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V4 receptive field dynamics as predicted by a systems-level model of visual attention using feedback from the frontal eye field

Fred H. Hamker*, Marc Zirnsak

Allgemeine Psychologie, Psychologisches Institut II, Westf. Wilhelms-Universität, Münster, Germany

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Abstract

Visual attention is generally considered to facilitate the processing of the attended stimulus. Its mechanisms, however, are still under debate. We have developed a systems-level model of visual attention which predicts that attentive effects emerge by the interactions between different brain areas. Recent physiological studies have provided evidence that attention also alters the receptive field structure. For example, V4 receptive fields typically shrink and shift towards the saccade target around saccade onset. We show that receptive field dynamics are inherently predicted by the mechanism of feedback in our model. According to the model an oculomotor feedback signal from an area involved in the competition for the saccade target location, e.g. the frontal eye field, enhances the gain of V4 cells. V4 receptive field dynamics can be observed after pooling the gain modulated responses to obtain a certain degree of spatial invariance. The time course of the receptive field dynamics in the model resemble those obtained from macaque V4.

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1. Introduction

Attention refers to the net effect of multiple mechanisms that leads to a focusing of the available processing resources. It is known to improve visual perception and action in a number of ways, such as speeding up the reaction time towards a stimulus (Posner, Snyder, & Davidson, 1980), improving change detection (Rensink, O'Regan, & Clark, 1997), enhancing the perceived contrast (Carrasco, Ling, & Read, 2004) and increasing the spatial resolution (Yeshurun & Carrasco, 1998). A large number of models have been inspired by the classical idea of a 'spotlight of attention' that highlights an area of interest by routing that information into higher areas for further processing. Such general approaches raise at least two fundamental issues.

First of all, what is the source that determines the location and shape of a spatially selective attentional focus? More than 10 years ago, due to the lack of detailed electrophysiological

data, attention has been described as a selection or winner-takes-all process within a saliency (or master) map (Koch & Ullman, 1985; Treisman & Gelade, 1980; Wolfe, 1994). Such a map has been defined to indicate potentially relevant locations by an enhanced activity at the corresponding spatial location. In the search for the saliency map a number of brain areas have been identified. Among those are the frontal eye field (Schall, 2002; Thompson & Schall, 2000), the superior colliculus (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Muller, Philiastides, & Newsome, 2005) and LIP (Bisley & Goldberg, 2006). However, area V4 has also been shown to reflect aspects of a saliency map (Bichot, Rossi, & Desimone, 2005; Mazer & Gallant, 2003; Ogawa & Komatsu, 2004), which suggests that saliency alone might not be a sufficient criterion for defining the source of spatial attention in the brain. In fact, we suggested a model in which the information of saliency in V4 can be task relevant immediately after the presentation of a visual scene regardless of spatial attention (Hamker, *in press*). This selective enhancement at intermediate levels of the cortical hierarchy could be used to guide visuomotor processes such as eye movements. Inspired by electrophysiological and behavioral observations (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995; Kustov & Robinson, 1996;

* Corresponding address: Allgemeine Psychologie, Psychologisches Institut II, Westf. Wilhelms-Universität, Fliegenerstrasse 21, 48149 Münster, Germany. Tel.: +49 251 83 34171; fax: +49 251 83 34173.

E-mail address: fhamker@uni-muenster.de (F.H. Hamker).

Moore & Armstrong, 2003; Rizzolatti, Riggio, Dascola, & Umiltà, 1987), we have provided computational evidence that, at least one, spatially selective feedback signal arrives from premotor cells of the oculomotor system such as the frontal eye field movement cells (Hamker, 2005a). This assumption makes specific predictions, since it constrains the timing and the spatial location of the feedback signal. Movement cells show only little, if any, response related to the onset of the stimulus and they start to increase in firing prior to saccade onset (although there is a continuity of frontal eye field visuomovement cells from showing only little to having a strong onset response). Thus, a spatially selective feedback at the saccade target occurs just prior to saccade onset but not immediately after the saccade target onset, since the movement cells require time to build up. However, spatially selective processing can occur earlier, due to feature-specific top-down signals (Hamker, *in press*).

The second issue is the impact of a spatially selective feedback signal on visual processing. The most simple and common mechanism is that of a gating mechanism according to which the cells which receive feedback gate their input to higher areas for object perception. Even when this gating can be gradual with respect to the strength of the feedback signal, it nevertheless implements an on/off switch depending of the presence/absence of the feedback signal. Inspired by the observation that object recognition can be very fast and probably even possible without prior spatial selection (Li, VanRullen, Koch, & Perona, 2002; Rousset, Thorpe, & Fabre-Thorpe, 2004) we suggested that feedback affects just the gain (Hamker, 2003, 2004, 2005a) and showed that this mechanism is consistent with the frameworks of multiplicative scaling (McAdams & Maunsell, 1999) and biased competition (Desimone & Duncan, 1995) if, in addition, lateral interactions exist. The framework of biased competition is built upon the following observation: When two stimuli are presented within the receptive field of a neuron, the influence of the non-attended stimulus is suppressed, as if the receptive field shrinks around the attended stimulus (Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999). The idea of a receptive field shift has been supported by the observation that the response profile is distorted towards the attended location, even when attention is directed outside of the receptive field (Connor, Preddie, Gallant, & Van Essen, 1997). Receptive field shifts might be an indirect result from a multiplicative scaling further upstream (McAdams & Maunsell, 1999). However, little work has been done to directly measure the receptive field profiles in attended and non-attended situations. A direct mapping of the receptive field profile has been done peri-saccadically (Tolias, Moore, Smirnakis, Tehovnik, & Siapas, 2001) and it can be inferred from this study that similar effects occur in covert shifts of attention.

In this article we will demonstrate that our framework is able to qualitatively reproduce the above mentioned receptive field effects. We suggest that gain modulation occurs in the same area where the receptive field effects are observed, after the response of the feature detectors (“simple cells”) and before the activity is spatially pooled

onto “complex cells”. This hierarchical processing is consistent with feedforward models of object recognition (Fukushima, 1980; Riesenhuber & Poggio, 1999; Spratling, 2005), where in addition, feedback increases the gain prior to spatial pooling. Since the computation of area V4 in our present large scale model of visual attention (Hamker, 2005b, 2005c, 2005d, *in press*) has been simplified to a single layer in which the gain modulation takes place, we extend area V4 to three (functional) layers. The first layer combines the input from cells of earlier areas in the hierarchy — a layer of feature detectors. These cells project to the next layer in which feedback enhances the gain. The third layer spatially pools the responses of the second layer to implement a limited range of spatial invariance. The feedback signal originates in IT and in the FEF movement cells. We show here that this extended model shows peri-saccadic receptive field dynamics similar to that observed in V4 (Tolias et al., 2001).

2. Model

The present model is an extension of an earlier model which has been described in detail on tasks such as object detection in natural scenes, change detection, visual search, feature-based attention and other attentional experiments (Hamker, 2005b, 2005c, 2005d, *in press*). The full model description is located in Appendix A.

The model consists of visual areas V4, inferotemporal (IT) cortex, prefrontal areas that contain the frontal eye field (FEF) for saccade planning and more ventrolateral parts for implementing functions of working memory (Fig. 1).

If we present a visual scene to the model, features such as color, intensity and orientation are computed from the image. The fact that features that are unique in their environment ‘pop-out’ is accounted for by computing an initial stimulus-driven saliency which determines the input into V4. We consider this stage a simplification with respect to its location in the brain. Pop-out effects are not necessarily generated early in the visual pathway. They are probably also computed in later areas, such as IT.

In extension to the original model (Hamker, 2005a, 2005c) V4 is now simulated by 3 layers: V4in, V4gain and V4pool. Feedback from the FEF and IT increases the gain of the cells in V4 gain. Pooling these gain modulated responses results in a larger degree of spatial invariance. However, for simplicity the complexity of features is not increased from V4 to IT. We have shown earlier that such a hierarchy of processing in V4 allows to quantitatively replicate single cell recordings of experiments investigating the ‘biased competition’ of two stimuli in a receptive field of a V4 cell under variable attentional conditions (Hamker, 2004, 2005b).

The growing receptive field size along the processing hierarchy requires that a number of V4 pool cells project to a single IT cell. Search in this model can be goal directed since IT receives feature-specific feedback from the prefrontal memory (PFmem) cells.

The planning of an eye movement is implemented as follows. The FEF visuomovement (FEFv) neurons receive convergent afferents from V4in and V4pool. The input activity at each location is summed across all dimensions (e.g. color,

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