



Spatial remapping in visual search: Remapping cues are provided at attended and ignored locations

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ABSTRACT

We experience the world as stable and continuous, despite the fact that visual input is overwritten on the retina with each new ocular fixation. Spatial remapping is the process that integrates selected visual information into successive (continuous) representations of our spatial environment, thereby allowing us to keep track of objects, and experience the world as stable, despite frequent eye (re-)fixations. The present paper investigates spatial remapping in the context of visual pop-out search. Within standard instances of the pop-out paradigm, reactions to stimuli at previously attended locations are facilitated (faster and more accurate), and reactions to stimuli at previously ignored locations are inhibited (slower and less accurate). The mechanisms that support facilitation at previously attended locations, and inhibition at previously ignored locations, serve to enhance the efficiency of visual search. It is thus natural to expect that information about which locations were previously attended to or ignored is stored and remapped as a concomitant to successive representations of the spatial environment. Using variants of the pop-out paradigm, we corroborate this expectation, and show that information concerning the prior status of locations, as attended to or ignored, is remapped following attention shifts, with some degradation of information concerning ignored locations.

1. Introduction

Our visual system compensates for changes in the outside world and for self-movements, in order to generate a stable and continuous representation of the environment. At a given instant, the “raw material” of visual perception consists of the content of the present eye fixation on the retina. In the next instant this content is immediately overwritten by the content of the next ocular fixation. To a great extent, we owe it to spatial remapping that selected visual input is preserved across saccades and accompanying overt attention shifts, and integrated into meaningful representations of our spatial environment (Bays & Husain, 2007; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Hall & Colby, 2011). Neurons in the lateral intraparietal area, the frontal eye fields, and the superior colliculus, frequently studied in monkeys (Duhamel, Colby, & Goldberg, 1992; Kusunoki & Goldberg, 2003; Merriam, Genovesi, & Colby, 2003; Mirpour & Bisley, 2015), have been found to accomplish remapping by bringing future target locations into their dynamic receptive fields, in advance of a saccade. These neural

mechanisms are highly selective, and although we have the subjective impression of maintaining an extensive gapless sensory representation of our spatial environment, only those stimuli that have attracted visual attention due to the relevance for the task at hand, or to the salience of their physical properties, are selected for representation and remapping (Gottlieb, Kusunoki, & Goldberg, 1998; Pisella & Mattingley, 2004; Melcher, 2007; Golomb, Chun, & Mazer, 2008). Theories of spatial remapping attempt to explain how it is that visual attention guides these remapping processes (e.g., Pisella & Mattingley, 2004; Cavanagh et al., 2010). As an element of such theories, the idea of a “salience map” was introduced (Niebur & Koch, 1997; Itti & Koch, 2001), as a model of the means by which an agent's visual system measures its “interest” in varied locations within the spatial environment, which in turn directs the priorities of visual attention in surveying that environment. According to such theories, spatial remapping employs a salience map to ensure spatio-temporal continuity between successive eye fixations, by, first, preventing highly salient information (above a certain probabilistic threshold) from being overwritten, and, second, by

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refreshing and “repositioning” select information from past representations within the current representation of the spatial environment (Pisella & Mattingley, 2004). According to this view, activity on the saliency map provides “remapping cues”, and information concerning those locations that feature the highest current activity is remapped.

The present study investigates spatial remapping in situations such as they occur during visual search, where the deployment of visual attention to certain locations in a visual scene is mediated by previous experience concerning those locations: attention is primed and thus quickly driven towards salient target locations that were previously attended, but it is - at the same time - slowed (“inhibited”) when the current target location was previously occupied by a distractor stimulus. Priming effects signal the successful integration of visual information across successive trials. We make use of this fact, in the experiments described in this paper. In these experiments, we investigate the extent to which target and distractor locations provide remapping cues.

1.1. Saccadic remapping into spatiotopic coordinates

The initial representation of visuo-spatial information is in a retinotopic format, whereas objects in our environment reside within a spatiotopic, “world-centered”, frame of reference. While a subject's retinotopic representation changes with each eye-movement, the spatiotopic coordinates associated with the subject's environment remain stable. To enable interaction with our environment and to keep track of objects in the world, it is thus essential that visuo-spatial information be reoriented to a spatiotopic frame of reference (for a review, see Melcher & Morrone, 2015). Empirical evidence suggests that visuo-spatial information is maintained in retinotopic coordinates across saccades in trans-saccadic memory, but is also *remapped*, in the course of saccades, into world-centered coordinates (Irwin, Zacks, & Brown, 1990; Golomb et al., 2008; Golomb & Kanwisher, 2012a, 2012b; Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013). For example, Golomb et al. (2008) found that reactions to target stimuli were facilitated at attended locations in a retinotopic coordinate system after saccades (i.e., at the same attended location relative to the position of the eyes) as well as within a post-saccadic spatiotopic coordinate system (i.e., at the same attended location in terms of “absolute” world-based coordinates). However, while retinotopic facilitation occurred independently from task requirements, it appears that spatiotopic facilitation occurs only “on demand”, i.e., when the target stimulus is task-relevant (but see recent work by Jonikaitis, Szinte, Rolfs, and Cavanagh, 2013, for evidence that spatiotopic facilitation also occurs in response to salient attention-capturing stimuli that are not task-relevant). Furthermore, Golomb et al. (2008) found that retinotopic facilitation was strongest immediately (100–200 ms) after saccades and weaker at later points in time, while the strength of spatiotopic facilitation followed a reverse pattern (weaker first, and stronger later), matching the finding that trans-saccadic (retinotopic) memory is limited and decays as a function of time (Irwin, 1992; Irwin & Gordon, 1998; Carlson-Radvansky, 1999; Deubel, Schneider, & Bridgeman, 2002; Prime, Tsotsos, Keith, & Crawford, 2007). The differential pattern for spatiotopic and retinotopic information is explicable, since it makes more sense to maintain enduring spatiotopic representations of the environment, as opposed to retinotopic representations which become obsolete with each movement.

Further corroborating the hypothesis that spatial attention operates on retinotopic coordinates, while remapping operates over spatiotopic coordinates (Golomb et al., 2008), Sapir, Hayes, Henik, Danziger, and Rafal (2004) found prolonged reaction times for post-saccadic targets at locations that were “pre-cued” (an effect known as “inhibition of return”; IOR; Klein, 2000) *both* in the case where the location was invariant according to retinotopic coordinates (but not spatiotopic coordinates), and in the case where the location was invariant according to spatiotopic coordinates (but not retinotopic coordinates). Sapir et al.

(2004) also probed for the same effects in patients with right parietal lesions, known to exhibit spatial remapping deficits (Duhamel, Goldberg, Fitzgibbon, Sirigu, & Grafman 1992; Heide, Blankenburg, Zimmermann, & Kömpf 1995; Pisella, Berberovic, & Mattingley, 2004). In these patients, IOR was found within retinotopic, but not within spatiotopic coordinates. These results support the idea that spatiotopic representations rely on spatial remapping, while retinotopic representations are held in trans-saccadic memory.

In summary, the available evidence suggests that, following overt attention shifts, visuo-spatial information about previously attended locations is maintained in retinotopic coordinates, and remapped to spatiotopic coordinates as needed, thereby resulting in facilitation (Golomb et al., 2008) and inhibition (Sapir et al., 2004) for stimuli at respective retinotopic and spatiotopic coordinates.

1.2. Location priming as a method to assess spatial remapping during visual search

The target in a visual pop-out search display is a prime example of a salient stimulus. It is identified by a unique feature (e.g., its color), the so-called singleton, which makes it distinct from simultaneously presented distractor stimuli. The singleton “causes” the target to “pop-out” from the display among a set of distractors. The effect is based on the extremely fast bottom-up allocation of selective attention to the (pop-out) target (Treisman & Gelade, 1980). In a visual search task, embedded in a cross-trial priming paradigm, there are multiple consecutive trials where the targets and distractors are presented at different locations in respective trials. At target locations that were also target locations in the preceding trial (trial $n-1$), reactions (e.g., pressing certain keys to indicate the presence of a specific characteristic of the target) are facilitated compared to reactions to targets that appear at locations that were “empty” (i.e., not occupied by any stimulus in trial $n-1$). The effect is variously known as “positive priming” or “facilitation”. Positive priming is supposed to advance visual search by facilitating reactions at locations that proved to be relevant on prior trials. The reverse effect is obtained for a target that occurs at a location that was previously occupied by a distractor. Here, reactions are slowed and less accurate, an effect termed “negative priming” or “inhibition”. See Fig. 1 for an illustration of priming of pop-out effects. Negative priming presumably reflects the assignment of some inhibitory tag that marks a location where reactions should be suppressed, and contributes together with facilitation to the efficiency of visual search in a complementary manner.

The above described paradigm, which is used in the experiment presented here, is well-established and its effects have been repeatedly and reliably obtained under static viewing conditions in numerous studies (e.g., Maljkovic & Nakayama, 1996; Kristjánsson, Vuilleumier, Malhotra, Husain, & Driver, 2005; Geyer, Müller, & Krümmenacher, 2007; Finke, Bucher, Kerkhoff, Keller, v. Rosen, et al., 2009; Kristjánsson & Campana, 2010; Geyer, Gokçe, & Müller, 2011; Gokçe, Müller, & Geyer, 2015). Recently, a study by Gokçe et al. (2015) used a similar paradigm to shed light on the short-term memory mechanisms that underlie the representation of target and distractor stimuli in visual pop-out search in various spatial reference frames. While Gokçe et al. (2015) focus on the mechanisms that underlie priming, the focus of the present paper is on the mechanisms used by our visual system to stabilize perception across saccades and accompanying overt attention shifts. In the experiment presented in this paper, we employed the paradigm as the basis for measuring the extent of the successful transfer of visual input following saccades and overt attention shifts.

The first condition of our experiment was meant to replicate facilitation and inhibition under conditions where no saccades and overt attention shifts occur between successive trials. Visual search arrays were presented around a central fixation cross and participants kept the cross fixated throughout successive trials. However, under static viewing conditions, one cannot distinguish between post-saccadic

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