



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

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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.

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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 inte-

gration 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

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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, Papa-thomas, & 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, fol-

lowed 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; McPeck, 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 Doshier (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

attention to initiate selective feature-based enhancement may be particularly valuable during visual search (Bichot, Rossi, & Desimone, 2005; Bichot & Schall, 1999; Motter & Belky, 1998; Murthy, Thompson, & Schall, 2001).

2.2.3. Neural mechanisms of pre-saccadic shifts of attention

Several neural pathways have been identified that can account for pre-saccadic shifts of attention. For example, neurons in areas involved in saccadic control (LIP, FEF and, SC) show enhanced firing when the target of a saccade falls in the receptive field of the cell, with effects comparable to those observed when attention is drawn to a target in the receptive field by means of cues (Ipata et al., 2006; Kustov & Robinson, 1996; Murthy, Thompson, & Schall, 2001; Schall, 2004; Thompson, Bichot, & Sato, 2005; Wurtz & Mohler, 1976). Neurons in SC also show enhanced contrast sensitivity prior to saccades (Li & Basso, 2008).

Visual areas (V1, V4) also show pre-saccadic enhancements in firing (Bichot, Rossi, & Desimone, 2005; Fischer & Boch, 1981; Moore, 1999; Supèr et al., 2004) and pre-saccadic increases in sensitivity to features (Moore & Chang, 2009). There is also evidence that signals from FEF may trigger the pre-saccadic enhancements in V4 (Moore & Armstrong, 2003; Zhou & Desimone, 2011). The direction of these functional connections – FEF to V4 – is consistent with the behavioral findings, summarized above, showing that top-down decisions about where to direct saccades (which may be represented in areas such as FEF or SC) result in pre-saccadic enhancements in visual perception at the target location.

2.3. The visual consequences of attention during maintained fixation

The research reviewed up to this point shows that perception is enhanced at the goal of the saccade relative to other locations. “Enhancement” can be achieved by a variety of mechanisms, and a central goal of this paper is to investigate which mechanisms may account for the pre-saccadic perceptual changes, and which can be ruled out.

Psychophysical studies of the effects of attention on perception have examined mechanisms of attention by using spatial cues (not saccades) to direct attention to selected locations during maintained fixation. Spatial cues have been found to reduce contrast thresholds at attended locations in a variety of visual tasks. Analysis of the effects of cues as a function of contrast in the presence or absence of external noise have made it possible to evaluate different candidate mechanisms underlying the effects of attention. These mechanisms include changes in the tuning of visual analyzers so as to exclude interference from external noise, increases in the contrast sensitivity of visual analyzers, or reductions in additive or multiplicative internal noise, (for review and discussion of proposed mechanisms, see Carrasco (2011), Doshier and Lu (2000a, 2000b) and Liu, Doshier, and Lu (2009). For consideration of neurophysiological correlates, see, for example, Reynolds & Heeger, 2009).

A different set of mechanisms may be involved when attention is divided among tasks or locations (Bahcall & Kowler, 1999; Huang & Dobkins, 2005; Joseph, Chun, & Nakayama, 1997; Lee et al., 1999; Liu, Doshier, & Lu, 2009; Morrone, Denti, & Spinelli, 2004; Reeves & Sperling, 1986; Wilder et al., 2009). In these dual-task or dual-report studies, the effects of dividing attention on visual performance were typically found even at high levels of target contrast. These effects have been attributed to interference among neighboring visual analyzers (Bahcall & Kowler, 1999), imprecise targeting of attention (Palmer & Moore, 2009), reductions in the activity level of visual analyzers (Huang & Dobkins, 2005), or reduced signal sensitivity coupled with increases in multiplicative internal visual noise (Liu, Doshier, & Lu, 2009).

2.4. The visual consequences of attention during pre-saccadic intervals

How can we connect what has been learned about mechanisms of attention in psychophysical studies under conditions of maintained fixation (Section 2.3) to the shifts of attention associated with the planning of saccades (Section 2.2.2)? This is a significant question if we assume that one of the most important functions of spatial attention is to act in concert with saccades to control the exploration of the environment. The prior studies of pre-saccadic attention (Section 2.2.2) were not done to test particular hypotheses about the mechanisms of visual attention. Experimental manipulations that have proven to be valuable in the psychophysical studies of attention described above, such as comparing performance with and without external visual noise, testing stimuli across a wide range of contrasts, or imposing secondary perceptual tasks, were typically not employed in the pre-saccadic attentional research.

There were good reasons for this strategy. The stimuli and tasks used in the previous studies of pre-saccadic attention were chosen in order to find out whether attention played a role in saccadic control. As a result, stimuli and tasks were chosen because they imposed high processing loads and unambiguously high attentional demands, thus increasing the likelihood of detecting any contribution of attention to pre-saccadic perceptual performance. For example, most tasks required analysis of the contents of several display locations (between 4 and 12) that contained multi-featured visual characters (letters or numerals) (Baldauf & Deubel, 2008; Deubel & Schneider, 1996; Gersch et al., 2008; Godijn & Theeuwes, 2003; Hoffman & Subramaniam, 1995; Kowler et al., 1995; McPeck, Maljkovic, & Nakayama, 1999). Such tasks are likely to benefit from attention because they require observers to remember and analyze the content of many display locations, and to use high-level perceptual analyzers appropriate for recognizing complex targets. In all but two studies (Hoffman & Subramaniam, 1995; Kowler et al., 1995), no cues were given to indicate which of the several available locations would be probed until well after the displays were removed. Thus, achieving high levels of performance would require the processing of multiple locations, and holding the results in memory until the report would be required.

2.4.1. Pre-saccadic attention with reduced load on perception and memory

Some studies of pre-saccadic attention abandoned the letters and numerals in favor of presumably simpler stimuli, that would not require involvement of higher-level perceptual analyzers. Caspi, Beutter, and Eckstein (2004) studied search for a single Gaussian target that was brighter than four other Gaussian distractors. Rolfs et al. (2011) also used displays with multiple stimuli, specifically, six Gabor patches, one tilted and the rest oriented vertically. Their displays were presented during the latency interval prior to executing a pair of saccades, and the orientation of the tilted Gabor was reported after the trial. Nevertheless, memory remains a factor in these studies because the procedures required attending to the contents of multiple locations to find the target, thus, limits in pre-saccadic performance could reflect the selection of which locations had the highest priority for analysis.

Other studies of pre-saccadic attention avoided overtaxing memory by reducing memory load (i.e., the number of Gabors that had to be analyzed). These studies nonetheless found effects of saccadic planning on attention, and will be considered in some detail below because of their relevance to the goals of the new experiments that will be reported.

Castet et al. (2006) measured angular thresholds for discriminating the orientation of high-contrast Gabor patches. Displays contained 8 Gabors (100% contrast), followed by masks. The location of the probed Gabor relative to the saccadic target remained

the same throughout a block of trials, thus, only one location had to be monitored for the perceptual report. Castet et al. (2006) found lower thresholds for orientation discrimination at the saccadic target relative to the neighboring locations. Using a similar display of 8 locations, Montagnini and Castet (2007) varied the probability that the probed Gabor would be located either at or opposite to the saccadic goal. They found better performance at the saccadic goal, but performance opposite to the saccadic goal improved, without cost to saccades, when the probability of probing the opposite location was high (75%). Montagnini and Castet (2007) concluded that locations opposite to the goal of a saccade can be attended to some extent while saccadic planning is in progress without noticeable cost to saccades.

Gersch et al. (2004, 2009) presented only a single Gabor per trial and measured perception during pauses between saccades made in sequences. The Gabor target could appear in one of 6 (Gersch, Kowler, & Doshier, 2004) or 9 (Gersch et al., 2009) locations during a randomly-selected inter-saccadic pause. Gersch, Kowler, and Doshier (2004) measured contrast thresholds for identifying grating orientation, while Gersch et al. (2009) measured the proportion of correct identifications of orientation at a single, moderate contrast level. Both studies found better performance when the grating appeared at the goal of the next saccade in the sequence than when it appeared at non-goal locations (see also Section 2.2.2).

These four studies found effects of pre-saccadic shifts of attention using simple stimuli (tilted Gabor patches) that presumably imposed less of a load on perception than the letters or numerals used in other studies of pre-saccadic attention (see Section 2.2.2). These studies also reduced the load on perception and memory by either presenting only a single perceptual target stimulus per trial, or by pre-cuing the location of the perceptual target stimulus prior to the saccade. However, these studies were limited in the types of inferences that could be drawn about the attentional mechanisms involved in producing the pre-saccadic changes in perception. This is because experimental manipulations that have proven useful in the prior psychophysical studies of attention (Section 2.3), such as comparison of performance with and without superimposed external noise fields, or reporting performance across a range of contrasts, were not featured in these studies. The goal of the present paper was to learn about mechanisms of pre-saccadic attention by testing a variety of targets, target contrast levels, and by varying the presence/absence of external noise.

2.5. Present study

The present study investigates perceptual characteristics of pre-saccadic shifts of attention during sequences of saccades. The psychophysical tasks were modeled after those used to study attention during steady fixation in that perceptual performance (stimulus identification, and in one case, detection) was studied across a range of stimulus contrasts, and in the presence or absence of superimposed visual noise. As in prior work (Gersch, Kowler, & Doshier, 2004; Gersch et al., 2008, 2009), attention will be assessed during the pauses between saccades made in sequences. This is because the saccadic planning processes during ongoing saccadic sequences may be different from, and more representative of natural viewing, than the planning processes during the latency interval prior to a single saccade, or prior to the first saccade of a sequence (Motter & Belky, 1998; Sternberg et al., 1978; Zhou & Desimone, 2011; Zingale & Kowler, 1987). Note that we are not assuming that the plans for the sequences were fully prepared prior to sequence initiation, and then executed automatically without reference to visual details in the array, nor are we concerned in this study with the question of whether attention may be allocated to the targets of more than one upcoming saccade. For discussion of the question

of allocating attention to multiple targets, see Gersch et al. (2004, 2009), Godijn & Theeuwes (2003) and Baldauf and Deubel (2008).

Each of the three experiments to be reported used a dual-task methodology in which perceptual judgments were made about stimuli presented during the pauses between successive saccades. Carrying out dual-tasks studies such as these, particularly when sequences of saccades are involved, is a formidable enterprise because of the opportunity for task trade-offs, such as delaying the saccade in an attempt to improve perceptual performance. Thus, it is important to report (as we will do) both perceptual and saccadic performance, and to both look for, and take into account, evidence for tradeoffs between the two.

3. Experiment 1: Pre-saccadic attention with multiple perceptual targets

Experiment 1 studied the ability to identify the orientation of a target presented during the pause between two consecutive saccades made along a specified path. The perceptual task was modeled after Lu and Doshier (2000). Four targets (oriented letter T's) appeared briefly, each in a different location, during the pause between consecutive saccades, and subjects were asked to identify the orientation of one of the T's after the trial. The contrast of the target letter T was varied from trial to trial. The 4 T's had the same contrast within a trial. T's were presented with or without superimposed external noise. Performance when the probed T was located at the saccadic goal was compared to performance when it was located at one of the 3 non-goal locations.

3.1. Methods

3.1.1. Eye movement recording

Two-dimensional movements of the right eye were recorded by a Generation IV SRI Double Purkinje Image Eyetracker (sensitivity <1') (Crane & Steele, 1978). The observer's left eye was covered and the head was stabilized on a chin-rest.

The voltage output of the tracker was fed online through a low pass 100 HZ filter to a 12 bit analog to digital converter (ADC). The ADC, controlled by a PC, sampled eye position every 2 ms. The digitized voltages were stored for later analysis. Voltage from a photocell (out of the subject's view) that recorded stimulus onset and offset directly from the display monitor was fed into a channel of the ADC and recorded along with the eye position samples to ensure accurate temporal synchronization between stimulus display and eye movement recording.

Tracker noise level was measured with an artificial eye after the tracker had been adjusted so as to have the same first and fourth image reflections as the average observer's eye. Filtering and sampling rate were the same as those used in the experiment. Noise level, expressed as a standard deviation of position samples, was 0.4' for horizontal and 0.7' for vertical position. Recordings were made with the tracker's automatically movable optical stage (autostage) and focus-servo disabled. These procedures are necessary with Generation IV Trackers because motion of either the autostage or the focus-servo introduces artifactual deviations of Tracker output. The focus-servo was used, as needed, only during inter-trial intervals to maintain observer alignment. This can be done without introducing artifacts into the recordings or changing the eye position/voltage analog calibration.

3.1.2. Observers

Four paid volunteer participants were tested (JC, LM, KW and TH), each with normal uncorrected vision. Each was unaware of the purpose of the experiment.

3.1.3. Stimulus display

Stimuli were displayed on a Dell P793 CRT monitor (13° horizontally \times 12° vertically; viewing distance 115 cm; resolution 1.5 pixels/minarc; refresh rate 75 Hz). Background luminance was 66 cd/m^2 and maximum luminance was 129 cd/m^2 at the refresh rate used.

The stimulus display (see Fig. 1) consisted of four outline squares ($1.4^\circ \times 1.4^\circ$) arranged around a central fixation cross. The distance between the centers of adjacent squares was 4.8° and the distance between the center of each square and the center of the display was 3.4° . The target to be identified was a letter T (0.7° deg horizontally, 0.4° deg vertically with line width 0.1°) which could be displayed in one of the four cardinal orientations. The T was shown with or without superimposed visual noise. The noise was a matrix of 40×40 dots (dot size = 3×3 pixels) whose luminance levels were Gaussian distributed ($SD = 33\%$ maximum display contrast). For cases where no superimposed noise was tested, the noise contrast was set to 0%. Frames containing the letter T, denoted as signal frames, were sandwiched between noise frames. There were four noise frames and three signal frames in the order N–S–N–S–N–S–N (duration 93 ms).

The pre-trial display contained a central arrow that disclosed the start and end locations of the V-shaped saccadic path. The path markers remained on throughout the trial. The saccadic path always started from one of four locations, went to the central location, and ended at one of two locations flanking the start location. This V-shaped path meant that each of the 4 outline squares could be classified as follows: (1) start location; (2) saccadic goal location; (3) location opposite to the goal; (4) neutral location.

3.1.4. Procedure

Observers fixated the designated start location before each trial and pressed the button to start the trial when ready. After a short random delay (200–600 ms), a brief (50 ms) tone was the signal to begin making saccades along the path. Subjects were instructed to make saccades at the fastest possible rate that allowed them to stay on the path. They were also told to give priority to making saccades at a high rate, even if errors in the perceptual reports resulted.

Eye position was monitored online to detect the first large saccade, directed to the center of the display. After a random delay (30–70 ms) following detection of the saccade, the 7 display frames appeared (3 signal frames containing the T, interspersed with 4 noise frames or 4 frames of mean luminance). The report cue – a caret (1.2° on a side; eccentricity 1.7°) pointing to the location to be reported at the end of the trial – appeared simultaneously with the onset of the last signal frame and indicated which location would be probed at the end of the trial. Report cues delivered along with the stimulus display are used in order to minimize performance loss due to memory decay and to uncertainty about which display location will be probed (Doshier & Lu, 2000a, 2000b; Gould, Wolfgang, & Smith, 2007).

At the end of the trial (1.5 s from the button press) the report frame appeared and remained on until the report was given by a button press. This was followed by visual feedback (the critical frame with the T reappeared) and an auditory signal indicating whether the report was correct. Subjects were asked to make saccades as quickly as they could, giving primary weight to the saccadic task even if that produced perceptual errors.

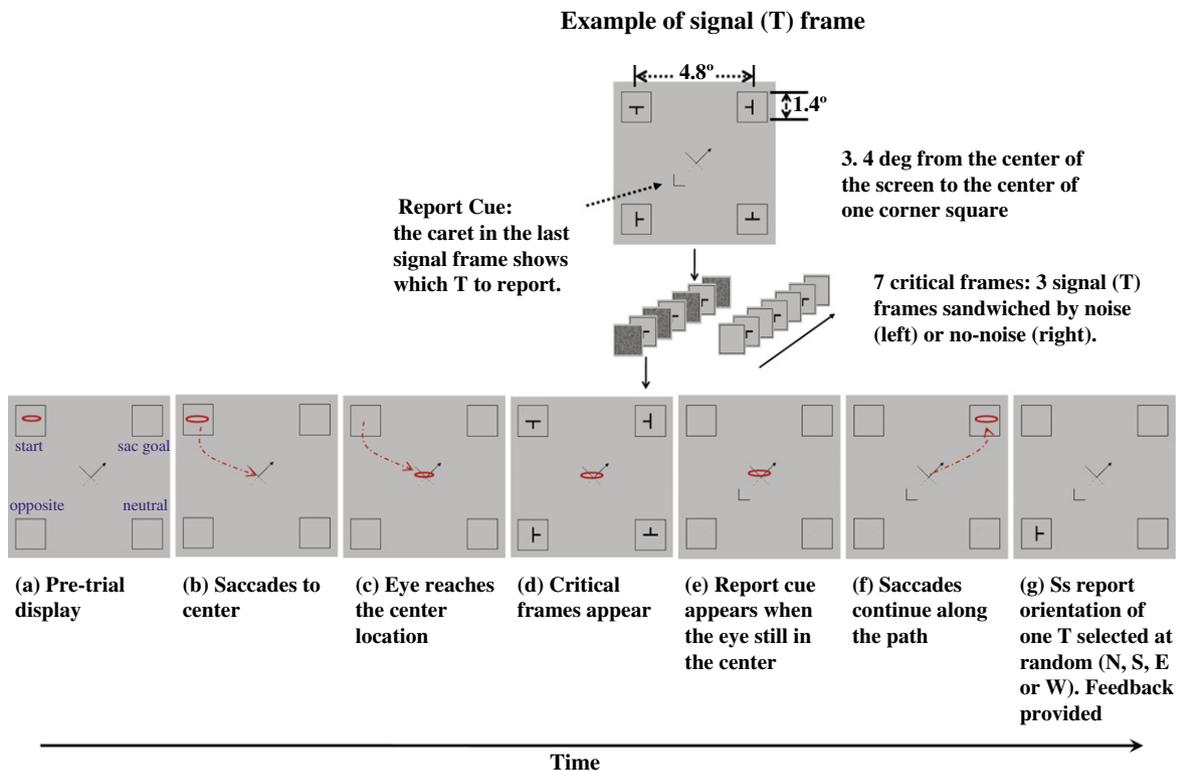


Fig. 1. Stimulus and procedure for Experiment 1. The red oval markers and dotted lines (not visible to the subject) indicate the position and the path of the eye. The V-shaped saccadic path was selected at random on each trial and shown by the central arrows. (a) At the beginning of the trial, subjects fixated the start location and pressed the button to start the trial. After 200–400 ms delay, a brief tone sounded as the signal to begin making saccades along the path. (b and c) Subjects made the first saccade from the start location to the center. (d) With 30–70 ms delay after eye reached the center, the critical frames appeared, 4 noise and 3 signal “T” frames. (e) The report cue appeared simultaneously with the onset of the last signal “T” frame. (f) The second saccade was made. (g) The second saccade was made. (g) At the end of the 1.5 s trial subjects report the orientation of a randomly selected T indicated by the report cue. Visual and auditory feedback was provided.

3.1.5. Analyses

The beginning and end positions of saccades were detected by means of a computer algorithm employing an acceleration criterion based on differences in eye velocity between successive 14 ms intervals whose onsets were separated by 2 ms. The criterion for saccade offset was more stringent in that 12 consecutive velocity differences had to meet the criterion in order to ensure that the overshoot at the end of the saccade would be bypassed. The values of the criteria were determined and confirmed empirically by examining a large sample of analog records of eye position.

The “critical saccade” was defined as the first saccade that occurred after the appearance of the T and noise frames. This is the saccade that was being planned while the perceptual targets appeared. Eye positions at the onset and offset of the critical saccade were analyzed offline using a nearest neighbor criterion to confirm that the central square (rather than any other display location) was fixated at the time of the presentation of the critical frames, and that the critical saccadic endpoint landed at the next target in the sequence. Critical pause duration included pause durations preceding any secondary saccades that did not take the line of sight away from the central square (the durations of the secondary saccades themselves were excluded). Pause durations containing secondary saccades were rare (<1% for all subjects). The few trials in which the critical saccade did not land within the saccadic target were excluded (see below for proportion of excluded trials). In addition, all measures of the saccade onset and offset positions were computed relative to a reference position defined as the eye position at the start of the trial when one of the four start location boxes was fixated. This was done to correct for any trial to trial drifts in measured eye position.

Perceptual data were analyzed by fitting Weibull functions to the psychometric functions showing percent correct reports as a function of stimuli contrast, using ‘psignifit’ algorithm (Wichman & Hill, 2001), with three free parameters (threshold, slope and upper asymptote). Contrast at 62.5% of correct level was taken as the contrast threshold.

3.1.6. Number of trials and sessions tested

Experimental sessions contained 50 trials. Observers usually were tested in 300–350 trials/day. Two subjects (JC and LM) were tested both with and without external noise. JC finished 90 dual-task sessions (45 no noise and 45 with noise), and LM 55 sessions (27 no noise and 26 with noise). TH and KW only participated in the sessions without noise. TH finished 30 sessions and KW finished 35 sessions.

A portion of trials were eliminated: Trials in which tracker lock was lost (0.66% for JC, 0.18% for TH), trials with no saccade occurring (0.06% for TH), trials in which the observers made their first saccade before the go-signal (42% for JC, 2% for LM, 5% for TH, 14% for KW), trials in which T or noise frames occurred during any part of a saccade (5% for JC, 2% for LM, 24% for TH, 4% for KW), trials in which there was no saccade detected before the critical frames appeared (3% for JC, 2% for LM: 1% for TH, 17% for KW) and trials in which either there were no saccades detected after the frames, or the critical saccade went to the wrong location (0.1% for JC, 0.2% for TH, 0.2% for KW). Data were based on a total of 1207 trials without external noise and 1118 with noise for JC; 1268 trials without noise, 1215 with noise for LM; 1042 trials for TH and 1155 trials for KW.

3.2. Results

3.2.1. Perceptual performance at the different locations

As expected, perceptual reports of orientation were best at the goal of the saccade (see psychometric functions in Fig. 2). Performance at the other locations was poorer across contrasts, in fact, for three of the four subjects (all except JC) performance at the

non-goal locations did not reach an upper asymptote at the highest contrasts tested. There were also differences across the non-goal locations. Performance at both the start location and the location opposite to the saccadic goal were generally poorer than performance at the remaining “neutral” non-goal location. Results were similar with or without superimposed external noise.

3.2.2. Saccadic performance

Saccadic performance was assessed by the duration of the critical pause between saccades when the perceptual targets appeared (Fig. 3). For three of the four subjects (JC, LM and KW) critical pause durations were shortest when the probed location coincided with the saccadic goal. The exception, TH, showed about the same pause durations for the different locations, which were also considerably shorter than those of the other subjects. Pause durations were analyzed using ANOVA for each subject. LM and KW showed significant differences in pause durations among the different locations, with or without external noise (see Table 1).

The increases in pause durations observed when the probed location did not coincide with the saccadic goal was likely to be a response to the detection of the report cue indicating that a non-goal location would be probed. The report cue was presented along with the final frame of the perceptual target display (Fig. 1). Subjects may have delayed the saccade and shifted some attention away from the saccadic goal, perhaps as part of an attempt to improve perceptual performance at the non-goal locations.

3.3. Discussion

Perceptual performance was better at the goal of the saccade than at any of the non-goal locations. The differences between goal and non-goal locations were prominent at high levels of target contrast and did not depend on the presence of external noise. This pattern of performance, in which large losses are found at high stimulus contrasts, is similar to the results obtained when attention is divided between tasks or locations (see summary in Section 2.3). It is possible that mechanisms similar to those proposed in the dual-task perceptual studies, such as interference among limited capacity perceptual analyzers, or effects of increased multiplicative internal noise, could also apply to the current dual-task situation.

Before considering whether mechanisms involving interference or increased noise due to saccadic planning can account for the results, it is important to consider the consequences of presenting multiple targets. The use of a report cue removes decisional uncertainty about which location would be probed, and also indicates which location should receive priority for processing or for maintenance in a short-term memory store. The small increase in the critical pause durations (Fig. 3) when the report cue pointed to a location other than the saccadic goal shows that the cue was noticed while saccadic preparation was in progress on at least a portion of the trials for some subjects. However, it is possible that on some trials the report cue was not noticed until after the critical saccade was completed. This means that information needed to determine which of the 4 locations to remember for the report might not have been available soon enough to avoid memory decay. Memory decay might have been greater at non-goal locations than at the saccadic goal.

A role for memory decay at non-goal locations is consistent with the results of Gersch et al. (2008), who found better memory for targets presented at the saccadic goal than other locations. They also found that cues indicating which of the 9 target location would be probed were effective if presented before the saccadic sequence began, however, the effectiveness of these cues came at a cost, namely, slower saccade rates when a non-goal location was cued.

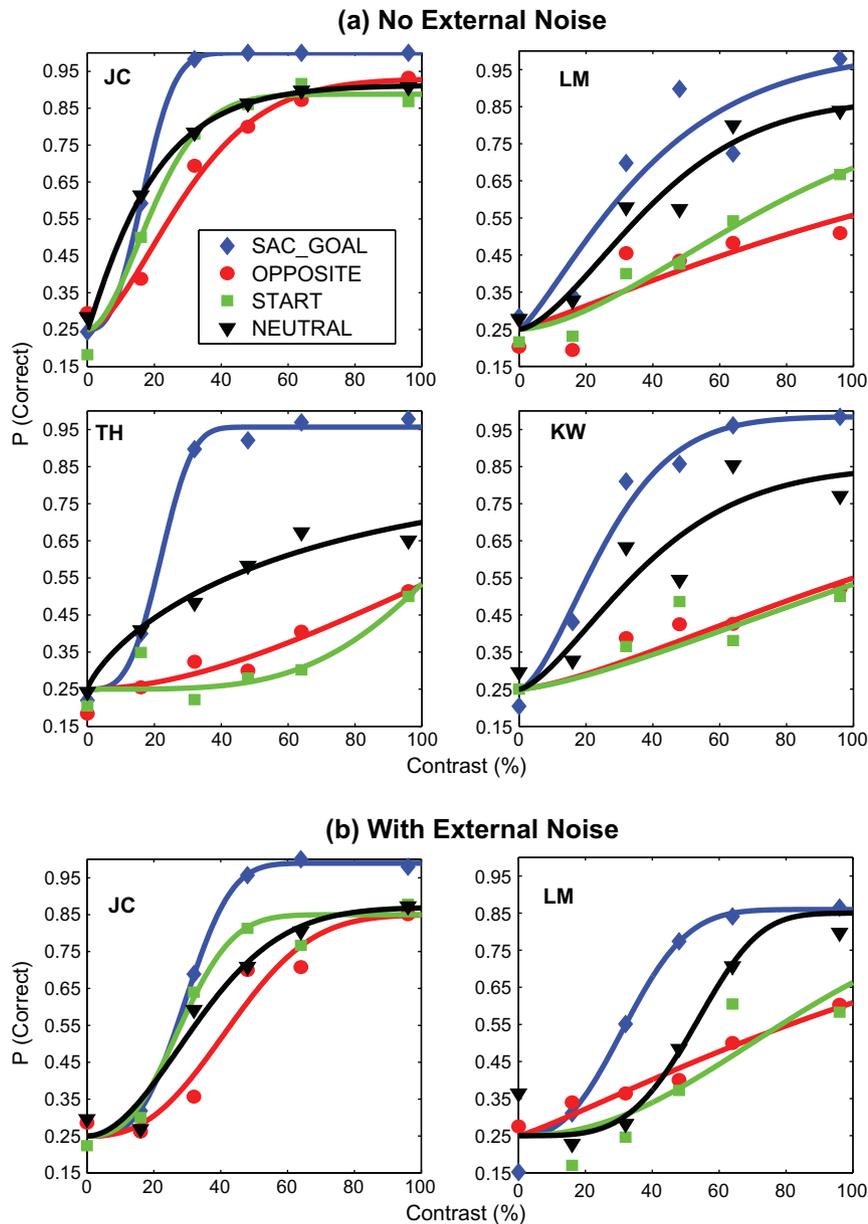


Fig. 2. Experiment 1. Psychometric functions showing proportion of correct reports of the orientation of the T as a function of contrast (a) without or (b) with external noise for the four test locations: saccadic goal (blue), opposite the saccadic goal (red), start location (green) and neutral location (black). Dots are data points and lines are best-fit lines (see text).

The above considerations suggest that one of the consequences of pre-saccadic shifts of attention in a display with multiple targets is that the saccadic goal location receives priority for limited-capacity processing or for entry into limited-capacity memory (see also Section 2.4).

Experiment 2 was done to determine the effects of pre-saccadic shifts of attention when demands on processing and on memory were reduced relative to those in Experiment 1 by presenting a single perceptual target on each trial.

4. Experiment 2: Pre-saccadic attention: identifying the orientation of a single target

In Experiment 2 we reduced the target processing load by reducing the number of perceptual targets from four to one, the number of possible locations for the target from four to two, and the number of possible responses from four to two. The target was a tilted Gabor, in one of only two possible orientations

($\pm 22.5^\circ$) and it could appear either with equal probability at the saccadic goal or at the location opposite to the saccadic goal.

Performance was once again tested with and without superimposed external noise and at a range of target contrasts. The length of the saccadic path was increased to four targets rather than the two targets used in Experiment 1. This was done because two-saccade sequences can be special cases, encouraging concurrent and overlapped programming of a pair of saccades (Araujo, Kowler, & Pavel, 2001; Caspi, Beutter, & Eckstein, 2004; McPeck, Skavenski, & Nakayama, 2000). Longer sequences are more representative of natural viewing.

4.1. Method

4.1.1. Observers

Five paid volunteer participants were tested (VK, KM, KW, AT and AUT), each with normal, uncorrected vision. Each was unaware of the purpose of the experiment. AT and AUT were tested after

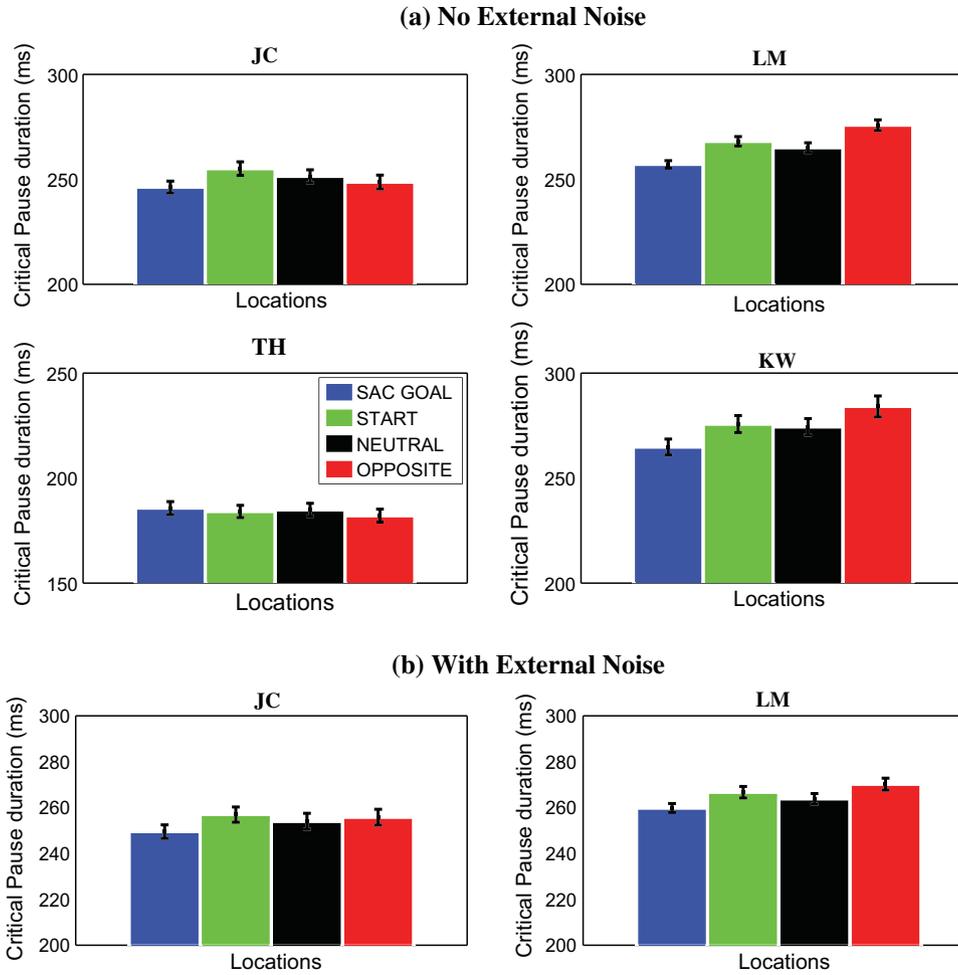


Fig. 3. Experiment 1. Critical pause duration for reports at the four different locations.

Table 1
ANOVA for the critical pause duration for each subject in Experiment 1. Values marked with asterisks are significant with $p = .02$ (*), $p = .005$ (**) or $p < .001$ (***).

Noise Level	Subjects	df	F	p
No external noise	JC	3	1.29	.28
	LM	3	9.53	<.001***
	TH	3	0.61	>.61
	KW	3	3.27	.02*
External noise	JC	3	1.75	.15
	LM	3	4.24	.005**

they had completed testing in Experiment 3 (see Section 5), thus both had more experience judging the stimuli than the other three subjects.

4.1.2. Stimulus display

The stimulus display (Fig. 4) contained 13 outline squares ($1.2^\circ \times 1.2^\circ$). One square was located at the center of the computer screen, four squares formed an inner loop and the other eight squares formed an outer loop. The distance between the centers of adjacent squares in the same loop was 1.8° . The distance between the center of each inner loop square and the center of the display was 2.5° .

The target to be identified was a tilted Gabor that could be displayed in one of 2 orientations ($\pm 22.5^\circ$ from vertical). The Gabor was generated according to the following: $l(x,y) = l_0(1.0 + a \sin(2\pi f(x \cos \theta \pm y \sin \theta) * \exp(-(x^2 + y^2)/2\sigma^2)))$, where f is the

spatial frequency ($2.24 \text{ cycle/}^\circ$), l_0 the mean luminance (19 cd/m^2), θ the orientation ($\pm 22.5 \text{ deg}$), σ the standard deviation of the Gaussian window (0.7°), (x, y) the spatial coordinates in the display, and a the amplitude. The Gabor was shown with or without the superimposed external noise, and noise and Gabor frames were interleaved as in Experiment 1.

4.1.3. Procedure

The pre-trial display contained small arrows in the center square and lines connecting the squares to mark the V-shaped saccadic path, as shown in Fig. 4. A small open square indicated the start location and a small filled square indicated the end location of the path. The path started from one of the four outer corner locations. The four saccadic targets along the V-shaped path were: the nearest inner corner location, the central location, another inner corner location, and finally an outer corner position.

Observers fixated the designated start location before each trial and pressed a button to start the trial. As in Experiment 1, after a random delay (200–400 ms), a brief tone signaled the subject to begin making saccades along the path. 30–70 ms after a computer algorithm detected fixation within a region (radius $36'$) around the central location, the seven display frames appeared as in Experiment 1. Unlike Experiment 1, the report cue was presented only at the end of the trial in those trials requiring a report (see Section 4.1.4). Subjects were asked to make saccades as briskly as they could, giving primary weight to the saccadic task even if that produced perceptual errors.

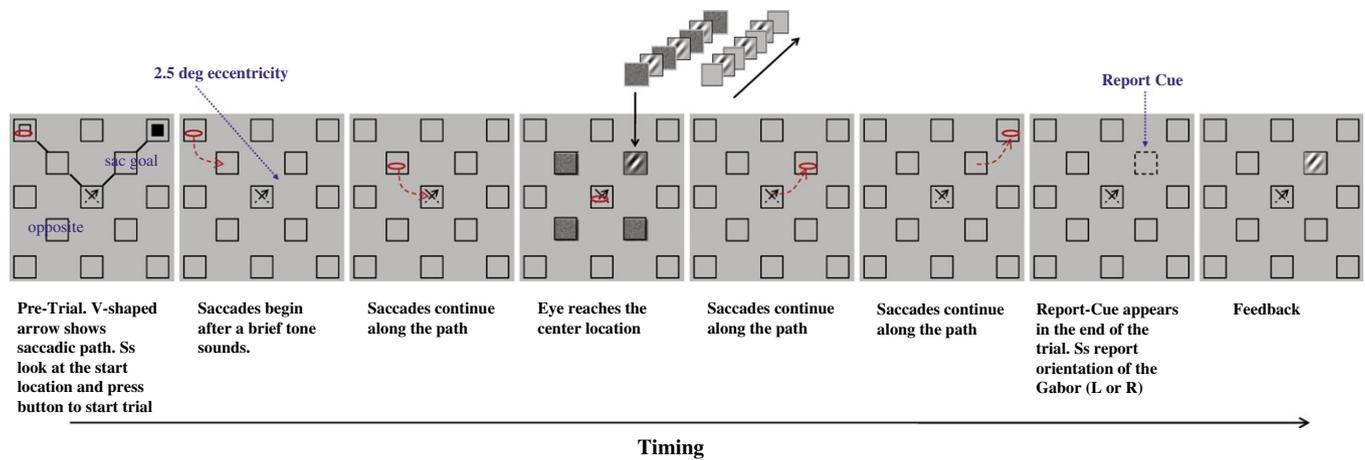


Fig. 4. Stimulus and procedure for Experiment 2. The open small square in the first frame indicated the start location, and the filled black square indicated the end location of the saccadic path. Red oval and dotted lines (not visible to the subject) show the instructed path of the eye over time. The critical frames (4 noise frame and 3 signal “Gabor” frames, interleaved) appeared when the line of sight reached the center after a 30–70 ms delay. Report cue (the report location turned into dash box) appeared after the path was completed. The trial duration was 2.5 s. Visual and auditory feedback was provided after the report was made.

4.1.4. Proportion of dual task trials

In an attempt to encourage subjects to maintain a brisk pace of saccades, and not to delay saccades in anticipation of the perceptual target, the probability of a perceptual report being required was set to either 80% or 20%, tested in separate experimental sessions. The types of sessions will therefore be denoted as 80% dual-task or 20% dual-task sessions.

4.1.5. Number of trials and sessions tested

All three observers ran both with and without external noise. VK finished 114 20% dual-task sessions (68 no noise and 46 with noise) and 37 80% dual-task sessions (21 no noise and 16 with noise). KM finished 138 20% dual-task sessions (57 no noise and 81 with noise) and 41 80% dual-task sessions (17 no noise and 24 with noise). KW finished 114 20% dual-task sessions (56 no noise and 58 with noise) and 30 80% dual-task sessions (15 no noise and 15 with noise). AT finished 90 20% dual-task sessions (46 no noise and 44 with noise) and 38 80% dual-task sessions (18 no noise and 20 with noise). AUT finished 114 20% dual-task sessions (56 no noise and 58 with noise) and 36 80% dual-task sessions (18 no noise and 18 with noise).

A portion of trials (15% for VK; 34% for KM; 5% for KW; 25% for AT and 26% for AUT) were eliminated for the conventional reasons: loss of track lock; no saccade detected or no saccade before the target/noise frames appeared, saccades during one or more target or noise frames, trials in which the critical saccade either did not start from the central location (defined as an offset error $>74^\circ$ from the center of the central location) or went to the wrong location, and trials in which the perceptual target did not appear due to failure to detect a critical saccade. Data were based on a total of 6723 trials for VK (2699 20% dual-task without noise, 670 80% dual-task without noise, 2688 20% dual-task with noise, 666 80% dual-task with noise), 5935 trials for KM (2002 20% dual-task without noise, 615 80% dual-task without noise, 2559 20% dual-task with noise, 759 80% dual-task with noise) and 6549 trials for KW (2669 20% dual-task without noise, 299 80% dual-task without noise, 2874 20% dual-task with noise, 714 80% dual-task with noise), 5501 trials for AT (2034 20% dual-task without noise, 680 80% dual-task without noise, 2118 20% dual-task with noise, 669 80% dual-task with noise) and 4824 trials for AUT (1794 20% dual-task without noise, 689 80% dual-task without noise, 1604 20% dual-task with noise, 734 80% dual-task with noise).

4.2. Results

Psychometric functions are shown in Fig. 5. Data were fit by Weibull functions with two parameters (threshold and upper asymptote) and the slope constrained to be the same for the two locations in each graph. Best fitting parameters were determined by using the “fminsearch” algorithm in Matlab 7.0 (see Appendix A for details).

The use of a single perceptual target that could appear in one of only two locations clearly had the sought-after effect of improving performance at high contrasts. The psychometric functions reached an upper asymptote of better than 90% correct in all cases.

Differences between performance at the goal and opposite locations were small. Contrast thresholds for orientation identification were either the same at the two locations, or (in about half the cases) lower when the Gabor appeared at the saccadic goal (Fig. 6). Overall, thresholds were lower for the saccadic target than the opposite location (paired t -test, $t = 3.8$, $p = 0.034$). Additional analyses showed that the better performance at the goal relative to non-goal locations was not a result of differences in retinal eccentricity of the Gabor targets at the two locations (see Appendix B).

Statistical tests using maximum likelihood procedures confirmed that performance was better at the saccadic goal, but differences between the locations were small. These tests determined whether the fits of the Weibull function were significantly better when the parameters of the Weibull (threshold and upper asymptote) for both goal and opposite locations were determined independently, rather than constrained to be the same (see Appendix A for details). In four cases (VK: 20% and 80% dual-task without external noise, KW: 80% dual-task without external noise and KW: 20% dual-task with external noise) fits for individual psychometric functions, were significantly better when parameters varied independently (Table 2). Applying the analyses to the data pooled over subjects showed significantly better fits in one case, 80% dual-task, without external noise. Fits in two other cases (20% dual task, with or without external noise) were also better when parameters were selected independently, however, significance was marginal (see Table 2). Thus, in contrast to some studies using spatial cues to direct attention (e.g., Doshier & Lu, 2000a, 2000b), effects of attention are not limited to situations in which superimposed external noise is present.

Saccadic strategies may have been a factor in reducing the differences between the two locations in two subjects, KM and KW.

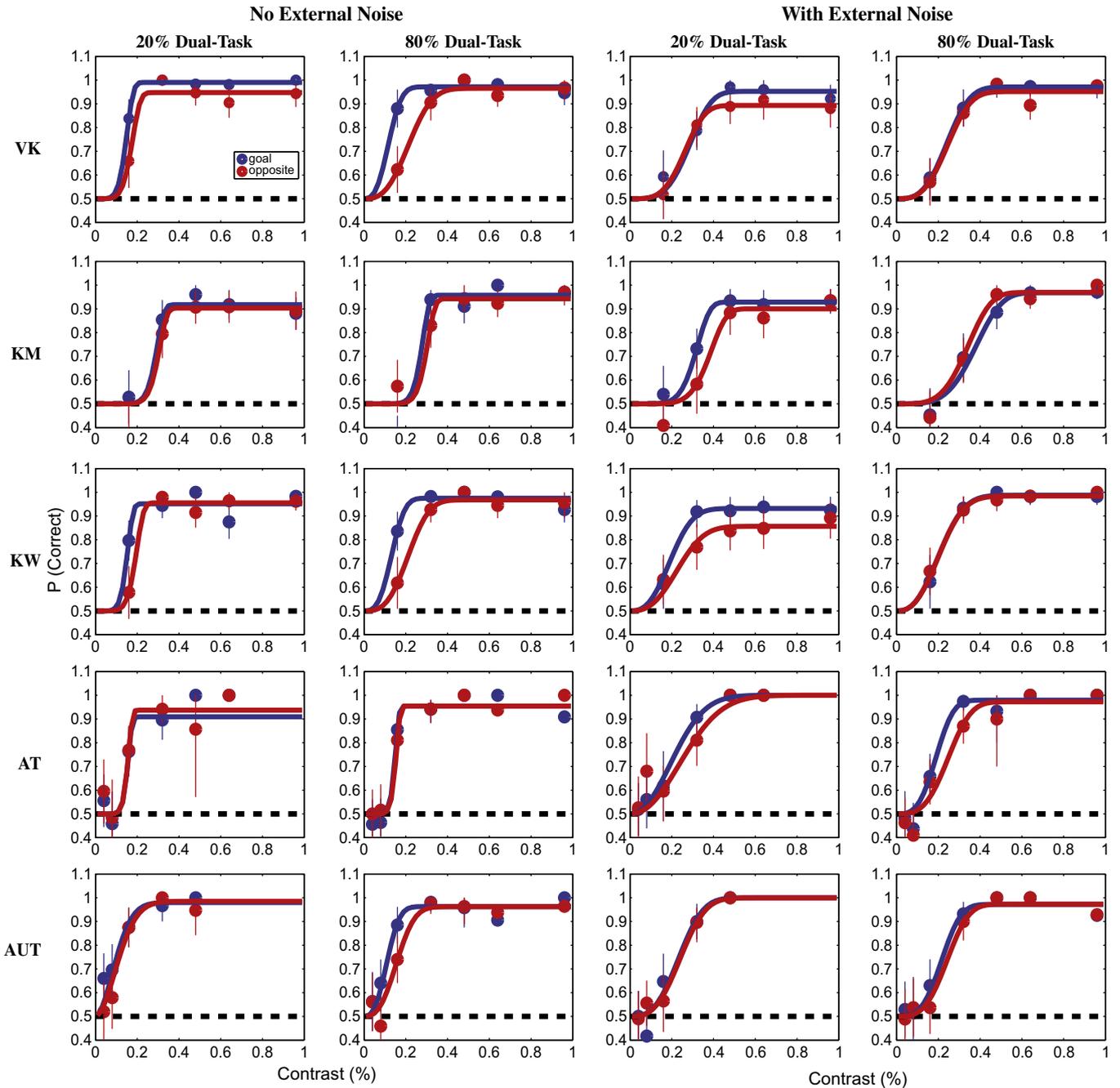


Fig. 5. Results of Experiment 2. Psychometric function for the 20% dual-task and 80% dual-task condition either with (right) or without (left) external noise when the Gabor appeared at (blue) or opposite (red) the saccadic goal. Bars represent 90% confidence interval based on the binomial variability of each observed probability. Lines are best fitting Weibull functions. The black dashed line is chance level. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 7 shows that these two subjects had longer critical pause durations when the Gabor appeared opposite to the saccadic goal, although KW's pause durations were much shorter than KM's. These increases in pause duration for the opposite location could have allowed extra time to process the orientation of the Gabor. Increased pause durations in the presence of external noise for three subjects, KM, KW and VK, could also have reduced perceptual differences between the goal and opposite locations. The two more practiced subjects (AT and AUT) had shorter pause durations than the other subjects regardless of the location of the Gabor. In one case (AT, with external noise) pause durations were longer when the Gabor appeared the saccadic goal than at the opposite location (see Fig. 7), however, analysis of his perceptual performance

showed that pause duration did not affect his perceptual performance and was not responsible for better perceptual performance at the saccadic goal (Appendix C).

4.3. Discussion

The results of Experiment 2 showed marginal improvements in contrast sensitivity for orientation identification at the saccadic goal relative to the location opposite to the saccadic goal. In contrast to some studies of attention that used spatial cues, improvements due to attention were not restricted to cases in which superimposed external noise was present, or to cases in which several (four or more) locations could be probed (Doshier & Lu, 2000a,

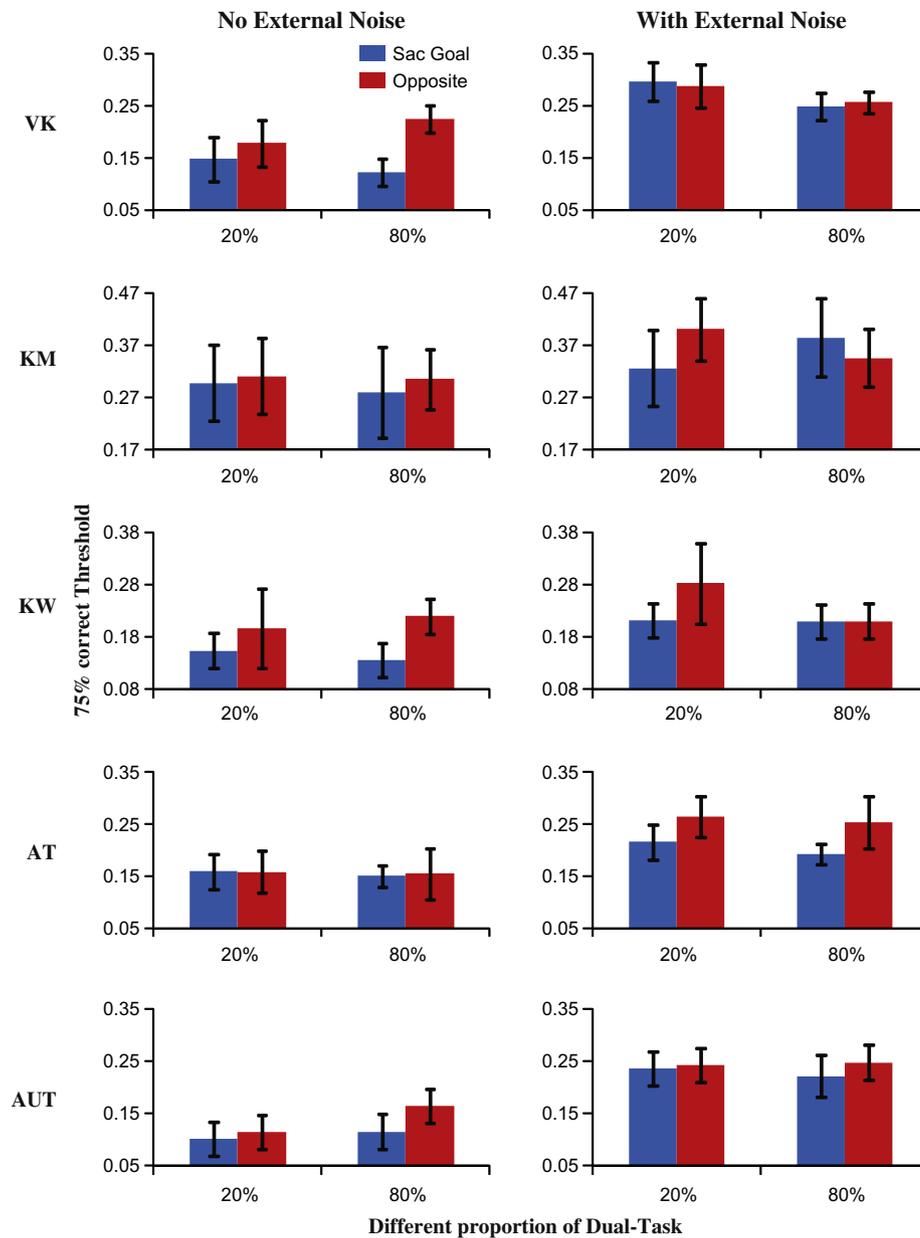


Fig. 6. Experiment 2. Seventy five percent thresholds for the 20% dual-task and 80% dual-task condition either with (right) or without (left) external noise when the Gabor appeared at (blue bar, left in each pair) or opposite (red bar, right in each pair) the saccadic goal. Error bars represent estimated ± 1 SD (see Appendix A for details). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Experiment 2. X^2 value for the maximum likelihood test of differences between psychometric functions (Fig. 5) obtained when Gabors appeared at and opposite to the saccadic goal (see Appendix A). Individual subjects results (top) and group results (bottom). Values marked with asterisks for the individual subjects tests are significant with $p < .001$ (***), $p < .01$ (**) or $p < .05$ (*).

Subjects	Without external noise		With external noise	
	20% Dual-task	80% Dual-task	20% Dual-task	80% Dual-task
VK	10.60**	11.21**	3.76	1.21
KM	0.71	3.31	4.10	1.32
KW	5.87	9.13**	7.86*	0.07
AT	0.29	0.40	1.48	5.10
AUT	0.37	5.04	0.08	0.80
Overall X^2 value (p value)	17.84 (.058)	29.10*** (.001)	17.29 (.068)	8.51 (.579)

2000b). We also found that for two of the five subjects, differences between performance at goal and opposite locations were reflected in the timing of saccades, with longer pause durations when a Gabor was detected at the opposite locations.

The use of a sparse display – a single Gabor that could appear in only one of two locations – contributed to the reducing the size of the differences in performance across locations relative to performance observed in Experiment 1, where four perceptual targets

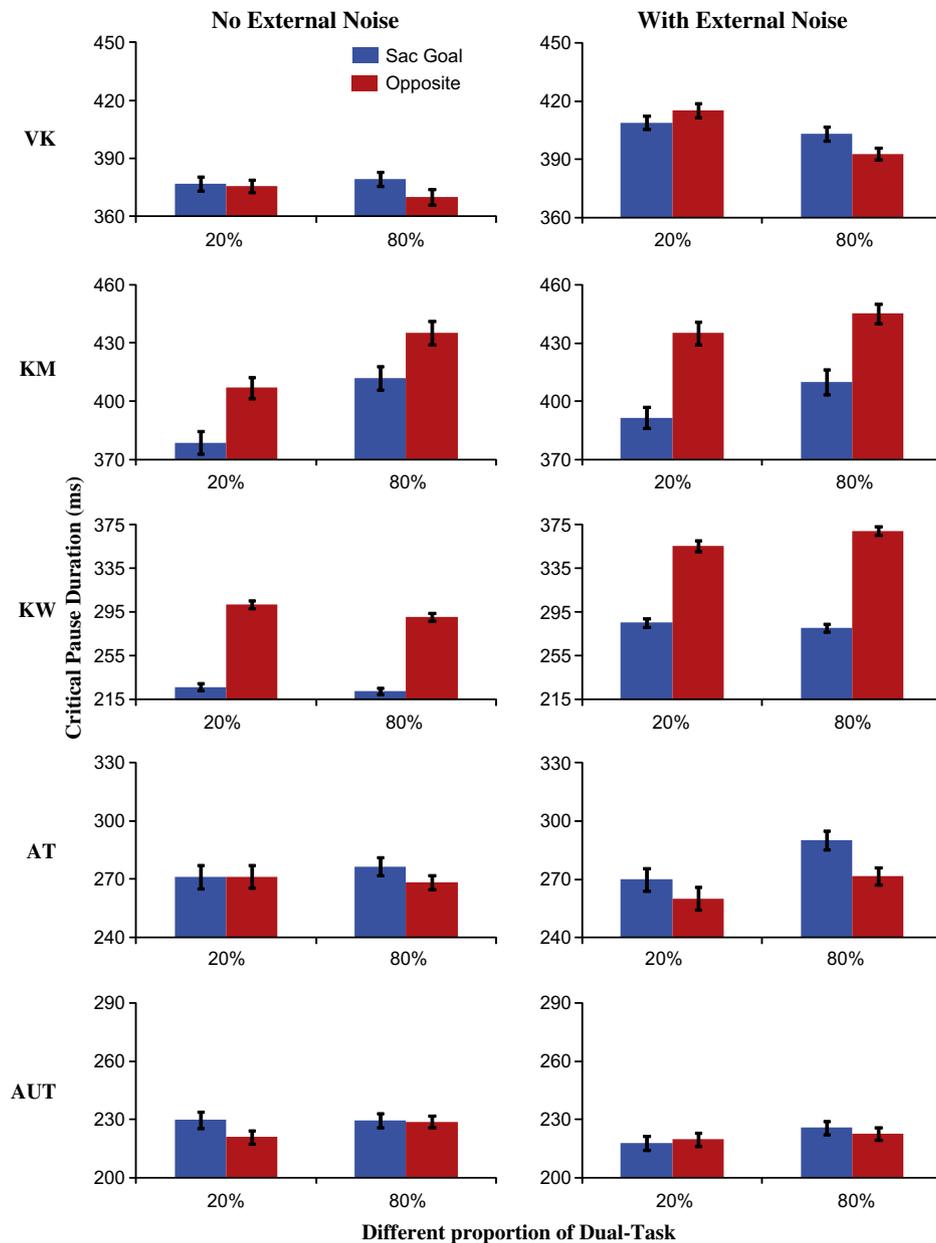


Fig. 7. Experiment 2. Mean (\pm SE) critical pause duration for the 20% dual-task and 80% dual-task condition either with (right) or without (left) external noise when the Gabor appeared at (blue bar, left in each pair) or opposite (red bar, right in each pair) the saccadic goal. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

were presented. With only a single Gabor that could appear in only two possible locations, the load on perception and memory was reduced (but not eliminated). Thus, it was interesting that under such conditions, where only two display locations had to be monitored for a single target, and where saccades were sometimes delayed in response to detection of the Gabor at the non-goal locations, that any enhancement at the goal of the saccade would be found. These results suggest that pre-saccadic shifts of attention may lead to modulation of early visual processes, even in the absence of superimposed visual noise.

5. Experiment 3: Effects of pre-saccadic shifts of attention on visual detection

Perceptual and memory load was reduced in Experiment 2 relative to that in Experiment 1 by presenting only a single percep-

tual target on each trial. But perceptual or memory limitations could still have been a factor because at low or moderate contrasts, when there would be a great deal of uncertainty about the location of the Gabor target, decisions about which location to preferentially encode or remember could have contributed to the results.

Experiment 3 was done in an attempt to reduce memory load, and perceptual processing requirements, even further. This was done by using a Yes/No detection task. We reasoned that detection imposes a smaller memory and processing load than identification because features of the perceptual target need not be stored. Previous results from Wilder et al. (2009) support this rationale. They found that subjects would delay saccades during active visual tasks in response to the appearance of a Gabor probe target when the judgments required reports of orientation, but not when reports of Gabor location were required. They also found less interference

from a concurrent task on reports of location than on reports of orientation, using the same Gabor orientations as tested here.

Measurements of detection within “yes/no” paradigms are sensitive to shifts in criteria. Results described below will include both hits, false alarms and measurements of d' to address this concern.

5.1. Method

5.1.1. Observers

Four paid volunteer participants were tested (VK, AT, JC and AUT), each with normal uncorrected vision. Each was unaware of the purpose of the experiment.

5.1.2. Stimulus and procedure

The procedures were similar to those in Experiment 2. The only difference is that the presence of the Gabor at each location was determined independently, so that on 25% of trials there was a Gabor at the saccadic goal location, 25% at the opposite location, 25% in both locations and 25% in neither location. The contrast and orientation of each Gabor was chosen independently. Subjects were asked to make saccades along the saccadic path and to report whether there was a Gabor in one of the locations at the end of the

trial. The location that was to be probed was disclosed at the end of the trial. In the first set of experimental sessions the Gabor contrasts were 8%, 16%, 24% or 32%. Based on these first results, a second set of sessions was run in which the contrast range was restricted to the narrow range (8%, 12%, 16% and 20%) where the performance difference between the two locations had been largest. In all sessions there was no superimposed external noise, and the central arrows and other markers denoting the path of the saccade were removed at the start of the trial. Subjects were again asked to make saccades as quickly as they could giving primary weight to the saccadic task, even if that produced perceptual errors.

5.1.3. Number of trials and sessions tested

VK finished nine sessions with large contrast range and 20 sessions with small contrast range. AT finished 14 sessions with large contrast range and 18 sessions with small contrast range. JC finished 18 sessions with large contrast range and 22 sessions with small contrast range. AUT only ran with small contrast range and finished 15 sessions. Subject AUT ran 30 with the small contrast range. (Initially, AUT showed much longer pauses between saccades than the other subjects, 500 ms for AUT vs. <470 ms for everyone else. AUT indicated that he could go faster, so AUT ran

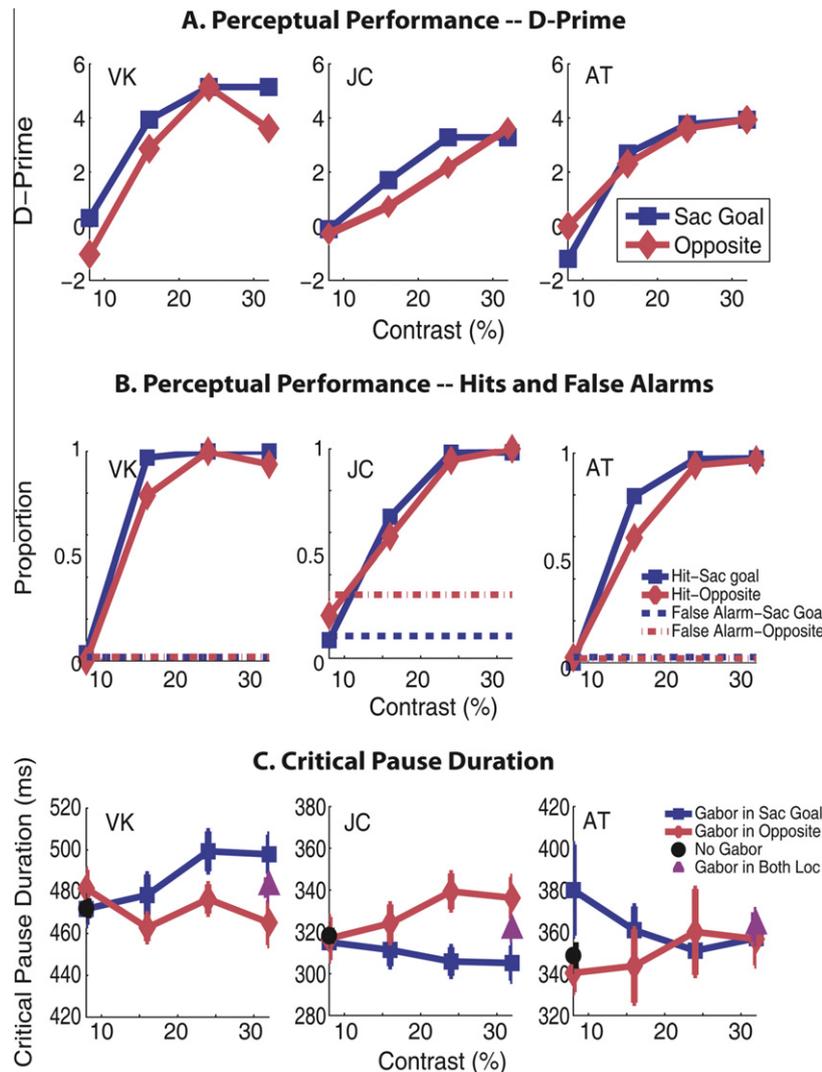


Fig. 8. Experiment 3. Detection performance as a function of contrast over the larger stimulus contrast range (8–32%). (a) d' Values (SE's are smaller than plotting symbols). (b) Proportion of hits (solid lines) and false alarms (dashed line). (c) Mean critical pause duration (± 1 SE) when the Gabor target appeared at (blue circle), or opposite (red circle) the saccadic goal. Average critical pause duration when the Gabor appeared in both (purple triangle) and in neither (black circle) location are also shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

another 30 sessions with faster saccadic pace at the small contrast range. Data from only these sessions will be reported.)

A portion of trials (2% for VK; 11% for AT, 12% for JC and 19% for AUT) were eliminated for the conventional reasons: loss of track lock; no saccade detected or no saccade before the critical frames appeared, saccades during one or more critical target frames, trials in which the critical saccades went to the wrong location, and trials in which the perceptual target did not appear due to failure to detect a critical saccade.

Data were based on a total of 1417 trials for VK (434 large contrast range and 983 small contrast range), 1432 trials for AT (616 large contrast range and 816 small contrast range), 1724 trials for JC (771 large contrast range and 953 small contrast range), 1145 trials for AUT (small contrast range).

5.2. Results and discussion

The proportion of correct detections and measurements of d' as a function of contrast showed better performance at the goal of the saccade than at the opposite location. Fig. 8 shows that effects of location were most apparent when contrast was less than about 25%. These effects were confirmed in a separate set of sessions comprising a smaller range of contrasts (8–20%; Fig. 9). At the same time, false alarm rates were low (<3%), and not higher at the saccadic goal. These results argue that the differences in detecting the

presence of the Gabor were not due to differences in criteria across the two locations.

Figs. 8 and 9 also show critical pause durations for trials in which the Gabor appeared at the saccadic goal, at the opposite location, both locations or neither. There was some modulation in pause duration as a function of Gabor location and contrast, but the differences were small, inconsistent across subjects, and not consistently related to psychophysical performance nor to the location of appearance of the Gabor.

The better detection performance for the saccadic goal suggests that the perceptual enhancements at the goal of the saccade are not due solely to selective memory for target features, and that perceptual enhancements due to saccades can be observed in the absence of external noise.

6. General discussion

The current study investigated the visual consequences of pre-saccadic shifts of attention. The experiments used manipulations comparable to those that have been used in the past to analyze the effects of attention during maintained fixation (Section 2.3), including variation of stimulus contrast, and presentation of targets either with or without superimposed external visual noise.

Perceptual enhancements for targets at the saccadic goal relative to non-goal locations were found across target contrast levels,

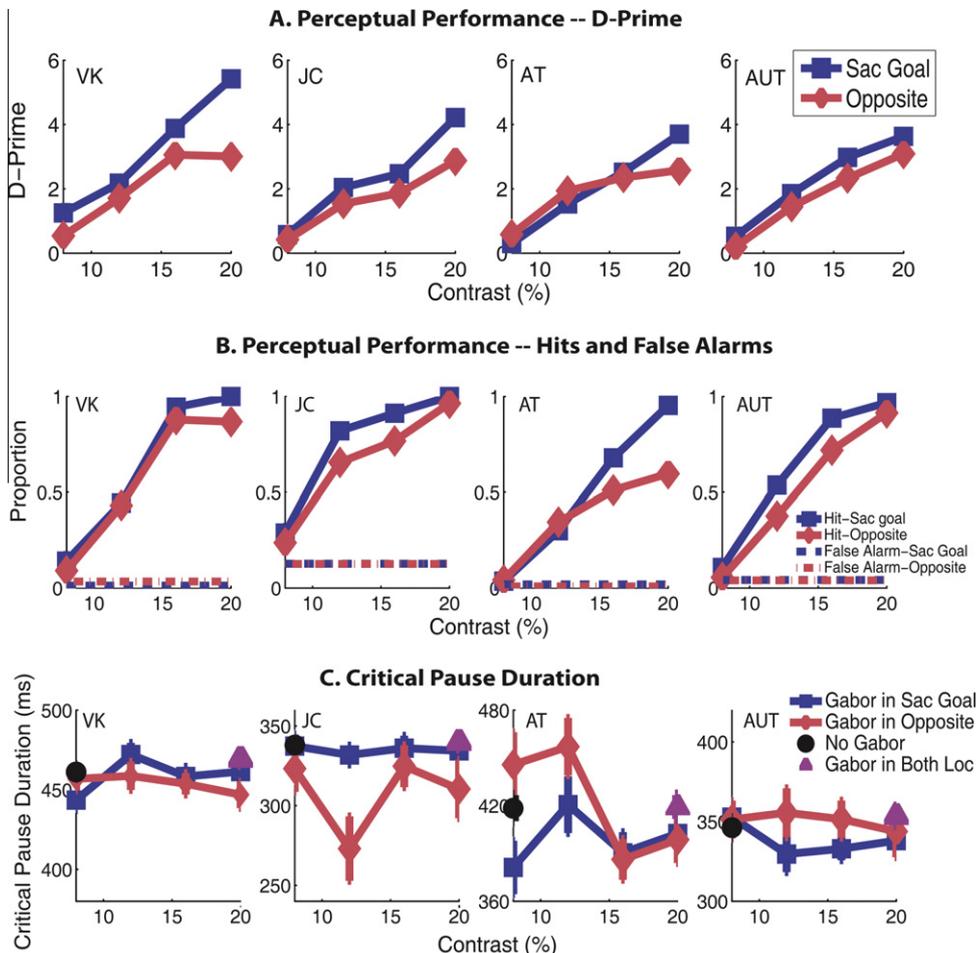


Fig. 9. Experiment 3. Detection performance as a function of contrast over the small stimulus contrast range (8–20%). (a) d' Values (SE's are smaller than plotting symbols). (b) Proportion of hits (solid lines) and false alarms (dashed line). (c) Mean critical pause duration (± 1 SE) when the Gabor target appeared at (blue circle), or opposite (red circle) the saccadic goal. Average critical pause duration when the Gabor appeared in both (purple triangle) and in neither (black circle) location are also shown. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

with or without superimposed visual noise. Perceptual performance was better at the saccadic goal, regardless of whether the task required encoding of stimulus features (Experiments 1 and 2) or simply detecting stimulus presence (Experiment 3), and for tasks that imposed a relatively high (Experiment 1) or low (Experiments 2 and 3) load on perception and/or on visual short term memory.

These results suggest that pre-saccadic shifts of attention can exert their effects in multiple ways and at multiple levels. Pre-saccadic shifts of attention may determine which objects or locations have priority for perceptual processing, or for storage in limited capacity memory (Experiment 1), or they may modify the thresholds for detecting or identifying low contrast images (Experiments 2 and 3). The results of Experiments 2 and 3 shows that pre-saccadic shifts of attention do not operate solely by exclusion of external noise since effects of pre-saccadic attention were found in the absence of external noise. This means that other mechanisms operate either in place of or in addition to external noise exclusion, such as enhancement of the attended signal, or reductions in internal noise (Doshier & Lu, 2000a, 2000b; Liu, Doshier, & Lu, 2009).

6.1. Effects of pre-saccadic shifts of attention in the presence of multiple targets

Experiment 1 used a demanding orientation identification task: four targets, each in one of four possible orientations, presented simultaneously in four different locations. The results showed that perceptual performance was best at the saccadic goal, and very poor at the other (non-goal) locations. The advantage at the saccadic goal existed even at the highest stimulus contrast levels, with or without superimposed external noise.

The advantage in performance at the saccadic goal in Experiment 1 could be related to memory, specifically, the inability to retain information about the entire stimulus display in a durable form until after the saccadic sequence was completed. Retaining information about the entire stimulus display may have been too difficult, particularly when a saccadic task was performed at the same time.

Psychophysical studies of attention effectively avoid memory loss by presenting a cue that discloses the probed location along with or very soon after stimulus appearance (e.g., Doshier & Lu, 2000a, 2000b; Gould, Wolfgang, & Smith, 2007; Lu & Doshier, 2000). Experiment 1 contained such a “report cue”, which disclosed the probed location beginning with the final frame of the critical display (see Fig. 1). The increased saccadic pause durations found when the report cue designated a location other than the saccadic goal (Fig. 3) shows that the cue was noticed on at least a portion of the trials for some subjects. The increased pause durations are likely to reflect the attempt to divide attention between the saccadic goal and the cued location as part of an effort to improve perceptual performance by delaying the saccade in at least a portion of the trials (Gersch et al., 2008; Kowler et al., 1995; Wilder et al., 2009). However, given that subjects were instructed not to delay saccades, we suspect that in some trials they simply ignored the report cue until after the saccadic sequence was completed. In that case information at the saccadic goal, rather than information at the location shown by the report cue, would have priority for storage in limited capacity memory. Such a strategy could account for the large losses in performance at non-goal locations that were observed even at high stimulus contrasts. Such large losses are not typical in studies of attention during maintained fixation with a similar displays, namely, only four locations tested and a report cue delivered near the end of the presentation of the perceptual targets (Lu & Doshier, 2000).

A role for pre-saccadic shifts of attention in memory has been supported by previous studies. For example, Gersch et al. (2008)

found better memory for targets at the saccadic goal than in other locations (including the foveally fixated location) during the performance of saccadic sequences. Baldauf and Deubel (2008) and Godijn and Theeuwes (2003), who presented displays containing multiple items (4–12 letters), found that performance in a letter discrimination task was much better when the target appeared at the saccadic goal than at a non-goal location. In their tasks subjects were not told the probed location until the end of trials. Thus, as in Experiment 1, subjects might not have been able to hold sufficient information from all possible probed locations until the end of the trial, and decided to give priority to the saccadic goal. Findings showing that performance in memory and change detection tasks is better at the saccadic goal (Currie et al., 2000; Henderson & Hollingworth, 1999; Irwin, 1992) are also consistent with the conclusion that one of the principal effects of pre-saccadic attention is to choose what should be stored in memory.

Although a case can be made for the involvement of memory, perceptual factors should be considered as well. Losses in performance similar to those observed in Experiment 1 (that is, at high contrasts and with or without superimposed noise) were found in studies of attention when reports of multiple targets (Bahcall & Kowler, 1999; Liu, Doshier, & Lu, 2009) or performance of concurrent perceptual tasks (Huang & Dobkins, 2005; Lee et al., 1999; Morrone, Denti, & Spinelli, 2004), were required. These losses were attributed to perceptual mechanisms. Liu, Doshier, and Lu (2009), for example, found performance losses when reports about two locations were required, particularly with high-precision judgments. The results were consistent with a model in which the need to attend to and report two locations led to higher levels of internal noise that increased together with the stimulus contrast. Huang & Dobkins (2005) found that judgments about the contrast of peripheral gratings were impaired by performance of a concurrent central identification task, and attributed the losses to effects of attention on either the contrast gain or response gain of the underlying visual analyzers. Bahcall and Kowler (1999) found losses when two closely-spaced targets were attended and attributed the losses to perceptual interference between signals from the attended locations. Palmer and Moore (2009) suggested that losses when targets were located near foils reflected the size and spatial precision of the attended region.

One difference between the present experiment and the prior psychophysical studies of perceptual attention summarized above is that the prior work used multiple perceptual tasks or targets, whereas we tested concurrent saccadic and perceptual tasks. Thus, the performance losses we found at locations other than the saccadic goal could be generated by events due to task interference (dividing attention between two types of tasks – perceptual vs. saccadic) or to perceptual interference (dividing attention between multiple visual targets). Given that the perceptual requirements at the saccadic goal were relatively modest – generating a representation of a location sufficiently precise to guide the saccade – it seems unlikely that performance losses would be generated solely due to perceptual interference. It is also unlikely that performance losses were generated by task interference because perceptual losses are not found when judgments are made about targets located at the saccadic goal (Gersch, Kowler, & Doshier, 2004; Kowler et al., 1995).

Rather, it seems more likely that the poor performance at non-goal locations in Experiment 1 occurred because the selection of the saccadic goal attenuates representations at non-goal locations (Li & Basso, 2008; Moore & Chang, 2009; Moore, Tolia, & Schiller, 1998). Attenuation can result from a variety of processes, including memory decay, reduced signal strength or signal/noise ratios (e.g., Liu, Doshier, & Lu, 2009), or reduced precision of perceptual encoding. All of these processes can produce performance losses at high stimulus contrasts, which is what we observed at locations other than the saccadic goal.

6.2. Effects of pre-saccadic shifts of attention on selection on contrast sensitivity

The perceptual tasks in Experiments 2 and 3 imposed a much smaller memory and perceptual load than those in Experiment 1.

Experiment 2 used an orientation identification task with only a single perceptual target that could appear in one of only two locations. Experiment 3 used a detection task. The results showed better performance, overall, at the saccadic goal than at the opposite location, with small differences between the locations that were evident primarily at low or moderate target contrasts. These results are similar to those of Gersch, Kowler, and Doshier (2004), who also presented a single Gabor target during saccadic sequences and found poorer orientation identification at non-goal locations at low or moderate stimulus contrasts. The effects Gersch, Kowler, and Doshier (2004) observed were larger than those reported here, perhaps because of the greater number of possible locations in which the Gabor could appear (six locations, with a post-stimulus report cue) and the greater uncertainty about when the Gabor could appear. Gersch, Kowler, and Doshier (2004) always used superimposed external noise, thus their effects could have been due to mechanisms of external noise exclusion (Doshier & Lu, 2000a, 2000b). The present results extend the effects of pre-saccadic shifts of attention to cases where external noise is absent, pointing to a role for other processes, primarily modulations in the gain of the signal, or in the level of additive internal noise, at the attended goal location relative to the non-goal locations (Doshier & Lu, 2000a, 2000b; Carrasco, 2011).

Could the performance losses in Experiments 2 and 3 be attributed to selective memory or selective encoding (as in Experiment 1), despite the modest task load? It is possible that when the low or moderate stimulus contrasts produced uncertainty about which of the two locations contained a perceptual target, priority for encoding orientation may have been given to the saccadic goal. This possibility seems less likely to apply to results of the detection task in Experiment 3 because it is only necessary to remember whether something appeared, not what has appeared.

We conclude that there are effects of pre-saccadic shifts of attention on perceptual judgments that are not readily accounted for solely by events at the level of memory encoding. This conclusion is supported by two prior studies. Castet et al. (2006) found lower thresholds for orientation discrimination using high-contrast targets and superimposed noise at non-saccadic-goal locations when subjects were told the probed location prior to the saccade, thus eliminating location uncertainty. Montagnini and Castet (2007) also found an advantage at the saccadic goal in the same orientation discrimination task when uncertainty about location was reduced by cuing the location in which the target was likely to appear (75% probability). These results, like those of our experiments using a single Gabor target (Experiment 2) or a detection task (Experiment 3) suggest that the performance loss at non-goal locations is due to effects of pre-saccadic shifts of attention on the quality of the visual representation of the targets.

6.3. Summary and conclusions

We investigated the effects of pre-saccadic shifts of attention on vision during sequences of saccades using the experimental manipulations that have been successful in the past for characterizing attention during maintained fixation. We found that perceptual performance during the pauses between saccades was better at the goal of the saccade than at non-goal locations under all conditions investigated, namely, across a range of stimulus contrasts, a range of memory loads, two different perceptual tasks (feature discrimination or simple detection), and with or without visual noise superimposed on the perceptual targets.

These results resolve unanswered questions about the basis of pre-saccadic shifts of attention by showing that the changes in visual performance prior to saccades are not due exclusively to changes in the content of short term memory that favor saccadic targets, nor to the operation of attentional mechanisms based on the exclusion of external noise. Rather, the effects of pre-saccadic shifts of attention cover a broader spectrum and include changes in the quality of visual representations. The visual changes may be attributed to modulations in the strength of the signal or the level of internal visual noise (Doshier & Lu, 2000a, 2000b; Liu, Doshier, & Lu, 2009; Carrasco, 2011). The pre-saccadic changes in vision are also consistent with neurophysiological findings of enhanced activity at the saccadic goal relative to non-goal locations (Li & Basso, 2008; Moore, Armstrong, & Fallah, 2003).

Spatial attention and saccades are often studied independently, but in natural vision the two must work in concert to explore the environment. The broad scope of the effects of pre-saccadic changes in attention supports the view that a major role for spatial attention in natural vision is to facilitate the accurate targeting of saccades and to ensure seamless perceptual transitions between discrete glances. These are accomplished by focusing resources on the saccadic goal across multiple levels of processing.

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Appendix A

A.1. Comparisons of psychometric functions when the Gabor target appeared at or opposite the saccadic goal (Experiment 2)

Psychometric functions in Experiment 2 were fit with Weibull functions

$$P_i = \min + (\max - \min) * (1 - 2^{-(c/\alpha)^\beta}) \quad (1)$$

where P_i is the predicted probability of a correct report of orientation at stimulus contrast c , and α is the threshold of the psychometric function at 75% correct, \min is the lower asymptote which is the chance level (0.5), \max is the upper asymptote, and β is the slope, which was constrained to be the same for both the goal and the opposite locations. In order to evaluate the significance of the differences between the psychometric functions obtained when the Gabor appeared at or opposite to the saccadic goal parameters were estimated for each psychometric function (i.e., for a given subject, location, noise level and proportion of dual-task trials; see Fig. 5) using Matlab function *fminsearch* under two possible models, as described below.

In the unconstrained model, the threshold (α) and asymptotic parameter (\max) were estimated independently for each psychometric function. In the constrained model, these two parameters were constrained to be the same for the two locations within a given subject and condition. The slope (β) was always constrained to be the same for two locations in both models. Thus, there were three parameters for the constrained model (1α , $1\max$ and 1β) and five parameters for the unconstrained model (2α , $2\max$ and 1β) for each subject and each condition.

The maximum likelihood under each model for each subject, condition and location was:

$$\text{Likelihood} = \prod_{i=1}^n \frac{N_i!}{K_i!(N_i - K_i)} P_i^{K_i} (1 - P_i)^{N_i - K_i} \quad (2)$$

where n is the number of stimuli contrast levels, N_i is the number of trials for each contrast, K_i is the number of correct reports for each stimuli contrast, P_i is the predicted proportion of correct reports for either the constrained or unconstrained model.

The log value of the maximum likelihood was determined for each location and condition within each subject and also pooled over subjects (s):

$$\text{Log(Likelihood)} = \sum_{s=1}^5 \sum_{i=1}^n \left[\log \left(\frac{N_i!}{K_i!(N_i - K_i)} \right) + K_i \log P_i + (N_i - K_i) \log(1 - P_i) \right] \quad (3)$$

A chi-square value was calculated for each condition based on the comparison of maximum likelihood values from the constrained and unconstrained models:

$$\chi^2(df) = 2.0 * [\log(\text{maxlikelihood}_{\text{unconstrained}}) - \log(\text{maxlikelihood}_{\text{constrained}})] \quad (4)$$

The df was defined as the number of free parameters of the unconstrained model minus the number of the free parameters of constrained model.

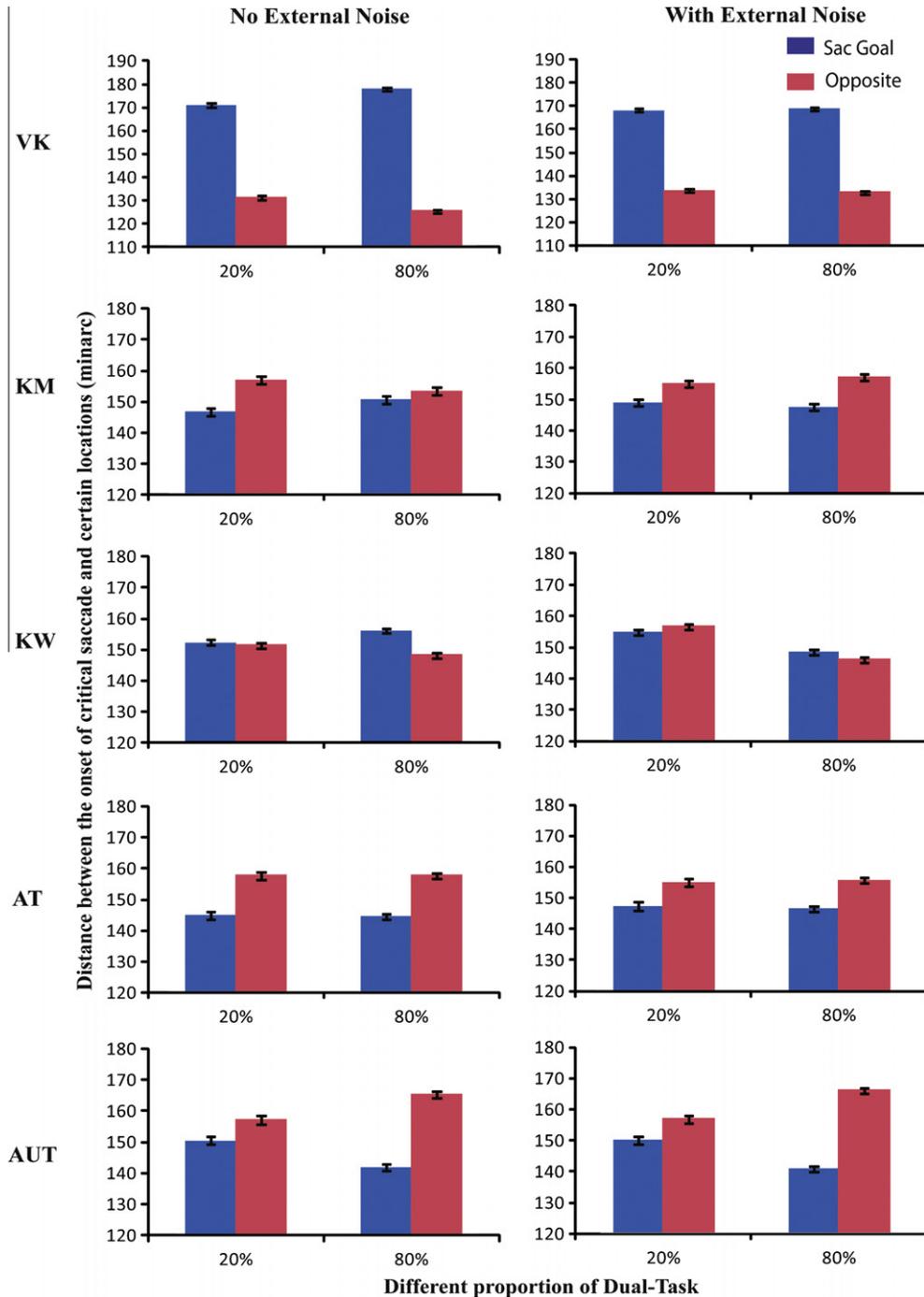


Fig. B1. Experiment 2. Mean retinal eccentricity (± 1 SE) of the goal (blue) and opposite (red) locations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

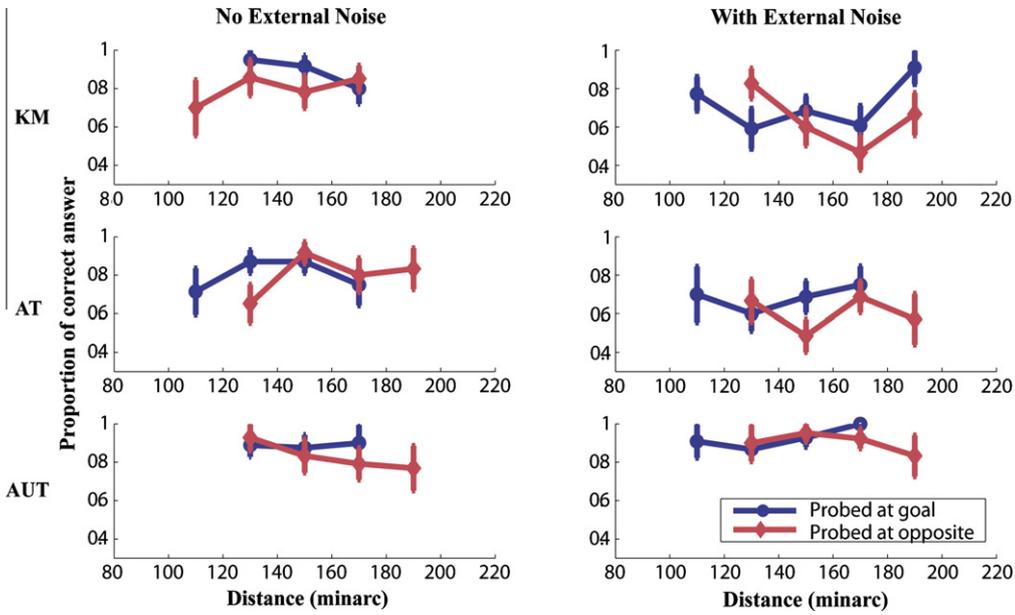


Fig. B2. Experiment 2. Percent correct for moderate contrast levels (see text) as a function of eccentricity when the Gabor appeared at (blue) or opposite (red) the saccadic goal locations. Eccentricities were sorted into bins 20° wide. Eccentricity was measured from the center of the Gabor to the eye position at the onset of the critical saccade. Data are pooled over the 20% dual-task and 80% dual-task conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

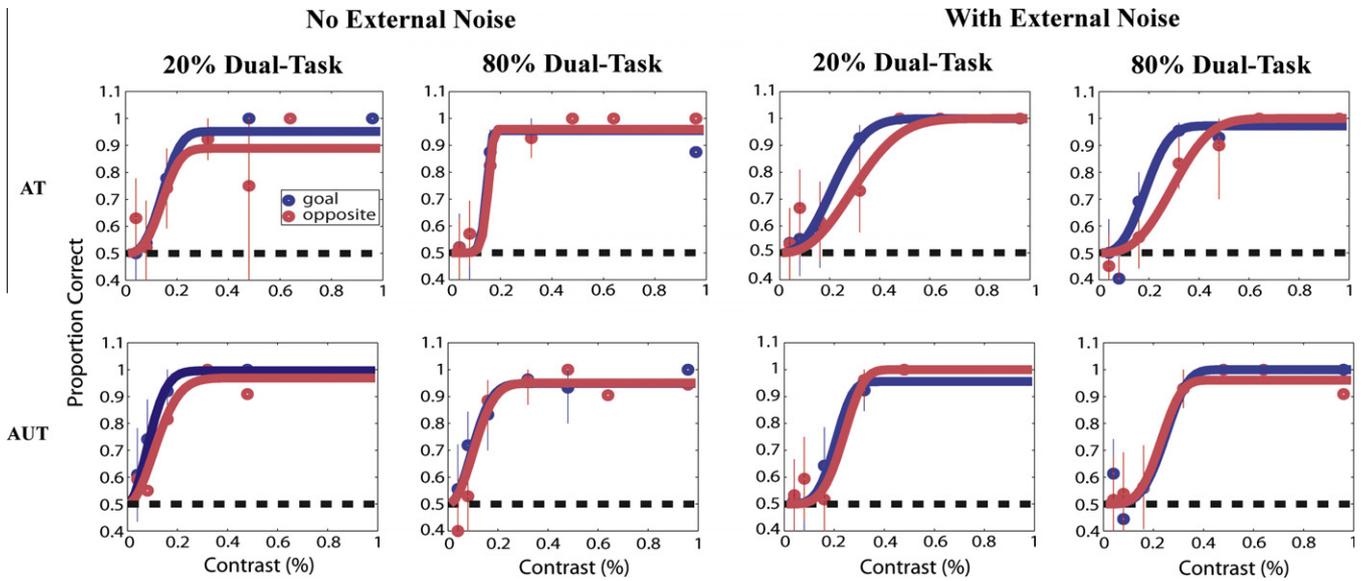


Fig. B3. Experiment 2. Psychometric function for 20% dual-task and 80% dual-task condition either with (right) or without (left) external noise when the Gabor appeared at saccadic goal (blue) or opposite (red) location. Trials with eccentricity of Gabor target larger than 180° were excluded. Bars represent 90% confidence interval based on the binomial variability of each observed probability. Lines are best fitting Weibull functions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

A2. Standard deviations of the threshold values in Experiment 2

Standard deviations of the reported thresholds in Experiment 2 (Fig. 7) were determined by re-sampling each point on each psychometric function from a binomial distribution whose parameters were determined by the total number of trials and the proportion of correct reports for each contrast in each psychometric function. The *binornd* function of Matlab was used to re-sample 100 new simulated data sets for each psychometric function. The mean threshold of the 100 fitted Weibull functions was determined, and the standard deviation of the obtained means plotted in Fig. 7.

Appendix B

In order to determine whether the advantage at the saccadic goal location in Experiment 2 was due to retinal eccentricity at the time of appearance of the Gabor target, we first determined the eccentricity of the Gabor target at the time of onset of the critical saccade. Fig. B1 shows the average (± 1 SE) distance from eye position at the onset of the critical saccade relative either to the center of the saccadic goal (blue bars) or to the center of the opposite location (red bars) in Experiment 2. For three subjects (KM, AT and AUT) the average retinal distance to the saccadic goal was shorter than the distance to the opposite location.

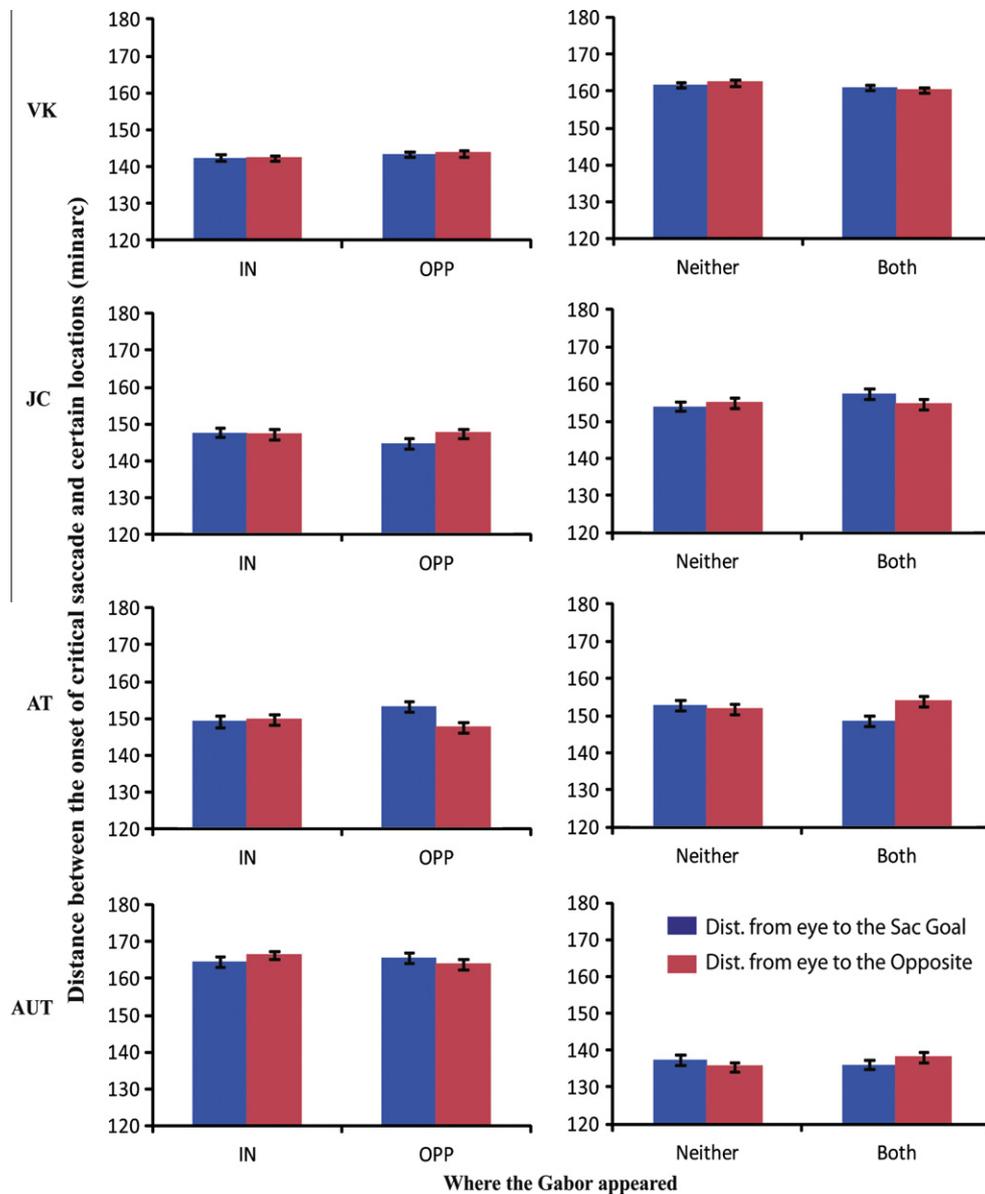


Fig. B4. Experiment 3. Distance from the eye position of critical saccades to different locations with small range of stimulus contrast (0–20%). The locations of the onset of the critical saccades were taken as the eye positions. We compared the distance from eye position to the saccadic goal location (blue bars) and to the opposite locations (red bars). The Gabor could appear only at the saccadic goal location (IN, first column), only at the opposite location (OPP, second column), at neither locations (neither, third column) and at both locations (both, fourth column). Error bars represent estimated ± 1 SE. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

To find out whether these differences in retinal eccentricity could have accounted for the better performance at the saccadic goal (Fig. 6) for these three subjects, the accuracy of perceptual reports was examined as a function of eccentricity and shown in Fig. B2. This analysis was done only for moderate contrasts (32% for KM, 16% for AT, 16% for AUT without external noise, and 32% for AUT with external noise) where effects of location were most evident (see Fig. 6). Psychophysical data were pooled across the 20% and 80% dual report conditions, and sorted into bins (20' wide) according to the eccentricity of the Gabor. Bins with fewer than 10 observations were not included. Fig. B2 shows percent correct reports (± 1 SE) as a function of eccentricity. For KM performance is better at the saccadic goal even for the equivalent eccentricities. AT and AUT shows a small drop with the largest eccentricities when the Gabor was in the opposite location. To determine whether these trials with large eccentricities could have contributed to their overall (but small) differences between performance

at the saccadic goal and the opposite location for these two subjects (Fig. 6), their psychometric functions were replotted with the largest eccentricities ($>180'$) omitted. The pattern of results (Fig. B3) is similar to that for the full data set (Fig. 6).

Fig. B4 shows the average eccentricities relative to both goal and opposite locations for Experiment 3. In that case, the mean eccentricities to both locations were about equal, meaning that any perceptual advantages at the goal location (Figs. 8 and 9) were not due to eccentricity effects.

Appendix C

In the Experiment 2, subject AT showed shorter critical pause durations at the saccadic goal (Fig. 7). In order to determine whether the better perceptual performance at the saccadic goal for AT when external noise was present (Figs. 5 and 6) was due to the longer critical pause duration, we examined perceptual

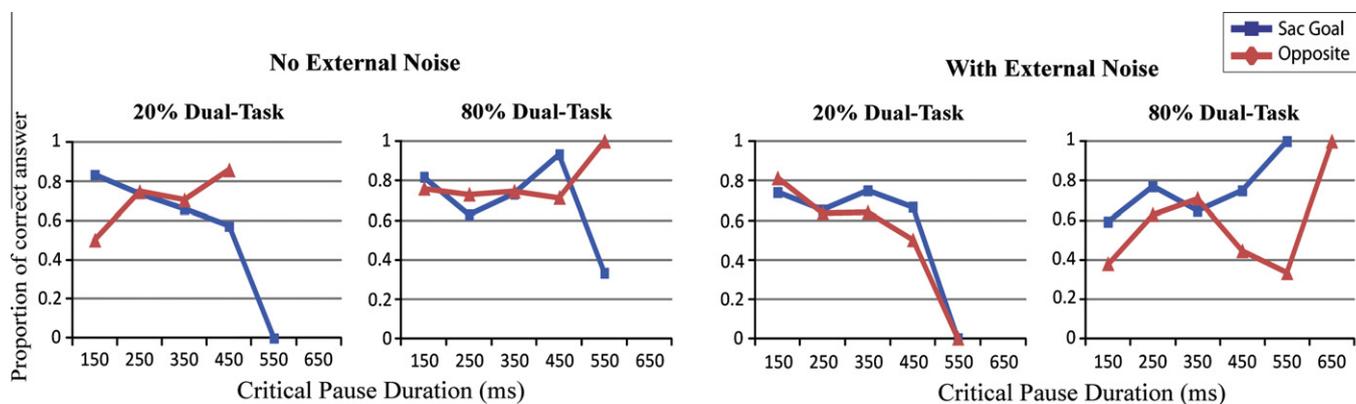


Fig. C1. Subject AT in Experiment 2. Percent correct as a function of critical pause duration when the Gabor appeared at (blue) or opposite (red) the saccadic goal. Data are pooled over stimuli contrast levels. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

performance as a function of the critical pause duration. Fig. C1 shows that there was no consistent relationship between AT's critical pause duration and perceptual performance. Performance was typically better at the saccadic goal across the range of pause durations, particularly in the presence of external noise (righthand graphs). Thus, the perceptual enhancement at the saccadic goal found for AT in the presence of external noise was not due to the saccadic performance.

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