



## Saccadic suppression of displacement in face of saccade adaptation

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### ABSTRACT

Saccades challenge visual perception since they induce large shifts of the image on the retina. Nevertheless, we perceive the outer world as being stable. The saccadic system also can rapidly adapt to changes in the environment (saccadic adaptation). In such case, a dissociation is introduced between a driving visual signal (the original saccade target) and a motor output (the adapted saccade vector). The question arises, how saccadic adaptation interferes with perceptual visual stability. In order to answer this question, we engaged human subjects in a saccade adaptation paradigm and interspersed trials in which the saccade target was displaced perisaccadically to a random position. In these trials subjects had to report on their perception of displacements of the saccade target. Subjects were tested in two conditions. In the 'blank' condition, the saccade target was briefly blanked after the end of the saccade. In the 'no-blank' condition the target was permanently visible. Confirming previous findings, the visual system was rather insensitive to displacements of the saccade target in an unadapted state, an effect termed saccadic suppression of displacement (SSD). In all adaptation conditions, we found spatial perception to correlate with the adaptive changes in saccade landing site. In contrast, small changes in saccade amplitude that occurred on a trial by trial basis did not correlate with perception. In the 'no-blank' condition we observed a prominent increase in suppression strength during backward adaptation. We discuss our findings in the context of existing theories on transsaccadic perceptual stability and its neural basis.

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### 1. Introduction

It is well known that the oculomotor system is able to retain its accuracy in case of changes in oculomotor conditions (e.g. muscle weakness or neural damage) that otherwise would lead to movement inaccuracy and poor vision. In the laboratory this effect, termed saccade adaptation, is typically studied by repetitive displacements of the saccade target while the eyes are moving. When the targets are shifted systematically in saccade direction, this process is called forward adaptation, for shifts against saccade direction it is called backward adaptation (McLaughlin (1967), Miller, Anstis, and Templeton (1981) and others, see Hopp and Fuchs (2004) for a review). During the first trials of an adaptation experiment, the motor error as induced by the target shift is corrected by secondary saccades. After a few tens of trials, however, human subjects adjust the gain of their first saccade until the displaced target position is reached with a single saccade.

The adaptation effect is not only relevant in the context of oculomotor learning. The investigation of saccade adaptation might also contribute to the understanding of the mechanisms that guarantee transsaccadic perceptual stability. Saccades in general

challenge visual perception (Bremmer & Krekelberg, 2003). Saccade adaptation specifically challenges perceptual stability as it interferes with the established mapping between pre- and post-saccadic perceptual space. Parts of the presaccadic visual field that were 'bound' to certain post-saccadic positions prior to adaptation will fall onto different spatial locations afterwards.

In the present study we aimed to investigate how the visual system would retain perceptual stability in the presence of motor distortions as induced by saccade adaptation. It is known that transsaccadic perceptual stability is supported by different mechanisms. On the one hand, specific aspects of visual perception are suppressed during saccades ((Bremmer, Kubischik, Hoffmann, & Krekelberg, 2009; Burr, Morrone, & Ross, 1994), see Ross, Morrone, Goldberg, and Burr (2001) for a review). On the other hand, mechanisms that guarantee space congruency across fixations are involved (see Wurtz (2008) for a review). Existing theories of transsaccadic stability can be grossly divided into those that emphasize post-saccadic (and in some notions rather 'passive') effects and others that focus on the contribution of active preparatory processes that operate prior to the saccade (see Wurtz (2008) for a review).

Evidence for the latter originates from physiological findings that were first made by single cell recordings in area LIP of the rhesus monkey while the animal performed a saccade task (Colby, Duhamel, & Goldberg, 1995; Duhamel, Colby, & Goldberg, 1992). In

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this study, some of the observed neurons showed a remarkable spatial response profile prior to the eye movements: they shifted their receptive fields (RFs) from their current position to their designated post-saccadic position thereby anticipating the spatial consequences of the upcoming saccade. Since the discovery of this effect, usually termed saccadic ‘remapping’ or ‘updating’, it has been replicated in slightly different variations in multiple other areas of the monkey brain including the FEF (Umeno & Goldberg, 1997), the SC (Walker, Fitzgibbon, & Goldberg, 1995) and earlier extrastriate visual areas (Nakamura & Colby, 2002) as well as in humans (Merriam, Genovese, & Colby, 2003). For the monkey, it has been demonstrated that the anticipatory shifting of the RFs in the FEF is caused by an internal copy of the motor command, termed corollary discharge or efference copy (Sperry, 1950; von Holst & Mittelstaedt, 1950), that represents the metrics of the upcoming saccades (Sommer & Wurtz, 2006). It is currently unknown, however, if and how RFs shift in case of saccade adaptation, i.e. if the shift would be based on the adapted or rather on an unadapted efference copy.

An alternative hypothesis concerning perceptual stability is mainly based on results obtained in human psychophysical experiments. One classical paradigm to study transsaccadic perceptual stability in humans is the so called ‘saccadic suppression of displacement’ paradigm (SSD) (Bridgeman, Hendry, & Stark, 1975). In this paradigm subjects perform a visually guided saccade. While the eyes are in flight, the saccade target is slightly displaced to a random position. Subjects report if (or alternatively in which direction) they have perceived a displacement of the target. Usually, displacement detection thresholds increase dramatically during saccades compared to fixation conditions (Bridgeman et al., 1975; Deubel, Schneider, & Bridgeman, 1996; Li & Matin, 1990). In other words, the visual system is rather tolerant against transsaccadic discrepancies in object positions. This tolerance, which typically is considered as evidence for perisaccadic perceptual stability, can be easily disrupted, though, using a simple manipulation termed blanking effect. In such case, the saccade target is briefly blanked (typically 200 ms) at the time the eyes land (Deubel et al., 1996). This cancels perceptual stability and subjects regain a remarkable precision in a displacement discrimination task. Based on these and other findings (Deubel, Bridgeman, & Schneider, 1998), Deubel and colleagues have proposed that re-afferent visual information (i.e. the post-saccadic visual scene) and in particular the presence of reference objects like the saccade target itself might play an important role in the preservation of transsaccadic perceptual stability (Bridgeman, 1995; Deubel, 2004; Deubel et al., 1998).

Following a slightly different approach, a couple of recent studies have found adaptation specific distortions in perceptual localization of stimuli that are presented before, during or after a saccade (Awater, Burr, Lappe, Morrone, & Goldberg, 2005; Bahcall & Kowler, 1999; Collins, Dore-Mazars, & Lappe, 2007; Collins, Rolfs, Deubel, and Cavanagh, 2009).

Bahcall and Kowler (1999) and Collins et al. (2009) asked subjects to indicate the position of a visual target that was used to elicit an (adapted) saccade in a blanking paradigm. Judgments were made by comparing the remembered target position to that of a probe stimulus, that was presented some time (200 ms) after the saccade had ended. In these experiments, the original saccade target was blanked before (Bahcall & Kowler, 1999) or during (Collins et al., 2009) the saccade. In non-adaptive control trials, localization of the saccade target was almost veridical. In adaptation trials, however, the probe stimuli had to be shifted in the direction of adaptation to match the remembered position of the saccade target.

In our present study we aimed at extending the existing literature on localization during saccade adaptation by investigating SSD in face of saccade adaptation. In contrast to Bahcall and Kowler

(1999) and Collins et al. (2009) we conducted our main experiments under conditions in which perceptual stability was not disrupted by the target blanking effect. Further, we did not only concentrate on the spatial aspect of SSD, but did also quantify suppression strength. We engaged subjects in saccade adaptation paradigms. Once adaptation was established, we interspersed trials in which perception of saccade target displacements was tested in a discrimination task (left/right), and, supplementary to former studies, also in a detection (yes/no) task. In addition to a *blank* condition we tested a *no-blank* condition in which the saccade target was not blanked when perceptual judgments were acquired. To avoid positional judgments with respect to external visual references, all our experiments were conducted in a completely dark environment.

## 2. Materials and methods

### 2.1. Subjects

Five subjects (three female and two male, mean age 26 years) gave written consent to participate in the experiments. All of them were experienced in psychophysical experiments, but were, except for one of the authors, naïve as to the goals of this study. The experiments were performed in accordance with the ethical standards of the 1964 Declaration of Helsinki.

### 2.2. Apparatus

Experiments were performed in a light and sound proof experimental chamber. Subjects were comfortably seated with their head supported by a chin rest. Eye position was monitored at 500 Hz using an infra-red eye tracker system (EyeLink II, SR-Research). Subjects were facing a large screen (80° × 60° of visual angle) on which stimuli were projected by a CRT projector (Marquee 8000, running at 150 Hz). Background luminance of the screen and its surroundings was below 0.1 cd/m<sup>2</sup>, i.e. there were no visual references available during the trials. Saccade onset detection that triggered target displacements in the adaptation conditions and target disappearance in the *blank* trials (cf. below) was based on a pure position criterion: eye position had to deviate from the initial fixation position by more than 2° in the direction of the intended saccade for more than two samples.

### 2.3. Task

Subjects always had to make a saccade from left to right in response to a jump of a fixation target. In some trials (‘probe trials’) they were prompted to report their perception of perisaccadic target displacements. In such case we collected two responses: the direction of the target displacement (left/right) and whether or not subjects had perceived such a displacement (yes/no). In the following, we will refer to the results of the yes/no task as the detection data, to those of the left/right task as the discrimination data. The detection data are dependent on the response criteria of the subjects (‘subjective data’), while the left/right response is bias free (‘objective data’). To give a response, subjects pressed one of four possible response keys on the number pad of the keyboard according to the following coding scheme: 7 – ‘left, yes’, 9 – ‘right, yes’, 1 – ‘left, no’, 3 – ‘right, no’. The given response was visible to the subject and could be corrected without temporal constraints.

### 2.4. Experimental conditions

Each subject was tested in the six conditions resulting from the combination of three adaptation conditions (*backward*, *forward* and *no-adaptation*) with two manipulations on the reappearance of the

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