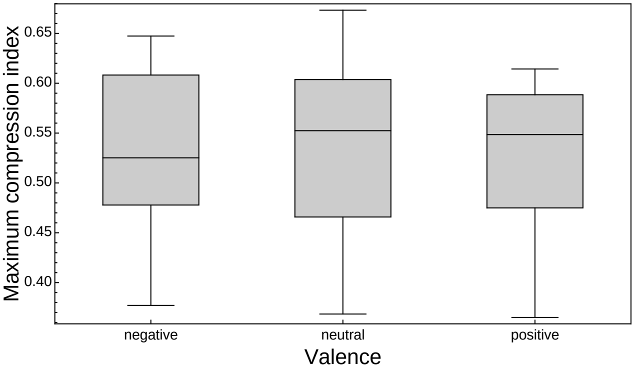

Figure 8.7: Maximum compression index in Experiment 1. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

Peri-saccadic suppression In the temporal vicinity of a saccade, perceptual thresholds are elevated and consequently peri-saccadic perception is suppressed. To assess the amount of this peri-saccadic suppression, the proportion of trials in which the localization stimulus was not perceived was calculated for each subject independently. This proportion is calculated as the ratio of suppressed trials over

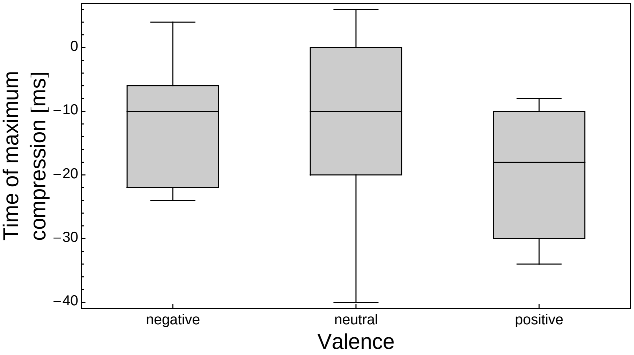

Figure 8.8: Time relative to saccade onset of the maximum peri-saccadic compression from Fig. 8.7. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. Negative times indicate pre-saccadic occurrence. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

all trials in the respective epoch. Results are shown in Figure 8.9 on page 139. The Friedman test revealed no significant influence of affective valence on peri-saccadic suppression ($p > .6$).

Significance of arousal

Experiment 1 was based on the assumption of potentially finding effects of affective saccade targets on saccade metrics or peri-saccadic perception. Hence, pictures were selected, among other criteria, with respect to their *pleasure* rating from the IAPS. Depending on this rating, pictures were subdivided into three categories with different affective valences. From Figure 8.2 on page 128 it appears that the selected target pictures can be described not only in terms of their *pleasure* rating but also in terms of their *arousal* rating. It is therefore necessary to control for influences of *arousal* on the observed saccadic and perceptual parameters.

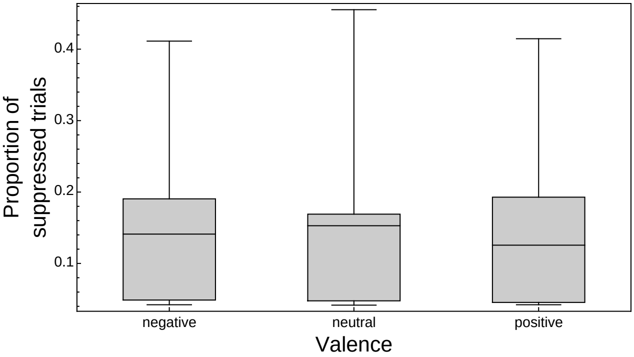

Figure 8.9: Peri-saccadic suppression in Experiment 1. The y-axis represents the proportion of suppressed trials The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

Arousal and *pleasure* ratings are unequally distributed across the set of target pictures. While positive and negative affective pictures both possess relatively high *arousal* ratings, their respective *pleasure* ratings differ largely. In contrast, pictures from the neutral affective valence category exhibit intermediate *pleasure* ratings together with relatively low *arousal* ratings (see Fig. 8.2). To assess the potential impact of *arousal*, data from Experiment 1 were re-evaluated. Therefor, target pictures were sorted according to *arousal* instead of *pleasure* ratings, and reassigned to four groups of about the same size. The quartiles of all *arousal* values thus marked the group limits. The assignment of target pictures to the four groups, mean *arousal* ratings, and the proportion of pictures with a certain affective valence in the respective groups can be gathered from Table 8.2.

Re-evaluation of the data was carried out analog to previous calculations. Saccade parameters and peri-saccadic perception were tested for systematic differences across the four groups represent-

Table 8.2: Assignment of the selected target pictures to four groups, with *arousal* rating being the partitioning variable. The corresponding .25, .5, and .75 quartiles marked the group limits. The Valence columns indicate the number of pictures with a specific affective valence in each group.

Quartile	**Arousal**	**Valence**		
	Mean ± SD	negative	neutral	positive
1*st*	2.62 ± .32	0	51	0
2*nd*	4.03 ± .58	9	15	26
3*rd*	5.36 ± .31	23	1	26
4*th*	6.42 ± .43	35	0	16

ing the quartiles of the target picture's *arousal* ratings. In summary, *arousal* appears not to have a systematic effect on either of the tested parameters. The Friedman test revealed no significant influence of *arousal* group on saccade latency and saccade metrics ($p > .5$ and $p > .1$, respectively), on the amount of maximum compression and the time relative to saccade saccade onset this maximum occurred ($p > .1$ and $p > .6$, respectively), and the strengt of peri-saccadic suppression ($p > .4$). Data are not diagramed here. It appears that the observed parameters do not depend on *arousal*. We therefore exclude the possibility of effects of *arousal* interacting or superimposing with *pleasure*.

8.4.2 Experiment 2: Validation of affective valence and perceptibility

In Experiment 1 we did not find a systematic effect of the affective valence of target pictures on saccade parameters or peri-saccadic localization. Initially, there are two antithetic explanations for these findings: Firstly, affective valence has no influence on the observed parameters, and therefore we do not find significant effects. Or, secondly, there are influences of affective valence that we were not able to substantiate. Potentially, our analyses were not sensitive enough to reveal smaller differences masked in noise. In Experiment 2 we aimed at testing the latter alternative. The objective of Experiment 2 was to assess the perceptibility of the presented target pictures and their affective valences. Subjects were instructed to indicate the affective valence of the target picture after each trial. The localization stimulus was of no importance for the task but was nevertheless presented. Each subject rated each picture only once.

Table 8.3: Results of Experiment 2. Subjects (N=7) judged the affective valence of each of the 202 target pictures. The first row indicates the complete set of target pictures. The second row indicates the percentage of correct identifications. The third row indicates the number of valid pictures as a subset of the totality of pictures. A picture was considered as valid if its affective valence was judged correct from at least 50 % of the subjects.

	Total	**Valence**		
		negative	neutral	positive
target pictures	202	67	67	68
% correct	74.4 %	65.7 %	86.3 %	71.1 %
valid pictures	178	53	66	59

Results of Experiment 2 are summarized in Table 8.3 on the previous page. In 74.4 % of all trials, individual judgments were consistent with the affective valence from the IAPS. This percentage of correct judgments varied with affective valence (see Tab. 8.3). Pictures with a neutral affective valence were judged correctly more frequently. This might be due to a bias of subjects to respond "neutral" in case of being uncertain. From the results of Experiment 2 a subset of only valid pictures was constituted. A picture was considered as being valid if at least 50 % of all subjects judged its affective valence in conformity with the ratings from the IAPS. Thus, pictures whose affective content could not be perceived—or was perceived only by a minority of subjects—were excluded. 178 valid pictures remained.

The eventuality of irrecognizable pictures being incorrectly judged as affectively neutral poses no problem, since the actual emotional content of irrecognizable pictures should have no effect. Although in Experiment 2 subjects might have paid more attention to the target picture than in Experiment 1, where the subsequently presented localization stimulus was task-relevant, we nevertheless demonstrated that the affective valence of these 178 valid pictures could in principle be recognized under the given experimental conditions.

However, we do not argue that the non-valid pictures are not effective in eliciting emotional reactions at all, or that subjects are under no circumstances able to identify the affective valence of the discarded pictures. This exclusively applies to the viewing conditions—i. e. size, duration, resolution, and subject's task—in our experiments.

8.4.3 Re-evaluation of the data for a restricted subset of target pictures

Data from Experiment 1 was re-evaluated for the restricted set of target pictures with higher validity gathered from Experiment 2. No novel experiment was conducted at this stage. From Experiment 1 only those trials were selected for analysis in which one of the 178 valid target pictures was presented.

Saccade parameters

Saccade latencies and saccade metrics were analyzed analog to Experiment 1. Results for saccade latencies are shown in Figure 8.10. The Friedman test revealed no significant influence of affective valence on saccade latencies ($p = .0603$), although the potential trend already observed in Experiment 1 almost reached significance during re-evaluation. Here, the median of saccade latencies is 3 ms and 4 ms higher for neutral compared to negative and positive affective

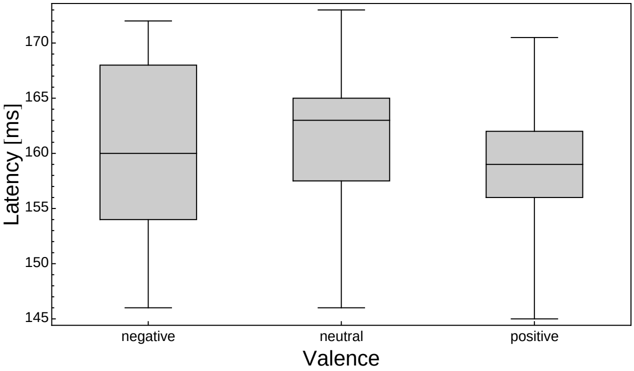

Figure 8.10: Saccade latencies from Experiment 1, re-evaluated for a restricted set of target pictures. Only trials in which one of the 178 valid pictures was presented were included in the analysis. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

pictures, respectively. No significant effect ($p > .8$) was revealed for the horizontal component of saccade amplitude.

Peri-saccadic localization

Peri-saccadic compression and peri-saccadic suppression were analyzed analog to Experiment 1. There were no statistically significant differences between valences for neither the amount of maximum compression nor its time relative to saccade onset (Friedman test, $p > .6$ and $p > .1$, respectively). In contrast, the amount of peri-saccadic suppression, i. e. the proportion of suppressed trials in the epoch 50 ms around saccade onset, differed significantly with affective valence (Friedman test, $p < .01$). Data are shown in Figure 8.11 on the next page. Subsequently calculated multiple comparisons revealed significant (Wilcoxon-Wilcox test, $\alpha = .01$) differences between negative and neutral, and between negative and positive affective valences. This means that pictures with negative affective valence—unpleasant pictures—, when presented as saccade targets, cause subjects to miss the localization stimulus more frequently compared to neutral or positive affective pictures.

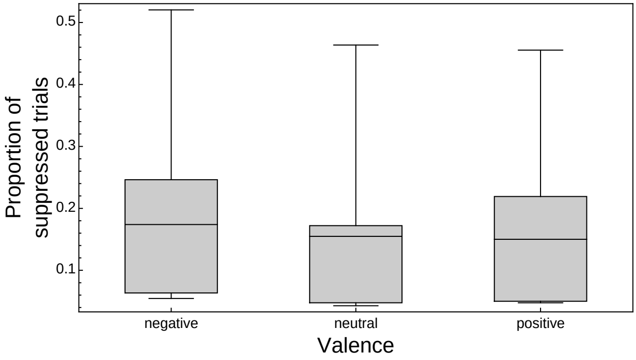

Figure 8.11: Peri-saccadic suppression in Experiment 1, re-evaluated for a restricted set of target pictures. Only trials in which one of the 178 valid pictures was presented were considered for analysis. The y-axis represents the proportion of suppressed trials. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

8.4.4 Experiment 3: Potential influence of low-level picture attributes

Experiment 2 allowed for selecting only target pictures whose affective valence was correctly identified by most subjects. In contrast to the complete picture set in Experiment 1, these valid target pictures effectively influence peri-saccadic suppression. A minor effect on saccade latency might also be existent.

A possible issue that had not been addressed so far is the role of low-level picture attributes—physical properties like contrast, color, brightness, and spatial frequency—defining the saliency of individual pictures or parts thereof. Saliency of the saccade target is known to influence saccade latency (Fischer, 1999). Furthermore, peri-saccadic suppression is affected by stimulus contrast (Michels and Lappe, 2004) and might therefore as well be affected by the contrast of the saccade target. Hence, at least some of the observed effects might be due to low-level differences in the target pictures from the IAPS. We designed Experiment 3 as a control condition to overcome this issue.

Saccade parameters

Saccade latencies and saccade amplitudes were analyzed analog to Experiment 1. The Friedman test revealed no significant influence of affective valence on neither saccade latency nor saccade amplitude ($p = 0.0886$ and $p > .5$, respectively). As per Experiment 1 and its re-evaluation after Experiment 2, a marginal trend for affective valence influencing saccade latency—with slightly higher latencies for neutral compared to negative and positive affective target pictures—remains in question. Furthermore, in Experiment 3 saccade latencies were systematically lower, about 10 ms, than in Experiment 1. This points at potential learning effects, since all subjects conducted Experiment 3 after completing Experiment 1 and Experiment 2.

Peri-saccdic localization

Peri-saccadic compression and peri-saccadic suppression were analyzed analog to Experiment 1. For one subject the number of valid trials was insufficient for calculating peri-saccadic localization. Thus, statistics concerning peri-saccadic compression were based on only six subjects. The Friedman test revealed no significant influence of affective valence on peri-saccadic suppression ($p > .8$), and on the amount of maximum compression ($p > .5$), but did indeed reveal a significant effect on the time relative to saccade onset this maximum occurred ($p < .01$). Data are shown in Figure 8.12 on the facing page. The median time of the maximum compression is much earlier for negative (−29 ms) compared to neutral (−12 ms) or positive affective pictures (−17 ms). Subsequently calculated multiple comparisons revealed significant differences between negative and neutral, and between negative and positive valences, respectively (Wilcoxon-Wilcox test, $\alpha = .01$). Neutral and positive affective pictures also differed significantly ($\alpha = .05$). This effect of affective valence on the time course of peri-saccadic compression was unanticipated, since the results of Experiment 1 and of the re-evaluation of Experiment 1 for exclusively valid pictures gave no evidence of such an effect. Thus, it remains unclear why inversion of the affective target pictures—probably going along with an impairment of its emotional effectivity—should uncover a potential effect not visible for pictures presented upright.

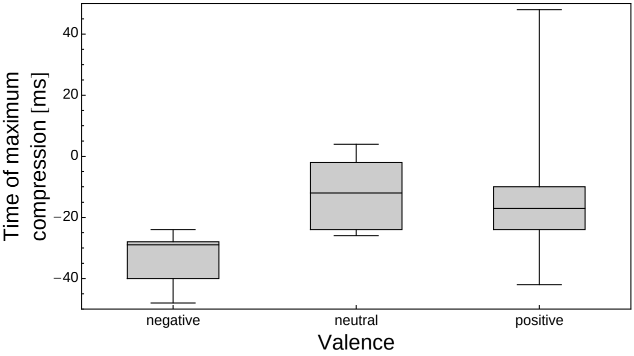

Figure 8.12: Time relative to saccade onset of the maximum peri-saccadic compression in Experiment 3. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. Negative times indicate pre-saccadic occurrence. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=6) in each column.

8.4.5 Re-evaluation of the data for a restricted subset of target pictures

According to Experiment 1, the results of Experiment 3 were likewise re-evaluated based on a restricted set of only valid target pictures. As per Experiment 1, potentially existent but undetected effects of affective valence should be revealed during this process. Motor and perceptual parameters were analyzed as above.

The Friedman test revealed no significant influence of affective valence on neither saccade latency ($p > .3$) nor the horizontal component of saccade landing position ($p > .2$). Data for peri-saccadic suppression are shown in Figure 8.13 on the next page. In contrast to the re-evaluation of Experiment 1, there is not even a tendency of affective valence taking effect on saccade latency in the re-evaluation of Experiment 3. The same is true for the amount and time course of peri-saccadic compression. For neither of them a significant effect of affective valence was revealed ($p > .8$ and $p > .2$, respectively). This is contrary to the initial analysis of Experiment 3 above (see Fig. 8.12), where the time course of peri-saccadic compression differed significantly with affective valence. However, similar to the re-evaluation of Experiment 1 there is a significant influence of affective valence on peri-saccadic suppression ($p < 0.01$) in the re-evaluation of Experiment 3. Data for peri-saccadic suppression are shown in Figure 8.14 on page 149. Suppression for negative affective pictures proved to be significantly higher than for neutral and positive target pictures (Wilcoxon-Wilcox test, $\alpha = .01$).

8.5 Discussion

The experiments described in this chapter were designed to explore the potential effects of affective stimuli—affective saccade targets in particular—on motor parameters of saccades and on peri-saccadic perception of briefly presented stimuli. In detail, the dependent vari-

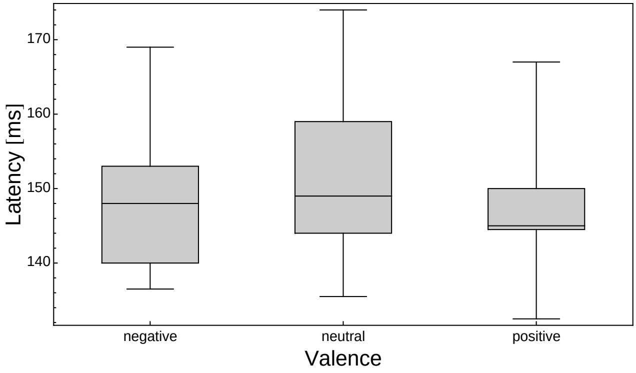

Figure 8.13: Saccade latency in Experiment 3, re-evaluated for a restricted set of target pictures. Only trials in which one of the 178 valid pictures was presented were considered for analysis. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

ables in our experiments were saccade latency, horizontal saccade amplitude, amount and time course of peri-saccadic compression, and strength of peri-saccadic suppression. In Experiment 1—the original experimental condition—we found no significant effects of affective target pictures on the motor and perceptual parameters in question. There only was a minor, non-significant trend towards higher saccade latencies for neutral target pictures compared to negative and positive pictures.

Longer saccade latencies for neutral saccade targets might be a sign of differential attentional processes before saccade start. This assumption is based on two aspects. Firstly, spatial attention is is known to be mandatorily shifting to the location of the saccade target during saccade planning (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996; Irwin and Gordon, 1998; Peterson et al., 2004; Baldauf and Deubel, 2008; see also Chapter 5 on

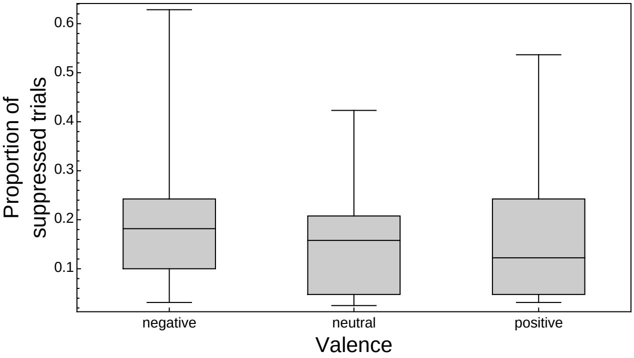

Figure 8.14: Peri-saccadic suppression in Experiment 3, re-evaluated for a restricted set of target pictures. Only trials in which one of the 178 valid pictures was presented were considered for analysis. The three columns represent affective targets with negative, neutral, or positive affective valence, respectively. The Box-Whisker-Plot represents median, quartiles, and variation range across subjects (N=7) in each column.

page 29 ff). This coupling between eye movement and attention shift is not consciously detachable during considerable phases of saccade preparation. Secondly, attention is known to be captured by emotionally relevant stimuli like potentially dangerous animals (Öhman et al., 2001; Vuilleumier and Schwartz, 2001), or erotica and mutilations (Bradley et al., 2006; Schupp et al., 2006, 2007b). See Phelps and LeDoux (2005) for a review on this subject. So when attention is "grabbed" by an affective stimulus, this shift of attention is more efficient or forceful compared to a neutral stimulus. One might further speculate that also the time course of this shift is differential for affective and neutral stimuli. In the case of the saccade target being constituted by such an affective stimulus, both issues could be combined. The attentional capture of the affective stimulus and the pre-saccadic attention shift to this very stimulus—at the same time representing the saccade target—might interact in some way. Theoretically, the necessary shift of spatial attention to the saccade target might be completed more swiftly, thereby facilitating faster saccade onsets—i. e., lower latencies—compared to affectively neutral saccade targets. In contrast, both mechanisms could also interfere with each other, potentially prolonging saccade latencies. Self-evidently, this hypothesis could not be proven or disproved from our data. It was nevertheless sufficient to justify further investigation of the potential influence of affective targets on saccade latency.

We designed Experiment 2 for two purposes. Firstly, we wanted to validate the presented target pictures with regard to the accessibility of their respective affective content. This is a prerequisite for drawing conclusions about the potential impact of their affective valence on the observed motor and perceptual parameters. Secondly, by discarding pictures whose affective content could not readily be identified, we aimed at sharpening the emotional relevance and thus reinforcing the potential impact of the picture sets. More subtle effects of affective valence might thereby become detectable. Subjects were able to correctly identify the valence of the depicted emotional content—whether it were negative, neutral or positive pictures—in about 75 % of the trials. Therefore, we assume that also in Experiment 1 the target picture's affective content was recognized in most cases. However, in Experiment 2 the the affectivity of the target pictures was task-relevant, while in Experiment 1 were only relevant as saccade targets. Nevertheless, we confirmed that the affective valence of most target pictures used in Experiment 1 was in principle accessible to the subjects.

In the re-evaluation of Experiment 1 the trend towards higher latencies for neutral compared to affective—negative or positive—pictures was more pronounced but again falls short of reaching significance. In principle this is consistent with findings of Hunt et al. (2007a), who did not find a significant effect of affective valence on reaction time in a visual search task, using highly abstracted facial expression. Instead, we found a significant effect of affective valence on the amount of peri-saccadic suppression, taking higher values for negative compared to neutral and positive pictures. This effect has not been visible in the original analysis of Experiment 1.

But the question remained which of these differences were potentially based on the emotional content of the target pictures, and which were rather due to low-level attributes of the pictures. Delplanque et al. (2007) pointed at differences in spatial frequencies for different subgroups of the IAPS, although not necessarily identical to our target pictures.

The inverted control condition in Experiment 3 was designed to overcome this issue. The use of pictures turned upside down is a common approach to interfere with the emotional content of stimuli, especially faces (e.g. Phelps et al., 2006). We re-evaluated the data from Experiment 3 restricted to only valid trials. That allowed for comparing results to the re-evaluation of Experiment 1 summarized above. While initial analysis of Experiment 3 yielded somewhat different results—a slight, non-significant trend toward higher latencies for neutral target pictures, and a markedly earlier peak of peri-saccadic compression for negative pictures—we no longer found an influence of affective valence on saccade latency after re-evaluation, with statistical tests being far from reaching significance. This might point at a potential difference between the results from Experiment 1 and from Experiment 3. While in Experiment a trend towards higher latencies for neutral pictures was apparent, this was not the case in Experiment 3. However, since differences in Experiment 1 narrowly failed to reach statistical significance, an unambiguous answer to this question cannot be deduced. It remains nevertheless possible that saccade latency depends on affective valence differentially in both experiments. Moreover, saccade latency varied much stronger with experimental condition (Experiment 1 vs. Experiment 3) than with affective valences. This is most likely a sign of learning effects. To circumvent this problem, Experiment 1 and Experiment 3 could be repeated and modified, with pictures being presented either upright or upside down, pseudo-randomly intermixed within the same experimental block.

In contrast to saccade latency, results for peri-saccadic suppression are more consistent. In both Experiment 1 and Experiment 3 the proportion of suppressed trials—after re-evaluation—was significantly higher for negative compared to neutral and positive affective target pictures. There are at least two ways to explain these results. Firstly, affective valence has no influence on peri-saccadic suppression. In this case differences between groups had been due to low-level differences between individual pictures. Secondly, affective valence has an effect on peri-saccadic suppression, as revealed by the significant differences between groups of affective valences. Probably, the processing of the affective target picture was not completed at the time of stimulus presentation. The emotional content of such pictures has been demonstrated to affect the processing of subsequently presented pictures several hundreds milliseconds later (Schupp et al., 2006; Flaisch et al., 2008). In this case, the inversion of the target pictures had failed in disabling the impact of their emotional content. This might be a consequence of our affective pictures—unlike facial expressions, for example—being highly inhomogeneous in many aspects. Up to now, there is no evidence of the inversion of these pictures really reducing the impact of their emotional content. Even with facial expressions, several studies found effects for upright as well as for inverted faces (Öhman et al., 2001; Hunt et al., 2007a). A further control experiment analog to our Experiment 2 except with inverted pictures would be necessary to discriminate between these two possibilities.

In our experiments we aimed at assessing the potential impact of affective targets on motor and perceptual parameters relating to saccadic eye movements. Findings were discussed with respect to shifts of spatial attention preceding a saccade. However, saccade metrics and peri-saccadic localization errors are rather indirect and unexplored measurements of this pre-saccadic attention shift. In contrast, a converse approach might be more promising. Instead of analyzing the potential impact of affective targets on saccade metrics and on peri-saccadic (mis)localization, one could also aim at assessing their potential impact on the metrics of the attentional shift itself. One way of discriminating the locus of spatial attention is by measuring performance in certain discrimination tasks. For instance, contrast sensitivity is higher at the focus of spatial attention. Such experiments have been conducted to pinpoint the mandatory, pre-saccadic shifting of attention (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996; Godijn and Theeuwes, 2003; Gersch et al., 2004; Baldauf and Deubel, 2008). One could adopt these experiments by using affective pictures as saccade targets and measuring discrimination performance at different locations and in different epochs. Thus, one could test whether attentional modulations due to affective pictures are *per se* able to interact with the pre-saccadic attention shift. This is in no way self-evident, since emotion might indeed potentiate the effect of attention on perception but has also been shown to inherently enhance perception independently of attention (Phelps et al., 2006; Schupp et al., 2007b). A different alternative involves the peri-saccadic perception of time. Angrilli et al. (1997) already demonstrated that affective valence influences temporal interval estimation and temporal interval reproduction. In Chapter 5 on page 29 of this thesis, we conducted experiments dealing with a peri-saccadic error in temporal interval discrimination—the so-called *chronostasis*—and related this error to the pre-saccadic attention shift. Verifying an effect of affective saccade targets on chronostasis would produce further evidence corroborating this hypothesis. Recapitulatory, although the experiments presented in this chapter did not yield very conclusive results, there are several perspectives and connecting factors to different subject areas to encourage further research.

Part III

Attempt on a synthesis

Chapter 9

Synopsis of experiments

Contents

9.1 The peri-saccadic perception of time

In Chapter 5 on page 29 ff we addressed perceptual (temporal) stability across saccades by means of investigating the so-called *chronostasis*, a distortion of perceived timing immediately following a saccade. Visual perception is being suppressed during saccades. Although this peri-saccadic suppression lasts a considerable time interval, there is no “perceptual gap” around saccades. Chronostasis has been proposed to be a mechanism compensating for this perceptual gap—and more speculatively to be a general mechanism linking voluntary actions to their sensory consequences.

In our experiments we proved that chronostasis is not a global mechanism. It rather is a local effect, probably both temporally and spatially restricted—temporally to the time around saccades, and spatially to a circumscribed area around the saccade target. Although we did not succeed in specifying the exact spatial extent of this effect, we demonstrated that chronostasis lacks some characteristics necessary for such a global, compensational mechanism. Instead, we relate this distortion of perceived timing to the shift of spatial attention immediately preceding every saccade. The temporal and spatial dynamics of spatial attention are better suited to explain the observed limitations of the distortion of perceived timing following a saccade.

9.2 Perceptual consequences of saccadic adaptation

Chapter 6 on page 53 ff is concerned with the interrelation between action and perception by means of analyzing the perceptual consequences of short-term saccadic adaptation. Saccadic adaptation is a mechanism thought to adjust the amplitude of saccadic eye movements to accurately reach intended saccade targets. Short-term saccade adaptation is generated by repeatedly replacing the target of an intended saccade during saccade execution. This target step usually remains unnoticed. In the course of about 50 trials saccade amplitude gradually adapts to the intra-saccadic target step. This (motor) adaptation also affects peri-saccadic localization. Stimuli presented before an adapted saccade are localized shifted in the direction of adaptation. If a stimulus is presented pre-saccadically and localized post-saccadically, the metrics of the saccade have to be taken into account. Thus, saccadic adaptation is one tool to reveal how positional information is integrated across saccades.

In our experiments we successfully characterized the perceptual shift induced by saccadic adaptation—referred to as adaptation-induced shift—in much detail. For the first time we isolated the adaptation-induced shift from other peri-saccadic perceptual effects (peri-saccadic compression and peri-saccadic shift). This allowed us to examine the exact time course of this very effect relative to saccade onset. Furthermore, we were able to prove that the adaptation-induced shift becomes visible for stimuli presented up to about 1 s before saccade onset. In a last experiment we investigated the emerging of the adaptation-induced shift during the acquirement of saccadic adaptation. We were able to prove that—under the conditions given in our experiments—the visual system resolves the discrepancy between the intended and the actual saccade by weighting available visual references much higher than extraretinal information. Nevertheless, we also found evidence that—to a lesser extent—motor adaptation directly affects stimulus localization.

9.3 The peri-saccadic representation of object features

In Chapter 7 on page 91 ff we investigated the influence of peri-saccadic suppression and peri-saccadic compression on the retaining of object identity and the representation of object features across saccades. Due to peri-saccadic compression the perceived position of stimuli presented briefly around the time of saccade onset is shifted towards the saccade target. If multiple stimuli are perceptually shifted onto a single position, selected features of these stimuli—*form* and *color*, in particular—are retained independently of the object's position, and irrespective of the corresponding stimulus being explicitly perceived. The retained feature characteristics remain not only distinguishable but also independently compete for access to visual awareness in a manner comparable to perceptual rivalry. Thereby, single objects with multiple feature characteristics at the same time are perceived.

In our experiments we extended this approach by adding the object feature *motion*. *Motion* is different to *form* and *color* with respect to its representation in visual areas: *motion* is processed and represented in the dorsal stream, while *form* and *color* are features of the ventral stream. Unlike *form* and *color*, *motion* turned out not to be retained independently of objects' positions. If two stimuli with different *motion* attributes were perceptually shifted onto one location, both attributes interacted with each other. Furthermore, opposite motion directions explicitly impaired motion discrimination. We hypothesized that the parallel processing of *motion* attributes of different objects interfered with the process of feature binding, given that both attributes are assigned to the same object—or at least to some object at the same location—due to peri-saccadic compression.

9.4 Affective saccade targets

Experiments described in Chapter 8 on page 119 ff form an explorative study, investigating the potential impact of affective saccade targets on motor parameters of saccade execution as well as on parameters of peri-saccadic perception. For that purpose affective pictures of different emotional valences—either pleasant, neutral, or unpleasant—were presented as saccade targets. These pictures were taken from the IAPS, a well-established database for affective pictures. Around the time of saccade onset localization stimuli were briefly presented. The respective dependent variables were saccade latency, saccade amplitude, the amount and time course of peri-saccadic compression, and the strength of peri-saccadic suppression.

In our experiments a minor trend towards higher saccade latencies became visible in trials with neutral saccade targets compared to pleasant and unpleasant target pictures. However, this trend falls short of reaching statistical significance. Further on, we revealed higher proportions of localization stimuli that remained unnoticed due to peri-saccadic suppression in trials with unpleasant saccade targets. We ascribe these effects to the involvement of spatial attention, which is known to be attracted by emotionally relevant stimuli, and to improve visual perception. Attention is tightly coupled with saccade target selection, and with saccade planning and execution. Hypothetically, different attentional processes might interact with each other, thereby interfering with saccade preparation or hindering stimulus localization.

Chapter 10

Implications and perspectives

Contents

10.1 Preface

Individual experiments are extensively discussed in the relevant sections of the respective chapters. Therein, results are reconsidered from different angles, and conclusions and future perspectives are formulated as appropriate. Therefore, only selected aspects are specifically highlighted in this chapter.

10.2 Spatio-temporal coherence

10.2.1 Time

If taken literally, there is no *chronostasis*. Time does *not* stand still during saccades. Yarrow et al. described chronostasis as: "For a short period, the clock appears to have stopped" (Yarrow et al., 2001, p. 302). And this actually is consistent with the subjective impression, also in our operationalization of the stopped clock illusion (see Chapter 5 on page 29). However, Yarrow et al. (2001) explain this illusion in terms of being the product of a compensatory mechanism antedating the first visual impression after the saccade to a point in time immediately prior to the saccade. By doing so, chronostasis is thought to close the "perceptual gap" caused by peri-saccadic suppression.

This implies far reaching consequences. Peri-saccadic suppression affects—to some extent—the whole visual field. A mechanism compensating for peri-saccadic suppression should also cover the whole visual field. In Chapter 5 we were able to reproduce a chronostasis-like overestimation of time intervals subsequent to a saccade, given that the counter also constituted the saccade target. With the counter being located at different locations, interval discrimination was not different from conditions with steady fixation. Based on the results of our experiments we can reject this notion of chronostasis.

Furthermore, there might be no necessity for a mechanism compensating for a potential "perceptual gap" that is caused by peri-saccadic suppression, as this gap probably does not exist. Peri-saccadic suppression manifests in a gradual increase in perceptual thresholds, especially for contrast (Diamond et al., 2000; Michels and Lappe, 2004) and motion (Burr et al., 1994; Ross et al., 2001a). This threshold elevation reaches a maximum of about 1 to 2 log units around saccade onset. Moreover, peri-saccadic suppression mainly affects the magnocellular pathway (Burr et al., 1994). The parvocellular pathway is less affected, and thus the perception of higher spatial frequencies or colors is retained to some extent. Consequently, there is no "blank" time interval. Only less salient stimuli are prevented from reaching visual awareness.

Without a "perceptual gap" the maintenance of temporal stability across becomes self-evident. What remains is an overestimation of the time interval following a saccade. This overestimation is restricted to the saccade target or to the area around saccade target. We relate this overestimation to the fact that subjects mistake the pre-saccadic shift of attention with the actual eye movement, i. e. the subjective position of gaze shifts before the saccade (Deubel et al., 1999). This is also in line with findings that this overestimation does not scale with interval duration but is constant across different stimulus durations (Yarrow et al., 2004a). In short, subjective timing of gaze position and fixation duration rests upon the shift of spatial attention.

Interestingly, this characteristic overestimation of temporal intervals is critically linked to spatial stability. When space constancy, i. e. object constancy with respect to the saccade target, is broken "chronostasis" does not appear (Yarrow et al., 2001). This is in line with the *saccade target theory* (McConkie and Currie, 1996; Currie et al., 2000) and the *reference object theory* (Deubel et al., 1996, 1998; Deubel, 2004), respectively. Both theories postulate that space constancy is retained if the saccade target, as well as nearby items surrounding the saccade target, are found in a certain spatial window around their pre-saccadic locations. This spatial window is potentially defined by the focus of spatial attention, pre-saccadically being shifted to the future saccade target (see Hamker et al., 2007). If the reference objects are not regained post-saccadically, space constancy is broken and the complete scene is re-evaluated. This re-evaluation obviously extends to the temporal domain.

10.2.2 Space

In Chapter 6 on page 53 we addressed the perceptual consequences of short-term saccadic adaptation. With respect to *cancellation theories*, the difference in amplitude between initially planned and actually executed saccades results in an error in trans-saccadic integration of positional information, given that the efference copy is not affected by saccadic adaptation. This difference in amplitude between planned and executed saccades is induced by saccadic adaptation.

However, in our experiments we were able to highlight the relevance of post-saccadically available visual references. We were able to attribute a major part of the adaptation-induced perceptual shift to the usage of visual references. This is best explained in terms of the *reference object theory*. Thereby, the post-saccadically available references mediate space constancy. Note that under the given experimental conditions there actually is no space constancy since the saccade target is displaced intra-saccadically. Localization judgments of pre-saccadically presented objects are post-saccadically rendered relative to the displaced saccade target. The target displacement, i. e. the displacement of the reference object, thus gives rise to the adaptation-induced shift. Nevertheless, visual references are not the only source of information used in these experiments. A minor contribution is made by mechanisms underlying motor adaptation. However, the question whether the saccade amplitude gradually adapts while the efference copy remains unchanged, or whether motor space gradually structures perceptual space, as suggested by Collins et al. (2007), remains unresolved.

As stated in Section 10.2.1 spatial attention hypothetically defines the region around the saccade target from which information is stored for trans-saccadic integration. Only a small fraction of all pre-saccadically available information is integrated across saccades

(McConkie and Currie, 1996; Currie et al., 2000). Or, alternatively, only a small fraction of information is used for trans-saccadic comparison, analog to change detection paradigms (e.g. O'Regan et al., 2000; Mitroff et al., 2004). Thus, spatial attention potentially operates as a filter, selecting a sparse amount of information used for the post-saccadic retrieval of positional information.

10.3 The relevance of spatial attention

Not all findings and theories described in this thesis fit to one single line of reasoning. Nevertheless, several results and interpretations point in a similar direction. Once more, attention is highlighted as a key factor in peri-saccadic perception. In my opinion, the role of spatial attention in this context might be both, inadequately clarified as well as still underestimated. However, the most basic question in this context is: What is attention? At the same time this question is not easily answered comprehensively. There is endogenous and exogenous, overt and covert, spatial and feature-based attention, and so forth. For the interpretation of our results spatial attention is of capital importance.

The classic "zoom lens" model (e.g. Eriksen and Yeh, 1985; Eriksen and St James, 1986) of spatial attention is a rather mechanistic simplification, and falls far short of being biologically plausible, although some physiological evidence has been found (Müller et al., 2003). New approaches of spatial attention are to be developed. These should be adopted to explain and interpret experimental findings, both psychophysical and electrophysiological. In particular, models of spatial attention should make allowance for the dynamic nature of the visual system. In this respect, static and oversimplified models will not only be less predictive but might actually generate predictions that are per se deficient. One possible approach could be the *reentry hypothesis* (Hamker, 2005; Hamker and Zirnsak, 2006; Hamker et al., 2008), that inherently predicts the emerging of spatial attention from dynamic interactions between visual areas and oculomotor feedback circuitry.

To assume a linkage between oculomotor preparation and spatial attention seems obvious for several reasons. During saccade generation attention is closely associated with the future saccade target. Prior to saccade onset, attention is mandatorily shifted to the saccade target. The other way round, if attention is deviated during saccade preparation, for example by an abrupt stimulus onset, saccade landing position is likewise deviated towards this stimulus (Awater and Lappe, 2006). This further emphasizes the role of spatial attention for saccadic eye movements. Most likely, the pre-saccadic shift of spatial attention is not just one component amongst many of saccade preparation. Instead, spatial attention might be intrinsically tied to saccade preparation—or vice versa. There is evidence suggesting that spatial attention can be shifted without preparing a saccade (Juan et al., 2004; Montagnini and Castet, 2007). Nevertheless, the interplay between spatial attention and saccade preparation still contains a lot of unsolved issues.

Part IV

Appendices

Appendix A

Pictures from the International Affective Picture System (IAPS)[1]

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[1] The IAPS has been developed and made available to public by Lang et al. (2005)

Figure A.1: Negative affective pictures modified from the *International Affective Picture System*, as used in Chapter 8 on page 119. Pictures have been subject to clipping and scaling to meet experimental demands.

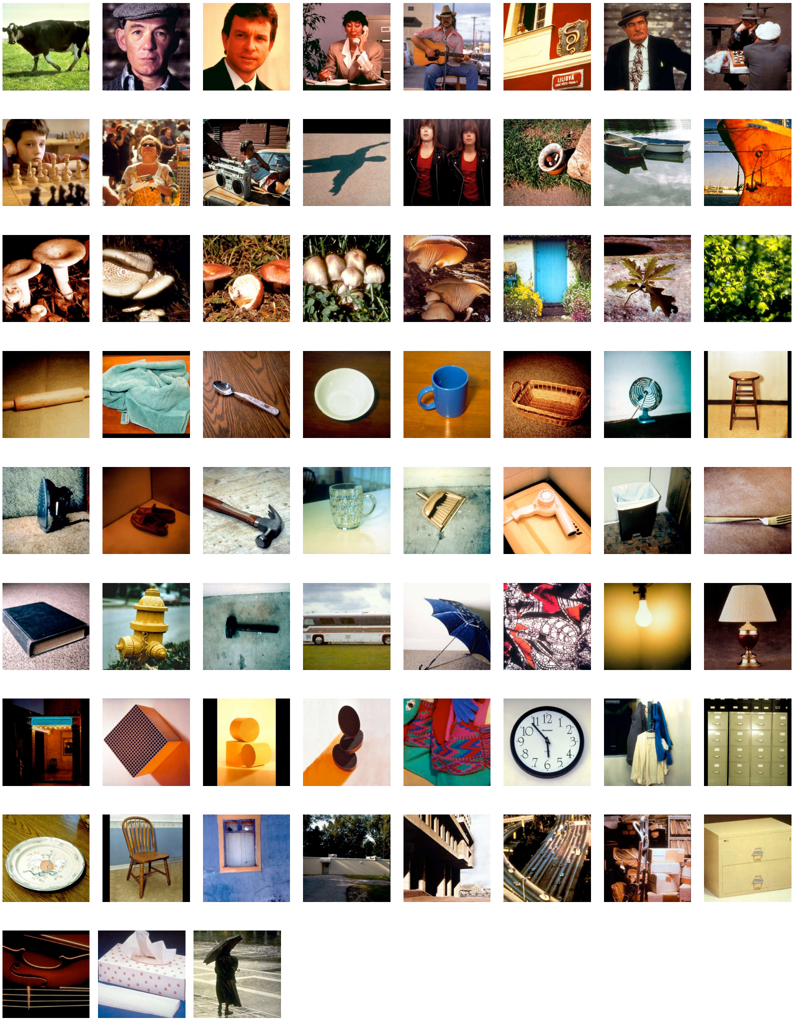

Figure A.2: Neutral pictures modified from the *International Affective Picture System*, as used in Chapter 8. Pictures have been subject to clipping and scaling to meet experimental demands.

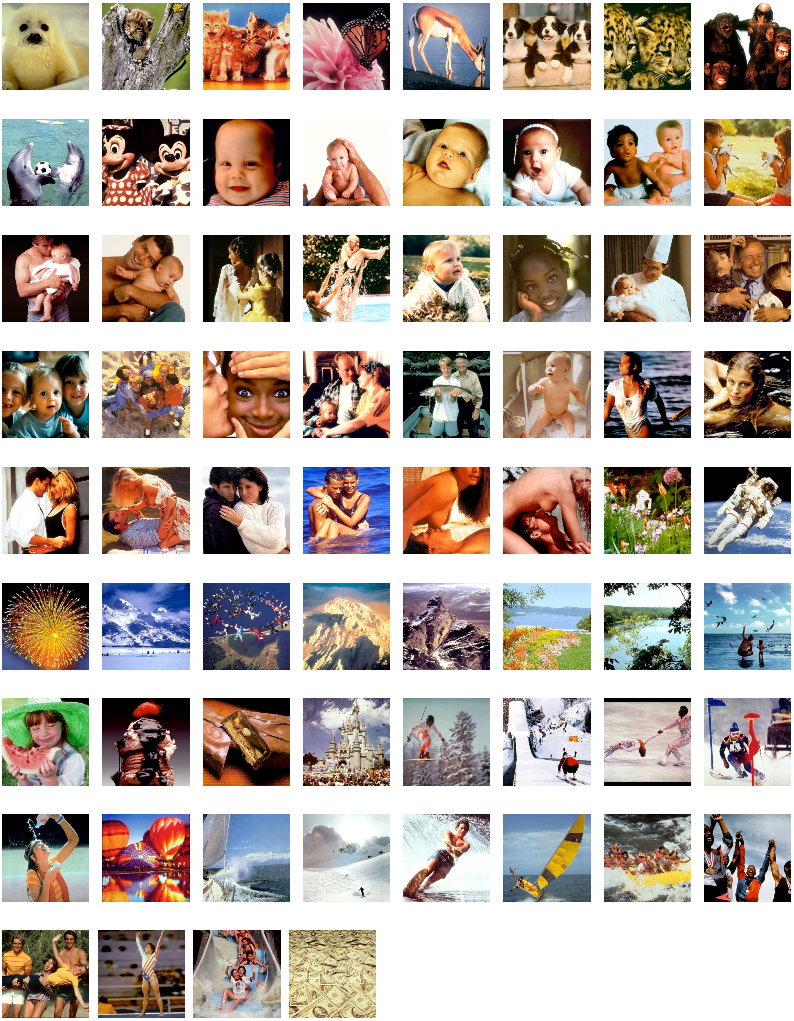

Figure A.3: Positive pictures modified from the *International Affective Picture System*, as used in Chapter 8. Pictures have been subject to clipping and scaling to meet experimental demands.

Appendix B

List of Abbreviations

2AFC two-alternative forced choice

3AFC three-alternative forced choice

ACTH adrenocorticotropic hormone

ANOVA analysis of variance

API application/advanced programming interface

C$_M$ Michelson contrast ($C_M = \frac{L_{max}-L_{min}}{L_{max}+L_{min}}$)

CI compression index

CoCoA Complex Covering Aggregation

CPD cycle(s) per degree

CRT cathode ray tube

EOM extra-ocular muscle(s)

ERP event-related potential

FEF frontal eye field

fMRI functional magnetic resonance imaging

IAPS International Affective Picture System (see Lang et al., 2005)

IDE integrated development environment

IOR inhibition of return

IR infrared

IT inferior temporal cortex

LED light-emitting diode

LGN lateral geniculate nucleus

LIP lateral intraparietal area

LPFC lateral prefrontal cortex

MRF mesencephalic reticular formation

NRTP nucleus reticularis tegmentis pontis

OFC orbitofrontal cortex

OKN optokinetic nystagmus

PSE point of subjective equality

PPRF paramedian pontine reticular formation

SC superior colliculus

SD standard deviation

SDL Simple DirectMedia Layer

SSD saccadic suppression of displacement

SE standard error

SEF supplementary eye field

SD standard deviation

STS superior temporal sulcus

T1 initial saccade target

T2 displaced saccade target

TE inferior temporal area

TEO temporo-occipital area

TMS transcranial magnetic stimulation

V1 primary visual cortex

V2 secondary visual cortex

Vx higher visual cortices

VOR vestibulo-ocular reflex

Appendix C

Zusammenfassung

Contents

C.1 Die peri-sakkadische Wahrnehmung von Zeit

Kapitel 5 auf den Seiten 29 ff. befasst sich mit der temporalen Dimension der trans-sakkadischen, perzeptuellen Stabilität, das heißt der Stabilität der Wahrnehmung über Sakkaden hinweg. Zu diesem Zweck untersuchten wir einen *Chronostasis* genannten Effekt. Chronostasis beschreibt eine Verzerrung der subjektiven Zeitwahrnehmung unmittelbar im Anschluss an eine Sakkade. Während Sakkaden wird die visuelle Wahrnehmung aktiv unterdrückt. Obwohl diese sogenannte peri-sakkadische Suppression einen beträchtlichen Zeitinterval einnimmt, gibt es im Zeitbereich um eine Sakkade keine bewusst wahrgenommene Unterbrechung der scheinbar kontinuierlichen, visuellen Wahrnehmung. Es wurde postuliert, dass Chronostasis ein Mechanismus sei, eben diese "Lücken" in der Wahrnehmung zu schließen, oder dass Chronostasis – noch weitgehender – ein grundlegender Mechanismus sei, um Willkürhandlungen und ihre sensorischen Konsequenzen miteinander zu verbinden.

In unseren Experimenten konnten wir beweisen, dass Chronostasis kein globaler, die ganze visuelle Wahrnehmung betreffender Mechanismus ist. Unsere Ergebnisse deuten vielmehr an, dass es sich um einen lokalen Effekt handelt, der vermutlich sowohl zeitlich als auch räumlich beschränkt ist – zeitlich auf den Bereich um eine Sakkade und räumlich auf eine umschriebene Region um das Sakkadenziel. Obwohl der Versuch einer exakten Bestimmung der räumlichen Ausdehnung dieses Effektes keine eindeutigen Ergebnisse lieferte, konnten wir dennoch nachweisen, dass Chronostasis nicht alle notwendigen Eigenschaften eines globalen Kompensationsmechanismus' aufweist. Stattdessen resultiert die Verzerrung der subjektiven Zeitwahrnehmung vermutlich aus dem Verschieben der räumlichen Aufmerksamkeit, das jeder Sakkade vorausgeht. Die zeitliche und räumliche Dynamik räumlicher Aufmerksamkeit scheinen weit besser geeignet, die beobachteten Beschränkungen in der Verzerrung der subjektiven Zeitwahrnehmung zu erklären.

C.2 Perzeptuelle Konsequenzen sakkadischer Adaptation

Kapitel 6 auf den Seiten 53 ff. behandelt die Wechselbeziehungen zwischen Handlung und Wahrnehmung am Beispiel der perzeptuellen Konsequenzen sakkadischer Adaptation. *Sakkadische Adaptation* ist ein Mechanismus, der die Amplitude von Sakkaden kontinuierlich anpassen soll, damit geplante Sakkadenziele möglichst akkurat getroffen werden. Kurzzeitige sakkadische Adaptation wird unter Laborbedingungen erzeugt, indem wiederholt das Sakkadenziel während der eigentlichen Ausführung der Augenbewegung um einen festen Betrag versetzt wird. Dieser Versatz des Sakkadenziels bleibt in der Regel unbemerkt. Im Verlauf von ungefähr 50 Versuchsdurchgängen passt sich die Sakkadenamplitude graduell dem intra-sakkadischen Versatz an. Diese motorische Adaptation hat auch Konsequenzen für die peri-sakkadische Lokalisierung. Stimuli, die vor einer adaptierten Sakkade präsentiert werden, werden anschließend in Richtung der Adaptation verschoben lokalisiert. Wird ein Stimulus prä-sakkadisch präsentiert und post-sakkadisch lokalisiert, so muss die tatsächliche Größe der Sakkade berücksichtigt werden, um die geänderten retinalen Bezüge auszugleichen. Sakkadische Adaptation ist somit ein mögliches Werkzeug, um aufzudecken, wie Positionsinformation über Sakkaden hinweg integriert wird.

In unseren Experimenten konnten wir die perzeptuelle Verschiebung, die durch sakkadische Adaptation hervorgerufen wird, detailliert charakterisieren. Diese wird im Weiteren als *adaptationsinduzierte Verschiebung* bezeichnet. Zum ersten Mal waren wir in der Lage, die adaptationsinduzierte Verschiebung isoliert von anderen peri-sakkadischen Wahrnehmungseffekten darzustellen. Dies erlaubte uns, den exakten Zeitverlauf dieses Effektes relativ zum Sakkadenbeginn zu bestimmen. Weiterhin konnten wir nachweisen, dass die adaptationsinduzierte Verschiebung noch bei Stimuli zu beobachten ist, die bis zu einer Sekunde vor Sakkadenbeginn präsentiert werden. In einem letzten Experiment untersuchten wir die Entstehung der adaptationsinduzierten Verschiebung im Verlauf der Entwicklung sakkadischer Adaptation. Wir konnten zeigen, dass – unter den Bedingungen unseres Experimentes – das visuelle System die Nichtübereinstimmung der geplanten mit der tatsächlich ausgeführten Sakkade auflöst, indem verfügbare visuelle Referenzen weit stärker gewichtet werden als extraretinale Informationen. Gleichwohl fanden wir Anzeichen dafür, dass – in einem weit geringeren Ausmaß – motorische Adaptation auch direkt die Lokalisation visueller Stimuli beeinflussen kann.

C.3 Die peri-sakkadische Repräsentation von Objekteigenschaften

In Kapitel 7 auf den Seiten 91 ff. untersuchten wir den Einfluss peri-sakkadischer Suppression und Kompression auf die trans-sakkadische Integration von Objektidentität und die trans-sakkadische Repräsentation von Objekteigenschaften. Peri-sakkadische Kompression verschiebt die wahrgenommene Position von Stimuli, die unmittelbar um den Zeitpunkt des Sakkadenbeginns herum präsentiert werden, auf das Sakkadenziel zu. Werden dadurch mehrere Stimuli perzeptuell auf eine einzige Position verschoben, bleiben bestimmte Eigenschaften dieser Stimuli – speziell *Form* und *Farbe* – erhalten. Dies ist unabhängig sowohl von der Position des jeweiligen Objektes, als auch davon, ob der entsprechende Stimulus überhaupt explizit wahrgenommen wird. Die erhaltenen Merkmalsausprägungen bleiben nicht nur voneinander unterscheidbar, sondern konkurrieren auch noch unabhängig voneinander um den Zugang zum visuellen Bewusstsein, vergleichbar mit der sogenannten "perzeptuellen Rivalität". Dadurch können einzelne Objekte mit mehrfachen Ausprägungen desselben Merkmals wahrgenommen werden.

In unseren Experimenten erweiterten wir diesen Ansatz um die Objekteigenschaft *Bewegung*. *Bewegung* unterscheidet sich von *Form* und *Farbe* besonders auch hinsichtlich ihrer Repräsentation in visuellen Hirnarealen: *Bewegung* wird im dorsalen Pfad verarbeitet und repräsentiert, während *Form* und *Farbe* Eigenschaften des ventralen Pfades sind. Im Gegensatz zu *Form* und *Farbe*, bleibt *Bewegung* in unseren Versuchen nicht unabhängig von der Position eines Objektes erhalten. Werden zwei Stimuli mit verschiedenen Ausprägungen des Merkmals *Bewegung* perzeptuell auf eine einzelne Position verschoben wahrgenommen, so interagieren beide Ausprägungen miteinander. In diesem Fall hemmen entgegengesetzte Bewegungsrichtungen ausdrücklich die Bewegungswahrnehmung. Möglicherweise wird die parallele Verarbeitung von Ausprägungen des Merkmals *Bewegung* verschiedener Objekte durch den Prozess des sogenannten "Feature Bindings" gestört, vorausgesetzt, beide Ausprägungen werden durch die peri-sakkadische Kompression dem gleichen Objekt zugeordnet – oder zumindest an der gleichen Position wahrgenommen.

C.4 Der Einfluss emotional relevanter Sakkadenziele

Die Experimente aus Kapitel 8 auf den Seiten 119 ff. bilden eine explorative Studie, die den potenziellen Einfluss emotional relevanter Sakkadenziele sowohl auf motorische Parameter der Sakkadenplanung und -ausführung, als auch auf Parameter peri-sakkadischer Wahrnehmung untersucht. Emotional relevante Bilder unterschiedlicher Wertigkeit – kategorisiert als angenehm, neutral oder unangenehm – wurden als Sakkadenziele präsentiert. Diese Bilder wurden dem *International Affective Picture System* (IAPS), einer etablierten Datenbank für emotionales Bildmaterial, entnommen. Um den Zeitpunkt des Sakkadenbeginns herum wurden außerdem kurzzeitig Lokalisierungsstimuli präsentiert. Die untersuchten abhängigen Variablen waren Sakkadenlatenz und -amplitude, die Stärke und der Zeitverlauf der peri-sakkadischen Kompression sowie die Stärke der (peri-)sakkadischen Suppression.

In unseren Experimenten konnte ein geringer Trend zu längeren Sakkadenlatenzen für neutrale Sakkadenziele, verglichen mit angenehmen und unangenehmen Bildern, festgestellt werden. Diese Differenz verfehlte jedoch die angelegte statistische Signifikanz. Weiterhin konnten wir nachweisen, dass ein größerer Anteil von Lokalisationsstimuli in Durchgängen mit unangenehmen Bildern unbemerkt blieb, verglichen sowohl mit neutralen als auch angenehmen Sakkadenzielen. Wir schreiben diesen Effekt der Beteiligung visueller Aufmerksamkeit zu, von der bekannt ist, dass sie von emotional relevanten Stimuli angezogen wird. Eine größere Zuteilung attentionaler Ressourcen verbessert die visuelle Wahrnehmung. Aufmerksamkeit ist eng mit der Auswahl eines Sakkadenziels verbunden, ebenso mit der Sakkadenplanung und -ausführung. Möglicherweise interagieren in diesem Fall unterschiedliche Aufmerksamkeitsprozesse, so dass die Sakkadenplanung verzögert und die Lokalisation von Stimuli erschwert wird.

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Loading Mercury with a Pitchfork[1]

Loading mercury with a pitchfork
your truck is almost full. The neighbors
take a certain pride in you. They
stand around watching.

Richard Brautigan (1935–1984)

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[1] from: Brautigan, R. (1976). *Loading Mercury with a Pitchfork.*

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