**VISION
RESEARCH**

On the superiority of visual processing in spatiotopic coordinates

Alon Mann[a], Ilana Naveh[b], Ehud Zohary[b],*

[a] Neurobiology Department, The Hebrew University of Jerusalem, Jerusalem 91904, Israel
[b] Neurobiology Department & The Edmond and Lily Safra Center for Brain Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

ARTICLE INFO

ABSTRACT

Organisms exploit spatiotemporal regularities in the environment to optimize goal attainment. For example, in experimental conditions, repetition of a stimulus at the same position speeds up response time. A recent study reported that this spatial priming occurs even when the eyes move between trials, indicating that the target is encoded in spatiotopic coordinates (Attention, Perception & Psychophysics 78, (2016) 114–132). However, in that study, the relevant position of the repeated stimulus eliciting spatiotopic priming, was always at the screen center. Using a similar paradigm, we find that reaction times for *screen-centered* targets are markedly shorter than for retinally-equidistant target positions. When this center preference is taken into account, the alleged spatiotopic priming effects are dramatically reduced, though not totally eliminated. In a second experiment, we show that the preferred central stimulus position is encoded in allocentric coordinates (e.g. screen position) rather than in an egocentric frame of reference (e.g. straight ahead). The better performance at the screen center, irrespective of gaze direction or seating position, is likely to reflect an optimal choice for the allocation of spatial attention.

1. Introduction

The brain is an efficient *prediction* machine. Organisms develop efficient internal representations of past sensory stimuli which provide valuable predictive information to optimize goal attainment. Thus, statistical regularities in the world are exploited to generate a better prediction of future events and the actions of others. This has been extensively studied in the visual modality. Numerous studies have shown that the visual system can exploit spatial regularities in the environment in order to improve behavioral efficiency. For example, in visual search tasks, if the target is placed in some locations at a greater frequency than in others, observers begin to search preferentially for the targets in the more likely parts of the display (Geng & Behrmann, 2002; Hoffmann & Kunde, 1999; Jiang, Swallow, Rosenbaum, & Herzig, 2013; Miller, 1988). Similarly, if the target item is repeatedly placed at a specific location per scene, that scene's spatial arrangement acts as a strong cue for the target location in the repeated trials: Within a few trials, observers are faster to find targets in familiar-setting trials than in non-familiar ones (Chun, 2000; Chun & Jiang, 1998; Jiang & Wagner, 2004).

Here, we focus initially on a phenomenon called spatial priming (or position priming), defined as response time facilitation in visual search when the target's spatial position is the same as in recent trials

(Maljkovic & Nakayama, 1996; see also Ball, Smith, Ellison, & Schenk, 2010; Geyer et al., 2007; Kumada & Humphreys, 2002; Leber, Lechak, & Tower-Richardi, 2013; Rabbitt, Cumming, & Vyas, 1977). Priming effects (i.e. shorter response times) are greatest when the target in the previous trial (n − 1) is placed at the same position as in the current trial (n). The priming gain decays rapidly, and is no longer evident if the position repetition is a few trials apart (e.g. n − 5). Spatial priming offers no net behavioral advantage when the events are uncorrelated in time (i.e. past trials do not convey any meaningful information about the target location in the coming trial). However, our sensory systems may be predisposed to assume and register "regularities" based on recent events even if the events are in fact uncorrelated when taking into account a much longer history of events.

Position priming effects have been repeatedly reported (for review see Kristjánsson & Campana, 2010) following the classical experiment by Maljkovic and Nakayama (1996). However, until recently, the issue of the *coordinate frame* at which priming occurs was not addressed, since participants maintained fixation throughout the trial. Thus, position priming could have occurred in a retinal or an extra-retinal (spatiotopic) coordinate system. Recently, Tower-Richardi, Leber, and Golomb (2016) addressed this issue by requiring participants to fixate at different positions on the screen at consecutive trials, thereby dissociating between retinotopic stimulus repetitions (when the target's

* Corresponding author.
  E-mail addresses: Alon.mann@mail.huji.ac.il (A. Mann), Ilana.Naveh@mail.huji.ac.il (I. Naveh), udiz@mail.huji.ac.il (E. Zohary).
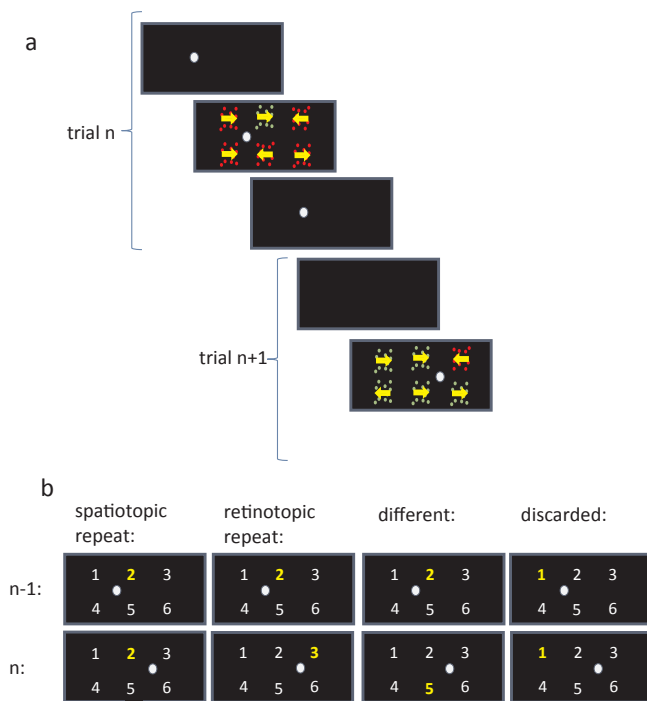
Fig. 1. Experimental design and trial classification method. (a) Trial design: subjects reported the direction of movement of the odd-colored random dot kinematogram (RDK). Fully coherent motion was present in six fixed positions. The motion in each was either right or left in an independent pseudorandom manner (arrows symbolize the movement). Each trial started with fixation on the new fixation point (white circle). Upon detection of fixation the stimulus array was shown (up to 3 s until response) and the subject's response (left or right movement) was recorded. After response, and an inter-stimulus-interval of 500 ms, the fixation point was moved to the alternate position. The subject was required to re-fixate the fixation point in its new location, initiating the next stimulus presentation. (b) Trial classification: the white circle is the fixation point. The numbers (1–6) correspond to the different stimulus locations on the screen. The yellow digit symbolizes the target RDK position. Trial conditions in the present trial (n) were classified into 4 different categories on the basis of the previous trial (n − 1). Spatiotopic repeat trials were those in which the target stimulus was at the same screen position as in the previous trial. Retinotopic repeat trials consisted of trials in which the target stimulus was at the same retinal position as in the previous trial. Different trials were the ones in which the target stimulus was neither at the same retinal position nor at the screen position as the previous trial, but at the same eccentricity. Discarded trials were ones in which the target stimulus at the present trial (n) was at a further eccentricity, and were not analyzed later. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

location on the *retina* was repeated) and spatiotopic stimulus repetitions (when the target was repeated at the same position on the *screen* but on different positions on the retina due to the change of gaze direction between trials). Somewhat surprisingly, Tower-Richardi et al. (2016) found strong spatiotopic position priming but only weak retinotopic position priming. They concluded that spatial priming occurs in an ecologically relevant coordinate system, and is likely to serve an adaptive role in human behavior.

The predominance of spatial priming effects in spatiotopic co-ordinates is an important finding, because the representation in the early visual system is strictly retinotopic, and the evidence for a non-retinotopic representation in higher order areas in the visual cortex is hotly debated (D'Avossa et al., 2007, Gardner, Merriam, Movshon, & Heeger, 2008; McKyton and Zohary 2006). Thus, our first aim (experiment 1) was to replicate the experiment by Tower-Richardi et al. (2016) with some changes, to test whether the spatiotopic priming effect is generalizable to other stimuli. In our task, subjects reported the

direction of motion of an odd-colored random dot stimulus (e.g. red leftward moving RDK) among other distractors (e.g. green RDKs moving left or right; see Fig. 1a). As in Tower-Richardi et al. (2016) subjects alternated their direction of gaze from trial to trial, to allow clear dissociation between stimulus repetition in retinotopic and spatiotopic coordinate frames. Note that both in the current study and in the previously reported study (Tower-Richardi et al., 2016) spatiotopic repetition trials were only included in the analysis if they were presented at the screen center/straight ahead (due to other required constraints, see below). This raises some obvious concern as recent evidence suggests that regardless of gaze position, visual processing of straight ahead stimuli is better than at other locations (Durand, Trotter, & Celebrini, 2010; Durand et al., 2012). These authors suggested that objects which are positioned straight ahead may form an immediate obstacle to a moving organism. If a straight ahead object is neglected when gaze is directed to other objects, this may result in a behavioral cost (Berkley, Kitterle, & Watkins, 1975). Therefore, there may be a strong evolutionary pressure for a mechanism to maintain vigilance to the straight ahead position even when gaze is directed elsewhere.

Another possible confounding factor is a bias for the screen center, as this is the optimal position for *spatial attention* given that the target could appear in various fixed locations around the screen center. Indeed, previous research found a strong "center bias" when freely viewing natural scenes as measured by the distribution of fixation positions (Tseng, Carmi, Cameron, Munoz, & Itti, 2009).

In this study we set to clarify the issue of position priming and its relevant coordinates, taking into account the above possible confounds.

2. Experiment 1 methods

2.1. Participants

All 24 participants were students (age, SD: 23 +/− 2.5 years) studying in the Hebrew University of Jerusalem. 17 of the participants were female. All were naïve to the goals of the current experiment and had normal or corrected to normal visual acuity by self-report. All subjects gave written informed consent and were paid for their participation. Experimental procedures were approved by the ethics committee of the Hebrew University of Jerusalem. Before beginning data collection, subjects had a short training block (consisting of 36 trials) to ensure that they understand the task requirements and can perform the experiment. Following this brief training block, the recording sessions were initiated.

We calculated the required sample size for our experiment (using the software G*Power 3.1.9.230) according to the results of a pilot experiment which consisted of 10 subjects (The first 10 subjects in the main experiment). Amazingly, the pilot group's effect size and standard deviation (using $\alpha = 0.05$ and Power $(1 − \beta) = 0.95$) was already sufficient to conclude that there was a significant spatial priming effect (cohen's d = 1.32). However, we decided to expand the sample size further to n = 24, to further enhance our statistical power and to match to previously reported articles' sample sizes in the field.

2.2. Stimuli

Our display comprised of six RDKs of colored dots that moved either to the left or to the right within a rectangular window (2.3 × 2.0 degrees). In each aperture, the motion was always fully coherent (100% coherence). The direction of motion was randomly chosen (left or right), per aperture. On each trial, the target stimulus (single RDK), was odd colored (i.e. red among green distractors, or green among reds).

2.3. Procedure

The experiment consisted of 1 training block and 64 recording blocks, each consisting of 36 trials, totaling in 2304 trials over 2 'daily