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Eye movements and attention: The role of pre-saccadic shifts of attention in perception, memory and the control of saccades

Min Zhao [a,*], Timothy M. Gersch [b], Brian S. Schnitzer [a], Barbara A. Dosher [c], Eileen Kowler [a]

[a] Department of Psychology, 152 Frelinghuysen Road, Rutgers University, Piscataway, NJ 08854, United States
[b] Center for Neurobiology and Behavior, Columbia University College of Physicians and Surgeons, 1051 Riverside Drive, New York, NY 10032, United States
[c] Department of Cognitive Sciences, University of California Irvine, Irvine, CA 92697, United States

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ABSTRACT

Saccadic eye movements and perceptual attention work in a coordinated fashion to allow selection of the objects, features or regions with the greatest momentary need for limited visual processing resources. This study investigates perceptual characteristics of pre-saccadic shifts of attention during a sequence of saccades using the visual manipulations employed to study mechanisms of attention during maintained fixation. The first part of this paper reviews studies of the connections between saccades and attention, and their significance for both saccadic control and perception. The second part presents three experiments that examine the effects of pre-saccadic shifts of attention on vision during sequences of saccades. Perceptual enhancements at the saccadic goal location relative to non-goal locations were found across a range of stimulus contrasts, with either perceptual discrimination or detection tasks, with either single or multiple perceptual targets, and regardless of the presence of external noise. The results show that the preparation of saccades can evoke a variety of attentional effects, including attentionally-mediated changes in the strength of perceptual representations, selection of targets for encoding in visual memory, exclusion of external noise, or changes in the levels of internal visual noise. The visual changes evoked by saccadic planning make it possible for the visual system to effectively use saccadic eye movements to explore the visual environment.

1. Introduction

Visual scenes contain far too much information to be apprehended in a single glance. Limitations come from several factors, including the decline in visual resolution with distance from the fovea, the interference produced by crowding, and the inability to identify or encode multiple visual objects or features within the same brief glance. These limitations mean that effective vision depends on saccadic eye movements and perceptual attention, working together in a coordinated fashion, to select the objects, features or regions with the greatest momentary need for limited processing resources.

This paper is organized in two parts. The first part reviews the connections between the planning of saccades and shifts of spatial attention. The review focuses on the shifts of attention to the goal of a saccade that occur when saccadic planning is underway. Evidence indicates that pre-saccadic shifts of attention are important both for ensuring saccadic accuracy, and for facilitating the integration of information across discrete glances. The signature characteristic of pre-saccadic shifts of attention is an enhancement of perception at the saccadic goal relative to other locations. Three new experiments are reported in the second part of the paper to investigate different ways in which the pre-saccadic perceptual changes may be produced, namely, by changing the strength or nature of the visual representations, by modulating the interference from external noise, or by selecting the contents of short-term visual memory. The results show involvement of all of these processes, supporting the view that saccadic preparation has effects on perception that operate at multiple levels of processing.

2. The links between saccadic eye movements and attention

2.1. Saccades are neither necessary, nor sufficient, for the control of attention…

Perceptual attention can act independently of saccades. We can attend to chosen locations, or switch attention between locations, without moving the eye. The manipulation of the locus of attention (typically, by the use of visual cues) while fixation is maintained has been the preferred way to study attention in psychophysical investigations because the retinal locations of stimuli are not

* Corresponding author.
E-mail addresses: minzhao@rci.rutgers.edu (M. Zhao), tmg2121@columbia.edu (T.M. Gersch), schintzb@rci.rutgers.edu (B.S. Schnitzer), bdosher@uci.edu (B.A. Dosher), kowler@rci.rutgers.edu (E. Kowler).

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altered. Some have argued that the ability to shift attention while keeping the eye fixated is not simply a laboratory convenience, but has survival value for primates in social situations by allowing them to avoid eye contact that may convey hostile intent (e.g., Moore, Armstrong, & Fallah, 2003).

Just as we do not need a saccade in order to shift attention to a target, it is also the case that fixating a target does not guarantee it will be attended. In the presence of a distracting task, there can be a surprising lack of awareness of objects or details that fall on the fovea (Droll et al., 2005; Kahneman, Beatty, & Pollack, 1967; Mack & Rock, 1998). Other phenomena that attest to the independence of perceptual attention from saccades include the ability to selectively attend to one of two superimposed images (Kowler et al., 1984; Neisser & Becklin, 1975), and the ability to attend in parallel to features in widely separated spatial locations (Melcher, Papathomas, & Vidnyanszky, 2005; Saenz, Buracas, & Boynton, 2002). These results, as well as others (e.g., Juan, Shorter-Jacobi, & Schall, 2004), argue against strong "pre-motor" theories (Rizzolatti et al., 1987) that equate the control of attention with the formation of sub-threshold saccadic commands.

2.2. ...But attention is necessary for the control of saccades

Attention may operate without saccades, but saccades cannot be planned without attention. Evidence (reviewed in detail below) indicates that attention will shift to the goal of a saccade while saccadic planning is underway.

Pre-saccadic shifts of attention to the saccadic goal can be useful for visual perception. For example, pre-saccadic shifts of attention can allow "perceptual previews" of material that is about to fall on the fovea (Henderson, Pollatsek, & Rayner, 1989). Pre-saccadic shifts of attention may also facilitate the maintenance of perceptual stability and continuity across saccades (Melcher, 2005, 2007, 2009), as well as contribute to the pre-saccadic neural remapping of visual receptive fields (Berman & Colby, 2009; Melcher & Colby, 2008).

2.2.1. Pre-saccadic attention and the accuracy of saccades

Pre-saccadic shifts of attention are also instrumental for the guidance and control of saccades. They define the effective input to the saccadic system, and suppress the influence of irrelevant signals.

In a cluttered visual environment, the suppression of irrelevant, non-target information by means of attention is necessary for avoiding saccadic landing errors. One well known type of landing error found in cluttered visual environments has been referred to as the "center-of-gravity" saccade, in which the saccade misses the target and instead lands near the center of a set of targets and non-targets (e.g., Cöeffé & O'Regan, 1987; Findlay, 1982; He & Kowler, 1989, 1991; Kowler, 2011; Ottes, Van Gisbergen, & Eggermont, 1985; Stritzke, Trommershäuser, & Gegenfurtner, 2009) .

Center of gravity saccades occur because saccadic landing position is determined by spatial pooling across the attended region. Pooling is valuable when aiming saccades to spatially-extended targets because it is only necessary to select (attend to) a target region; pooling can determine the precise saccadic landing position within the attended region (Melcher & Kowler, 1999; Vishwanath & Kowler, 2003, 2004). In the presence of non-targets, however, pooling can produce errors in landing whenever time, instructions, visual cues, or incentives are not sufficient to allow attention to focus on the designated target (e.g., Cohen et al., 2007; Findlay & Blythe, 2009; Ottes, Van Gisbergen, & Eggermont, 1985). Of course, any saccadic landing error can be corrected by subsequent saccades, and in many situations it may be more efficient (less time consuming) to make an inaccurate "center-of-gravity" saccade, followed quickly by a correction, rather than to delay saccades long enough to allow time to fully attend to the target (Araujo, Kowler, & Pavel, 2001; Cöeffé & O'Regan, 1987). The strategy of relying on saccadic corrections is particularly useful when targets are small relative to their eccentricity (Wu, Kwon, & Kowler, 2010).

2.2.2. Pre-saccadic shifts of attention and the link to perceptual attention

The importance of shifts of attention to saccadic localization raises questions about the underlying mechanisms that control and coordinate the two processes. How closely are saccades and attention linked? Do the saccades and the accompanying shifts of attention move in lock-step, as if under the direction of a single controller, or can these processes function independently, so as allow dissociations between movements of attention and movements of the eye? This question was raised in behavioral studies done beginning in the 1980s that used dual-task methods (concurrent saccadic and perceptual tasks) to measure perceptual performance during the latency interval of saccades (Klein, 1980; Posner, 1980; Remington, 1980; Shepherd, Findlay, & Hockey, 1986). The results of these early studies were not in agreement with one another, and several methodological factors complicated the interpretation of the outcomes (see Hoffman and Subramaniam (1995) and Kowler et al. (1995) for discussion).

The methodological difficulties were addressed in subsequent studies, which also used dual task methods. These studies found better perceptual identification of targets located at the saccadic goal than elsewhere, and concluded that pre-saccadic shifts of attention were an obligatory stage of saccadic preparation (Baldauf & Deubel, 2008; Deubel & Schneider, 1996; Godijn & Theeuwes, 2003; Hoffman & Subramaniam, 1995; Kowler et al., 1995; McPeek, Maljkovic, & Nakayama, 1999). The obligatory nature of the pre-saccadic shifts of attention can be illustrated by Kowler et al. (1995)'s finding that attempts to shift attention to targets remote from the saccadic goal interfered with saccadic performance, and resulted in increased saccadic latencies and decreased spatial precision of landing positions. There was an interesting asymmetry in the tradeoff between saccades and attention in that relatively small increases in saccadic latency (<20%), or small increases in the scatter of landing positions, could produce large improvements in perceptual performance at non-goal locations (see also Gersch et al., 2008; Wilder et al., 2009). This asymmetry can be useful in natural scanning because it creates the option to make relatively harmless sacrifices in saccadic timing and saccadic accuracy in order to improve perception across the visual array.

Pre-saccadic shifts of attention were also found during the performance of saccadic sequences. Gersch, Kowler, and Dosher (2004), Gersch et al. (2008, 2009) studied attention during pauses between saccades made in sequences along proscribed paths, where the sequences were either executed from memory, or guided by visual feature cues (color differences). They found that, in the absence of color cues marking the saccadic path, attention was allocated only to the target of the upcoming saccade. On the other hand, when saccades were made along paths marked by color cues, perceptual attention was greatest at the target of the next saccade, but could also be allocated to other locations along the path, including previously examined locations, without cost to the timing or accuracy of the saccades.

The ability to use feature cues to allocate attention to stimuli other than saccadic targets without cost suggests that feature-based attention (e.g., Saenz, Buracas, & Boynton, 2002) is not connected directly to the planning or control of saccades. This is useful. Gersch et al. (2008, 2009) proposed that during sequential scanning tasks, pre-saccadic shifts of attention to the selected target can initiate a spread of perceptual attention to other objects with similar features. The ability to use pre-saccadic shifts of