



## Reprint of: The effects of distractors and spatial precues on covert visual search in macaque <sup>☆</sup>

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### ARTICLE INFO

#### Article history:

Available online 16 May 2013

#### Keywords:

Attention  
Transient  
Cueing  
Rhesus monkey  
Set-size effects

### ABSTRACT

Covert visual search has been studied extensively in humans, and has been used as a tool for understanding visual attention and cueing effects. In contrast, much less is known about covert search performance in monkeys, despite the fact that much of our understanding of the neural mechanisms of attention is based on these animals. In this study, we characterize the covert visual search performance of monkeys by training them to discriminate the orientation of a briefly-presented, peripheral Landolt-C target embedded within an array of distractor stimuli while maintaining fixation. We found that target discrimination performance declined steeply as the number of distractors increased when the target and distractors were of the same color, but not when the target was an odd color (color pop-out). Performance was also strongly affected by peripheral spatial precues presented before target onset, with better performance seen when the precue coincided with the target location (valid precue) than when it did not (invalid precue). Moreover, the effectiveness of valid precues was greatest when the delay between precue and target was short (~80–100 ms), and gradually declined with longer delays, consistent with a transient component to the cueing effect. Discrimination performance was also significantly affected by prior knowledge of the target location in the absence of explicit visual precues. These results demonstrate that covert visual search performance in macaques is very similar to that of humans, indicating that the macaque provides an appropriate model for understanding the neural mechanisms of covert search.

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### 1. Introduction

Most real-world visual scenes contain more information than can be consciously selected and processed. Visuo-spatial attention is, therefore, critical for filtering incoming information according to the demands of the task at hand. Visual attention has been studied extensively in human subjects using covert visual search tasks, in which subjects must make a response based on some aspect of a peripheral array of stimuli while remaining fixated. However, there have been comparatively fewer studies of covert visual search performance during fixation in the monkey (e.g., Balan et al., 2008; Buracas & Albright, 1999; Golla et al., 2004; Monosov & Thompson, 2009; Wardak et al., 2006; Wardak, Olivier, & Duhamel, 2004). Most studies of visual search in monkeys have instead focused on overt search, in which monkeys are rewarded for making an eye movement to a target stimulus among distractors (e.g., Arai,

McPeck, & Keller, 2004; Bichot, Rossi, & Desimone, 2005; Bichot & Schall, 1999, 2002; McPeck & Keller, 2001), or on unconstrained search, in which monkeys are free to look anywhere in the scene while discriminating the target (e.g., Bisley et al., 2009; Motter & Belky, 1998a, 1998b; Motter & Holsapple, 2000, 2007; Shen & Paré, 2006). In order to link the results of single-unit studies of attention in monkeys with human attentional performance, it is important to determine to extent to which the performance of monkeys in covert attention tasks is comparable to that of humans.

Many studies of visual search have involved detecting the presence or absence of an odd target among distractors (e.g., Treisman & Gelade, 1980; Wolfe, 1994). However, it has been argued that when the target is easily discriminable from the distractors (e.g., pop-out search), such detection tasks require relatively few attentional resources (e.g., Braun & Sagi, 1990, 1991; Bravo & Nakayama, 1992; Sagi & Julesz, 1985), particularly in well-practiced observers (Braun, 1998). To examine pop-out in a more attentionally-demanding task, Bravo and Nakayama (1992) developed a visual search task in which the target is always present, and subjects must discriminate a fine shape detail of the target, rather than simply detecting it. They argued that this task is well suited for studying attention because discriminating the shape of the target requires subjects to focus attention on the target before responding. Furthermore,

DOI of original article: <http://dx.doi.org/10.1016/j.visres.2012.10.007>

<sup>☆</sup> This article is a reprint of a previously published article. For citation purposes, please use the original publication details; Vision Research, 76, pp. 43–49.

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unlike conventional target present/absent search, this task allows one to decouple the difficulty of the required discrimination (in this case, of the target shape) from the difficulty of locating the target among the distractors. To date, only a few studies have examined the behavioral performance of monkeys in this type of search task (e.g., Balan et al., 2008; Bisley et al., 2009; Monosov & Thompson, 2009). Most other studies of covert search in monkeys have instead focused on target present/absent search (e.g., Buracas & Albright, 1999; Wardak et al., 2006), or have examined tasks involving the discrimination of a target presented in isolation, without distractors (Golla et al., 2004).

In this study, we used an adaptation of Bravo and Nakayama's focal attention task to study covert attention during visual search in monkeys. Our goal was to systematically assess the performance of monkeys in a task similar to those used in humans (e.g., Bravo & Nakayama, 1992; Nakayama & Mackeben, 1989; Lu & Doshier, 2000; Maljkovic & Nakayama, 1994; Morgan, Ward, & Castet, 1998). In the first experiment, we compared the effect of varying the number of distractors on discrimination of a target which either does or does not pop-out from distractors. In the second experiment, we investigated the effects of peripheral cues on search performance, and mapped out the time course of the cueing effect. In the third experiment, we examined how prior knowledge of the target location influences search performance. In all three experiments, we used a limited-duration, masked target presentation, a procedure which captures variations in performance largely as changes in percentage correct performance (e.g., Braun, 1998; Braun & Sagi, 1990, 1991; Golla et al., 2004; Lu & Doshier, 2000; Morgan, Ward, & Castet, 1998; Nakayama & Mackeben, 1989; Sagi & Julesz, 1985) rather than as changes in reaction time (RT) or combined RT/error rate changes (e.g., Balan et al., 2008; Bravo & Nakayama, 1992; Buracas & Albright, 1999; Maljkovic & Nakayama, 1994; Monosov & Thompson, 2009; Treisman & Gelade, 1980; Wardak et al., 2006; Wolfe, 1994).

## 2. Experiment 1: Influence of distractors and pop-out

Studies in humans and monkeys have shown that a target which is highly discriminable from distractors, such as a color odd-ball, tends to rapidly and automatically attract attention to itself (e.g., Burrows & Moore, 2009; Constantinidis & Steinmetz, 2005; Egeth & Yantis, 1997; Thompson, Bichot, & Schall, 1997; Treisman & Gelade, 1980; Wolfe, 1994). In classic present/absent search tasks, this has been observed as a flat or shallow slope in the function relating search performance to the number of distractors in the display. In humans, using a search task which required discriminating the shape of the target, rather than detecting its presence or absence, Bravo and Nakayama (1992) showed that when the target popped-out, either in color or spatial frequency, the time required to discriminate the shape of the target did not increase when more distractors were added. In particular, when the colors of the target and distractors remained the same from trial to trial (blocked condition), search times were independent of the number of distractors. Here, we examined the effects of color pop-out on covert search in monkeys, comparing target discrimination performance when the target was the same color as the distractors and when the target was a unique color.

In the no pop-out condition, the colors of the target and distractors were identical, and we manipulated the number of distractors. We predicted that if the task requires monkeys to focus attention on the target, then target discrimination performance should decline when more distractors are present (e.g., Balan et al., 2008; Bisley et al., 2009). Presumably, this occurs because localization of the target is more difficult in the presence of same-colored distractors. In contrast, when the target has a unique color, and thus is

easily discriminable from the distractors, we predict that attention will be shifted rapidly to the target regardless of the number of distractors, resulting in little or no decline in performance with more distractors (e.g., Bravo & Nakayama, 1992). This pattern of results would support the conclusion that the attentional performance of humans and monkeys is similar.

### 2.1. Material and methods

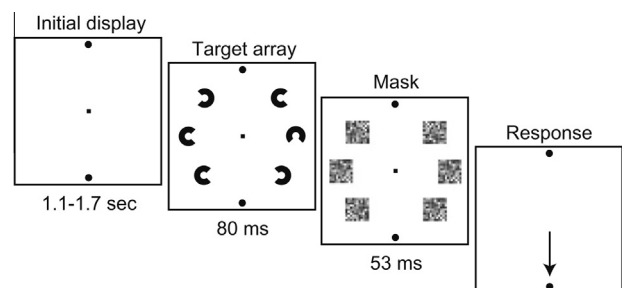
The experiments were conducted at the Smith-Kettlewell Eye Research Institute. All experimental protocols were approved by the Institutional Animal Care and Use Committee, and complied with the guidelines of the Public Health Service Policy on Humane Care and Use of Laboratory Animals. Two male rhesus monkeys (*Macaca mulatta*, H and F) weighing between 5 and 8 kg participated in the behavioral study. A scleral coil (Fuchs & Robinson, 1966; Judge, Richmond, & Chu, 1980) and a head holder system were implanted under isoflurane anesthesia and aseptic surgical conditions. At the completion of the surgery, animals were returned to their home cages, and then were trained for 6–8 months in the behavioral tasks.

The monkeys were seated in a primate chair with their heads restrained for the duration of the testing sessions, which were performed in a dimly illuminated room. They executed behavioral tasks for juice reward and were allowed to work to satiation. Records of each animal's weight and health status were kept, and supplemental water was given as necessary. The animals usually worked for 5 days a week and were allowed access to water on weekends.

Data collection and storage was controlled by a real-time program running on a Macintosh computer. Horizontal and vertical eye position and velocity were sampled at 1 kHz and digitally stored on disk. The computer also generated the visual displays using Psychtoolbox (Brainard, 1997; Pelli, 1997) running in Matlab. Visual stimuli were presented on a 29 in. color CRT (Viewsonic GA29), in synchronization with the monitor's vertical refresh. The monitor had a spatial resolution of 800 by 600 pixels and a non-interlaced vertical refresh rate of 75 Hz. The monitor was positioned 57 cm in front of the monkeys.

#### 2.1.1. Search task

The task was based on Bravo and Nakayama's (1992) search paradigm, in which the shape of a target among distractors must be discriminated. As summarized in Fig. 1, monkeys initially fixated a central fixation point for a randomly-determined interval of 82–127 frames (approx. 1100–1700 ms). Next, a search array was presented for a brief duration (6 frames; ~80 ms), followed



**Fig. 1.** Schematic representation of the stimulus sequence in Experiment 1. Each trial began with the presentation of a central white fixation point and two choice stimuli (above and below fixation). After a variably delay, a search array was briefly presented, followed by a masking stimulus. The target was defined as the Landolt-C with the gap aligned vertically, while the distractors were aligned horizontally. At the end of each trial, monkeys indicated the orientation of the target (up or down) by making a saccade to the corresponding choice stimulus.

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