Vision Research 50 (2010) 1235–1248

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Shape effects on reflexive spatial selective attention and a plausible neurophysiological model ☆

Saumil S. Patel, Xinmiao Peng [1], Anne B. Sereno *

Department of Neurobiology and Anatomy, University of Texas Medical School at Houston, Houston, TX 77030, United States

ARTICLE INFO

Article history:
Received 16 November 2009
Received in revised form 3 April 2010

Keywords:
Reflexive spatial attention
Shape processing
Neural model
Repetition suppression
Mutual inhibition

ABSTRACT

If a peripheral, behaviorally irrelevant cue is followed by a target at the same position, response time for the target is either facilitated or inhibited relative to the response at an uncued position, depending on the delay between target and cue (Posner, 1980; Posner & Cohen, 1984). A few studies have suggested that this spatial cueing effect (termed reflexive spatial attention) is affected by non-spatial cue and target attributes such as orientation or shape. We measured the dependence of the spatial cueing effect on the shapes of the cue and the target for a range of cue onset to target onset asynchronies (CTOAs). When cue and target shapes were different, the spatial cueing effect was facilitatory for short CTOAs and inhibitory for longer CTOAs. The facilitatory spatial effect at short CTOAs was substantially reduced when cue and target shapes were the same. We present a simple neural network to explain our data, providing a unified explanation for the spatial cueing effect and its dependence on shape similarities between the cue and the target. Our modeling suggests that one does not need independent mechanisms to explain both facilitatory and inhibitory spatial cueing effects. Because the neuronal properties (repetition suppression) and the network connectivity (mutual inhibition) of the model are present throughout many visual brain regions, it is possible that reflexive attentional effects may be distributed throughout the brain with different regions expressing different types of reflexive attention depending on their sensitivities to various aspects of visual stimuli.

1. Introduction

Despite the large number of neurons in the brain, the rate at which information can be processed, acted upon and remembered is limited. Due to the vast amount of external information at any moment, a dynamic or automatic adaptive mechanism may be helpful to indicate invariances that could enhance efficient use of the limited resources. Selection mechanisms are believed to filter signals arriving from the peripheral sensory organs thereby allowing the limited resources to only process signals important for the behavior at hand. This filtering can occur without movement of the eyes and is either automatic (reflexive attention) or willful (voluntary attention) (Jonides, 1981; Moore, 2006).

In a typical paradigm designed to study reflexive spatial attention, a stimulus, called a cue, is first presented randomly in one of two spatial locations. After a delay, a second stimulus, called a target, is presented randomly in one of the same two spatial locations. In Posner's and Cohen's (1984) original experiments, the observer indicated the spatial location of the target as quickly as possible by pressing a button. In subsequent experiments, the observer's responses have also been indicated by making an eye movement to the target (Briand, Larrison, & Sereno, 2000; Maylor, 1984). Normally, for short delays between the cue and target (cue onset to target onset asynchrony, CTOA), there is facilitation of target processing if the cue and target are presented at the same location compared to different locations, whereas for longer CTOAs, there are decrements in performance (Briand et al., 2000; Maylor, 1984; Posner & Cohen, 1984). This aspect of reflexive attention in which the cue impairs the response to the target is called inhibition of return, or simply IOR. The name arises because the phenomenon is often functionally interpreted as if the locus of attention were being inhibited from returning to the same spot (see Klein (2000), for a review).

It has also been suggested that color and shape attributes of the cue and the target produce a reflexive cueing effect. Law, Pratt, and Abrams (1995) and Fox and de Fockert (2001) showed that response times to detect the target were shorter when the color of the foveal cue and the foveal target were different compared to same (*color cueing effect*). Fox and de Fockert (2001) additionally showed that

---

☆ Parts of this manuscript have been presented at the Second International Conference on Cognitive Science in 2006 and the Society for Neuroscience annual meeting in 2007.

* Corresponding author.
E-mail address: Anne.B.Sereno@uth.tmc.edu (A.B. Sereno).

[1] Present address: Department of Neuroscience, Baylor College of Medicine, Houston, TX 77030, United States.

0042-6989/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2010.04.010

response times to detect the target were shorter when the shape of the foveal cue and the foveal target were different compared to same (*shape cueing effect*). Finally, Fox and de Fockert (2001) found that the inhibitory color and shape cueing effects observed for foveal cue and target did not occur for peripheral cue and target. However, using peripheral cues and targets (Riggio, Patteri, & Umilta, 2004) were able to demonstrate that response times to detect a target at 250 ms or greater CTOAs were longer when the shapes of the peripheral cue and target were same vs. different. This inhibitory *shape cueing effect* only occurred when cue and target were presented in the same location. In contrast to these studies, in one experiment, Kwak and Egeth (1992) found that response to detect a target was faster if its orientation was the same compared to different from that in a previous trial (*orientation cueing effect*). Spatial IOR is also found to be modulated by the relative shapes of the cue and the target (Morgan & Tipper, 2007). In a paradigm where observers knew *a priori* whether the cue and the target have the same or different shapes, Morgan and Tipper (2007) showed that spatial IOR is significantly larger when the cue and target have identical shapes compared to when they have different shapes.

One important question is whether there are two largely independent mechanisms mediating the facilitatory and inhibitory reflexive spatial cueing effects or whether there is a common network in which facilitatory and inhibitory reflexive spatial cueing effects occur. In spatial cueing paradigms, some studies have found IOR without concurrent facilitation (Lambert, Spencer, & Hockey, 1991; Tassinari, Aglioti, Chelazzi, Peru, & Berlucchi, 1994; Tassinari & Berlucchi, 1993), while others have found that IOR and facilitation occur under different stimulus conditions (Maylor & Hockey, 1985; Posner & Cohen, 1984). These results support the idea that facilitation and inhibition are separable processes (Collie, Maruff, Yucel, Danckert, & Currie, 2000; Klein, 2000; Maruff, Yucel, Danckert, Stuart, & Currie, 1999). However, as noted later in the discussion, the presence of an inhibitory cueing effect and concurrent absence of a facilitatory cueing effect does not necessarily imply that two independent mechanisms underlie facilitatory and inhibitory cueing effects.

The neural mechanisms underlying these facilitatory and inhibitory reflexive cueing effects are not well understood but it is clear that they occur for both spatial and non-spatial visual processing. Lehky and Sereno (2007) have suggested that the suppression of a neuron's response when a stimulus is presented in its receptive field multiple times (a phenomenon termed repetition suppression) may be linked to the IOR observed in behavioral cueing paradigms (also see Dukewich, 2009; Sereno, Lehky, Patel, & Peng, 2010). The first evidence of repetition suppression in inferotemporal cortex (IT) of awake behaving monkeys was reported by Gross and his colleagues (Gross, Bender, & Gerstein, 1979). Subsequently a large number of studies in inferotemporal cortex (IT) have replicated the repetition suppression effect (Baylis & Rolls, 1987; Brown & Bashir, 2002; Brown, Wilson, & Riches, 1987; Fahy, Riches, & Brown, 1993; Gross et al., 1979; Miller, Gochin, & Gross, 1991; Miller, Li, & Desimone, 1993; Rolls, Baylis, Hasselmo, & Nalwa, 1989; Sobotka & Ringo, 1993; Xiang & Brown, 1998). Recent work has demonstrated shape selectivity in dorsal stream areas (Peng, Sereno, Silva, Lehky, & Sereno, 2008; Sereno & Maunsell, 1998) and shown that neurons in the lateral intraparietal cortex (LIP) also exhibit a shape repetition suppression effect that is similar to the effects in AIT neurons (Lehky & Sereno, 2007). A reduced response to a repeated stimulus has also been demonstrated subcortically, in the superior colliculus (Fecteau, Bell, & Munoz, 2004). Could this repetition suppression phenomenon form the basis for the spatial and non-spatial facilitatory and inhibitory reflexive cueing effects observed in the behavioral cueing paradigms?

Here we utilized a model-based approach to explore the above question. Because (i) shape selectivity is found in area LIP (Sereno & Amador, 2006; Sereno & Maunsell, 1998), (ii) neurons in LIP exhibit repetition suppression (Lehky & Sereno, 2007), (iii) area LIP is linked to spatial attention (Bisley & Goldberg, 2006), we hypothesized that shape will systematically influence behavioral spatial cueing effects and that the repetition suppression effect may be critical for behaviorally observed facilitatory and inhibitory spatial cueing effects (Sereno et al., 2010). We tested this hypothesis by doing the following: (1) Using a modified reflexive/exogenous (i.e. peripheral cue) spatial cueing task (see Fig. 1 and Section 2 for more details), we investigated the psychophysical effect of shape on the performance of human observers. The main variables in our experiments were (a) the shape of the cue and the target, (b) the location of the cue and the target, and (c) the CTOA. If repetition suppression effects in shape selective neurons are the underlying physiological mechanism of reflexive spatial attention, we predicted that the shape of the cue and target would influence reflexive spatial attention. Given that many cells in the dorsal stream are shape selective, when the cue and target have the same shapes, these cells would have maximal neural repetition suppression effects. When the cue and target have different shapes, different cells would respond and there would be reduced repetition suppression effects. (2) We developed a mathematical model consisting of a network of shape selective neurons whose dynamic properties (e.g., repetition suppression, non-linear dynamics) are similar to those of neurons in area LIP of monkeys. A key network principle also used in the model was spatially localized mutual inhibition between the shape selective neurons. Using our model, we for the first time demonstrate that these simple dynamic properties of individual shape selective neurons along with a mutual inhibition among them are sufficient to account for the behaviorally measured facilitatory and inhibitory spatial cueing effects in Posner's cueing paradigms. (3) Finally, we demonstrate that the model can also explain the dependence of these facilitatory and inhibitory spatial cueing effects on the shape of the cue and target. Further, we "lesioned" the model to better understand the specific roles of repetition suppression and mutual inhibition on behavioral outcome and to show that both repetition suppression of neuronal responses and mutual inhibition between neurons in the network are critical for these facilitatory and inhibitory spatial effects and their dependence on shape.

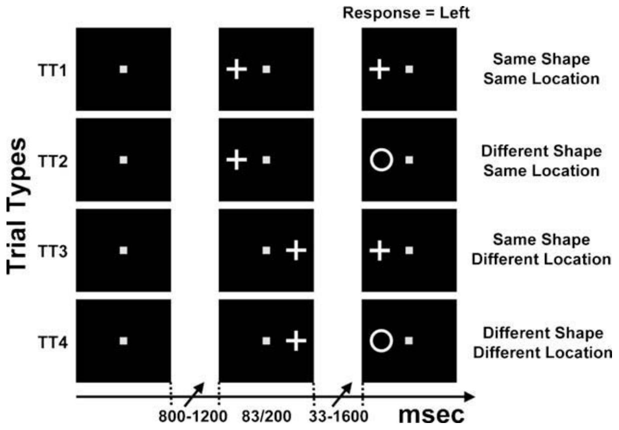

Fig. 1. Experimental paradigm. There were four types of trials (TT1–TT4) intermixed randomly in a single run. In this example, trials for a single cue shape (cross) and a single target location (left) are illustrated. The horizontal arrow at the bottom represents time. After fixation (left column; random duration between 800 and 1200 ms), a cue is flashed (83 or 200 ms) either to the left or right of the fixation point (middle column). After a random delay (33–1600 ms), a target is presented which remains on the screen until the observer responds. The observer's correct response in any of these trials is 'left'.