



Pre- and post-saccadic stimulus timing in saccadic suppression of displacement – A computational model



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ABSTRACT

When the target of a saccadic eye movement is displaced while the eyes move this displacement is often not noticed (saccadic suppression of displacement, SSD). We present a neurobiologically motivated, computational model of SSD and compare its simulation results to experimental data. The model offers a simple explanation of the effects of pre- and post-saccadic stimulus blanking on SSD in terms of peri-saccadic network dynamics. Under normal peri-saccadic conditions pre- and post-saccadic stimulus traces are recurrently integrated with reference to present and future eye position, whereas blanking diminishes the pre-saccadic stimulus trace and thus leads to an uninfluenced integration of the post-saccadic stimulus trace. We show that part of the intersubject variability in SSD can be explained by differences in decision thresholds of this integration process.

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1. Introduction

With each shift of our gaze, the image on the retina abruptly changes. However, we do not perceive these jumps during eye movements. Rather, the world appears stable to us. This phenomenon has been termed ‘visual stability across eye movements’. While multiple experiments explored different aspects of visual stability, we here focus on the experimental paradigm known as saccadic suppression of displacement (SSD, e.g., [Bridgeman, Hendry, & Stark, 1975](#)). It revealed that subjects are unable to perceive small peri-saccadic displacements of stimuli which they can well detect when they occur during fixation. In other words, subjects perceive the world as visually more stable than it actually is.

Meanwhile, several studies addressed different aspects of SSD. [Deubel, Bridgeman, and Schneider \(1996\)](#) found that the detectability of stimulus displacements can be considerably improved when the stimulus at the saccade target is not displaced during the saccade but first removed and then shown after a blanking period of about 250 ms at its displaced position, known as the blanking or (post-)gap effect. Less attention has been given to the observation by [Deubel et al. \(1996\)](#) that an improvement of the detection performance also occurs when the target stimulus is not blanked after but before the saccade (pre-gap effect).

[Zimmermann, Morrone, and Burr \(2013\)](#) found that a prolonged viewing time prior to saccade onset also improves the detection of stimulus displacements. [Zimmermann et al. \(2013\)](#) and [Zimmermann, Born, Fink, and Cavanagh \(2014\)](#) further revealed that a displacement detection reduction does not require a saccade: similar decrements in performance occur during fixation if, instead of the execution of a saccade, a mask is presented.

An early theory proposed to explain the SSD effect – the object reference or visual search theory ([Bridgeman, 2007](#); [Deubel et al., 1996](#)) states that the visual system uses visual objects, usually the stimulus at the saccade target, to recalibrate spatial perception after the saccade. According to this theory, small displacements of the saccade target are not noticed because the visual system assumes that the saccade target stays stable during the saccade and ascribes any deviances of the target which should be in the center of the fovea after the saccade to an imprecise eye movement. Only if the target displacements are too large the visual system uses other information such as proprioception to recalibrate spatial perception, which leads to the detection of the stimulus displacements. In this framework the blanking effect is explained by a spatiotemporal ‘constancy’ window: Only if the saccade target stimulus is found within this spatiotemporal window the world is perceived as stable. If the object reappears after this window has closed, the stability assumption is dropped and target displacements are detected ([Bridgeman, 2007](#)).

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Based on a similar assumption but spelled out in a computational framework, Niemeier, Crawford, and Tweed (2003) proposed a Bayesian transsaccadic integration model. They attempted to predict the perceived displacement of a stimulus by combining the stimulus position, an internal estimate of the eye positions (e.g. efference copy) and an expectation about the probability of peri-saccadic target displacements (the prior). The model rests on the assumption that the brain computes this prior for each experimental condition, while the underlying mechanisms however, are not part of the model. They fitted the model to their own recorded data by using a sharply tuned prior in the non-blanking condition and a broadly tuned one in the blanking condition.

Atsma, Majj, Koppen, Irwin, and Medendorp (2016) criticised this model as it necessarily relies on the integration of a displacement vector (the combined visual and motor signals) and a prior around zero displacement. Thus, independent of the size of the true displacement it always predicts a reduction of the perceived displacement. They proposed a different model which in parallel applies not only an integration but also a separation of the pre- and post-saccadic stimuli and weighting both using the factors displacement size and viewing time to compute the final percept. They found that the degree of integration and separation depends on displacement size, where small displacements show a stronger weight for integration. However, Atsma et al. (2016) do not address the blanking condition with their model. Further, viewing time is not explicitly modeled but only implicitly in the probability density function coding the precision of the stimulus.

Understanding SSD by computing a unitary percept from pre- and post-saccadic stimulus contributions as suggested by Atsma et al. (2016) is not novel and has been already proposed in a neuro-computational model of SSD (Ziesche & Hamker, 2014), which has the further advantage that time is explicitly part of the model description. This model explains the blanking effect as an uninfluenced integration of the post-saccadic stimulus as the neural trace of the pre-saccadic stimulus has declined during the blanking period. Further, the eye dependent parameters have been fully updated at the time of post-saccadic stimulus presentation. In the non-blanking condition, both the pre- and post-saccadic stimulus, are integrated into a single percept. However, as the model has to link the pre-saccadic with the post-saccadic view it uses an egocentric reference frame based on internal eye position signals. In the non-blanking condition, the eye position signals have not been fully updated as the displacement occurs during saccade. Ziesche and Hamker (2014) further explained how predictive remapping, first reported by Duhamel, Colby, and Goldberg (1992), and corollary discharge are linked to saccadic suppression of displacement. However, the model does not require a saccade to show a reduction of displacement detection. Bergelt and Hamker (2016) applied the model to a masking experiment without a saccade and could well account for the observation of Zimmermann et al. (2014).

To further investigate the properties of the neuro-computational model, in particular with respect to variations of the stimulus timings, we applied it to the most relevant experimental variations of Deubel et al. (1996).

2. Material and methods

The neuro-computational model has been originally introduced to explain the peri-saccadic mislocalization of briefly flashed stimuli in complete darkness (Ziesche & Hamker, 2011). It has then been slightly adapted to the paradigm of saccadic suppression of displacement (Bergelt & Hamker, 2016; Ziesche & Hamker, 2014). As the model has been described in detail before, we will here describe its properties on a coarse level.

2.1. Anatomy

Our proposed model rests on the assumption that parietal areas, such as the lateral intraparietal area (LIP), receive two different kinds of eye position information (Fig. 1). First, a proprioceptive information about eye position (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990; Bremmer, Distler, & Hoffmann, 1997), presumably from the somatosensory cortex (Wang, Zhang, Cohen, & Goldberg, 2007; Xu, Wang, Peck, & Goldberg, 2011; Xu, Karachi, & Goldberg, 2012), and second, a preparatory corollary discharge about the intended saccade displacement (Colby, Duhamel, & Goldberg, 1996; Melcher & Colby, 2008; Wurtz, 2008) which presumably originates in the superior colliculus (SC) and is routed via the mediodorsal nucleus (MD) and the frontal eye field (FEF, Sommer & Wurtz, 2004, 2008). However, the exact origins of these eye position signals are not critical assumptions but rather provide a source of inspiration for the model design. Importantly, both eye position signals are used to transform a visual stimulus position signal, which is encoded in a retinocentric reference frame coming from early extrastriate areas, into an intermediate reference frame. The representation of stimulus position in the intermediate reference frames is then used to compute the stimulus position in a head-centered reference frame (Galletti, Battaglini, & Fattori, 1995; Mullette-Gillman, Cohen, & Groh, 2005). The computation of an explicit head-centered reference frame is not a critical requirement of the model but slightly improves the simulation results (Ziesche & Hamker, 2011, 2014).

2.2. Model

We use the concept of basis function networks (Pouget, Denève, & Duhamel, 2002) to combine a retinotopic retinal signal (modeled in a one-dimensional neuron layer X_r) with proprioceptive (modeled in a 1D layer X_{ePC}) and corollary discharge (modeled in a 1D layer X_{eCD}) signals. The basis functions are realized in two two-dimensional layers X_{bPC} and X_{bCD} in which the retinal signal is modulated by proprioception and corollary discharge respectively. From these basis function representations we read out a head-centered stimulus representation in an output layer X_h (Fig. 2).

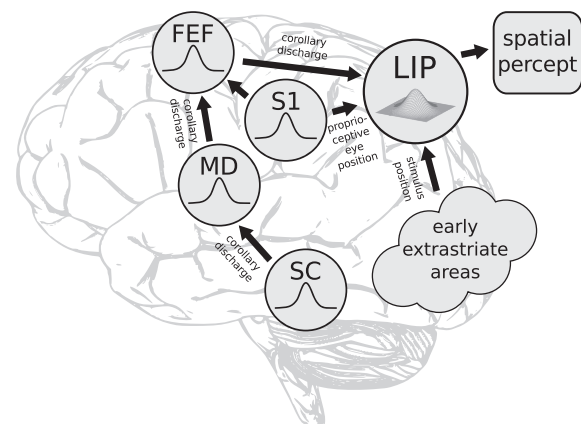


Fig. 1. Putative anatomical relationship of the model to the human brain. After the initial processing of stimulus properties in early visual areas, spatial information is represented in the parietal cortex in various reference frames. The core of the model may be localized in the human homologue of the lateral intraparietal area (LIP). It receives stimulus position information in retinotopic coordinates from early extrastriate areas, proprioceptive eye position information from primary somatosensory cortex (S1), and a phasic corollary discharge signal encoding planned saccade displacement originating from the superior colliculus (SC) and routed via mediodorsal nucleus (MD) and frontal eye field (FEF) to LIP. All this spatial information is integrated in LIP and then decoded to yield a spatial percept of the stimulus position.

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