



Eye movements selective for spatial frequency and orientation during active visual search

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ABSTRACT

Visual search can simply be defined as the task of looking for objects of interest in cluttered visual environments. Typically, the human visual system succeeds at this by making a series of rapid eye movements called saccades, interleaved by discrete fixations. However, very little is known on how the brain programs saccades and selects fixation loci in such naturalistic tasks. In the current study, we use a technique developed in our laboratory based on reverse-correlation¹ and stimuli that emulate the natural visual environment to examine observers' strategies when seeking low-contrast targets of various spatial frequency and orientation characteristics. We present four major findings. First, we provide strong evidence of visual guidance in saccadic targeting characterized by saccadic selectivity for spatial frequencies and orientations close to that of the search target. Second, we show that observers exhibit inaccuracies and biases in their estimates of target features. Third, a complementarity effect is generally observed: the absence of certain frequency components in distracters affects whether they are fixated or mistakenly selected as the target. Finally, an unusual phenomenon is observed whereby distracters containing close-to-vertical structures are fixated in searches for nonvertically oriented targets. Our results provide evidence for the involvement of band-pass mechanisms along feature dimensions (spatial frequency and orientation) during visual search.

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1. Introduction

It is well established by many physiological studies that neurons in various stages of the visual pathway are selective for spatial frequency and orientation attributes of visual stimuli. Selectivity for spatial frequency is present in early stages of the visual pathway and is refined in later ones, i.e. broad tuning at the level of the retina (Enroth-Cugell & Robson, 1966; Kuffler, 1953) and relatively narrower tuning in the visual cortex (Campbell, Cooper, & Enroth-Cugell, 1969; DeValois et al., 1982; Schiller, Finlay, & Volman, 1976). Tuning for orientation is a principal characteristic of cells in the visual cortex; neurons located in earlier stages, including in the lateral geniculate nucleus, have not been found to be orientation tuned (Hubel & Wiesel, 1962, 1968).

Psychophysical studies have further shown that spatial frequency and orientation are important features in visual processing,

generally using contrast sensitivity (Campbell & Robson, 1968; Graham & Nachmias, 1971), masking (Campbell & Kulikowski, 1966; Stromeyer & Julesz, 1972; Wilson, McFarlane, & Phillips, 1983), and spatial adaptation (Blakemore & Campbell, 1969; Blakemore, Carpenter, & Georgeson, 1970; Snowden, 1992; Tolhurst, 1972) paradigms. For example, Campbell and Robson (1968) conducted detection and discrimination tasks using gratings (e.g. sine-, square-waves, and so on) and showed that observers' contrast thresholds were directly related to the harmonic Fourier components of the gratings. They postulated the existence of independent band-pass mechanisms selective for spatial frequencies. Using stimuli consisting of rapid sequential presentations of sinusoidal gratings at random orientations and spatial phase, Ringach (1998) showed that observers' tuning for orientation generally presented a "Mexican hat" distribution peaking at orientations close to the orientation observers had to report, with valleys at either side of the peak.

Furthermore, studies of attention in visual search have demonstrated, through measurements such as reaction time and accuracy (percent correct), that spatial frequency and orientation can indeed guide visual attention (Sagi, 1988; Treisman & Gelade, 1980; Wolfe, 1998, chap. 1; Wolfe & Horowitz, 2004). Search efficiencies in many

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¹ For an explanatory discussion of the reverse-correlation technique, see Eckstein and Ahumada (2002), Ringach and Shapley (2004), Neri, Parker, and Blakemore (1999), and Chichilnisky (2001).

tasks were found to depend on target-distracter discriminability and distracter homogeneity along these feature dimensions (Foster & Ward, 1991; Verghese and Nakayama, 1994; Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992). Some asymmetries were also observed (Foster & Ward, 1991; Treisman & Gormican, 1988; Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992); for instance, the detection of a tilted line among vertical lines was shown to be easier than an otherwise identical search for a vertical line among tilted lines.

However, many of these previous search studies, despite intending to elucidate visual search, have avoided the analysis of eye movements, either as a result of using short stimulus display times or by instructing observers to keep their eyes still. The importance of incorporating eye movements to study observer strategies in visual search has been emphasized in the recent years (Findlay & Gilchrist, 2003; Geisler, Perry, & Najemnik, 2006; Rajashekar, Bovik, & Cormack, 2006; Zelinsky & Sheinberg, 1997). Observers naturally move their gaze when searching for a target and it has even been demonstrated in a few tasks that observers opt to perform eye movements even when such strategy is not optimal (Findlay, 1997; Findlay & Gilchrist, 1998).

A fundamental issue in earlier studies of eye movements in search has been whether saccades are visually guided. There have been somewhat disparate findings reported in the literature (Findlay, 1997; Findlay & Gilchrist, 2003; Hooge & Erkelens, 1999; Motter & Belky, 1998; Shen, Reingold, & Pomplun, 2000; Zelinsky, 1996; Zelinsky, Rao, Hayhoe, & Ballard, 1997). For instance, Motter and Belky (1998) discovered in experiments using tilted bars that saccades landed within 1 deg of the center of the target or of the distracters having similar features as the target. Yet, when using horizontal and vertical bars of different colors, Zelinsky (1996) found that distractors presenting no similarities in color and orientation with the search target were fixated almost as many times as those distractors presenting similarities (45% vs. 55%). Moreover, others have found different degrees of guidance. For example, Williams discovered that observers had a strong inclination to direct saccades to elements of the display having the same color as the target, while information on target size and shape were weakly used (Williams, 1967; Williams & Reingold, 2001). Scialfa and Joffe (1998) showed in experiments using tilted bars where targets and distractors differed in either contrast (black or white) or orientation (± 45 deg), that observers were more likely to direct their saccades to distractors that shared similar contrast as the target.

The question we have sought to address in our study has been whether saccadic targeting and target selection are guided by spatial frequency and orientation during visual search. We have hypothesized that visual search is effected by local spatial frequency and orientations in the objects being searched. An efficient experimental design presented previously (see Tavassoli, van der Linde, Cormack, & Bovik, 2007), extending earlier techniques (Ahumada, 1996; Eckstein, Beutter, Pham, Shimozaki, & Stone, 2007; Ludwig, Eckstein, & Beutter, 2007; Rajashekar et al., 2006), is used to study the behavior of humans seeking a grating of known characteristics embedded in noise with an amplitude spectrum closely resembling that found in images of natural scenes (Field, 1987). Note that the use of noise as distractors rather than geometric forms, gratings or real-world objects as used in many previous visual search studies, permits a much larger set of distracting items that possess differences across various feature dimensions (e.g. luminance, contrast, spatial frequency, orientation, color if colored stimuli were used, and so on).

2. Methods

2.1. Observers

Three male observers (aged 26–30) were tested in our experiments, of whom two were experienced (authors AT and IVDL)

and one was naïve to the purpose of the study (AJS), each with normal or corrected-to-normal vision. Each observer completed 10,500 trials (15 sets of 700 trials, each set with a different search target) over a period of several months.

2.2. Apparatus

Stimuli were presented on a 21" grayscale monitor (Image Systems Corp., Minnetonka, MN) driven by a Matrox Parahelia graphics card (Matrox Graphics Inc., Dorval, Québec, Canada) at a screen resolution of 1024×768 pixels, a grayscale resolution of 8 bits per pixel, and a refresh rate of 60 Hz. The screen was placed 134 cm from the observer and subtended a visual angle of 16×12 deg, giving approximately 1 min of arc per screen pixel. The luminance output was gamma-corrected and the ambient illumination in the laboratory was kept constant for all observers.

An SRI/Fourward Generation V Dual Purkinje eye tracker was used to record eye movements. This device has accuracy of better than 10 min of arc, a precision of about 1 min, and a response time of about 1 ms. A bite bar and forehead rest were used to minimize head movements. The output of the eye tracker was first low-pass filtered using a hardware Butterworth filter, with a 100 Hz cutoff to eliminate extraneous high frequency noise in the recording environment, and then sampled by a host computer at 200 Hz with a National Instruments data acquisition card.

2.3. Visual stimuli

Our 15 search targets were 64×64 pixel Gabor patches of spatial frequency 2, 4, and 8 c/deg with bandwidths 1, .5, and .25 octaves, respectively, oriented anticlockwise from the vertical at 0, 20, 45, 70 and 90 deg (see first row of Fig. 1 for examples of targets). Note that the bandwidths of the Gabor patches were such that targets of the same size were obtained. Also we would like to point out that the Gabors had isotropic envelopes. One hundred 7×7 tile mosaics were generated offline by creating one hundred 544×544 pixel $1/f$ noise images (with an amplitude spectrum of the form $1/f^a$ with $a = 0.8$) and then superimposing gray borders 12 pixels in width (Fig. 2b). On each trial, the Gabor target was added to a randomly selected tile of the $1/f$ noise grid (Fig. 2a and b; also see second row of Fig. 1 for examples of targets with added noise).

2.4. Procedure

Eye movements were recorded while observers searched the stimulus grid for the Gabor target. At the beginning of each experiment, observers were told which Gabor patch was the search target. Stimuli were presented for 5 s on the calibrated grayscale monitor using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Observers were required to fixate a central fixation mark to initiate each trial. Observers then searched the stimulus grid, and maintained their final fixation on the tile they believed to contain the target (over 80% of the dwell-times observed for final fixations were equal to or longer than 600 ms, an upper bound on typical fixation durations, indicating that observers were deliberately selecting a single tile as containing the target on most trials). The signal-to-noise ratio of stimuli was adjusted for each observer (i.e. we co-varied the contrast of the target and of the noise such that the entire grayscale was used but never exceeded) using the QUEST adaptive procedure (Watson & Pelli, 1983) to yield an average correct target detection rate close to 68%.

2.5. Analysis method

Observers typically performed close to five fixations on average per trial (fixations between tiles were disregarded), hence visiting

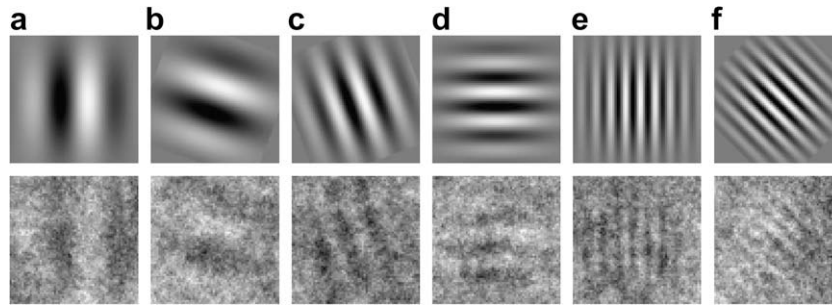


Fig. 1. Target embedded in noise. Examples of search targets, without (first row) and with (second row) the addition of noise, are shown. These targets are Gabor patches with the following [spatial frequency, orientation] characteristics: (a) {2 c/deg, 0 deg}, (b) {2 c/deg, 70 deg}, (c) {4 c/deg, 20 deg}, (d) {4 c/deg, 90 deg}, (e) {8 c/deg, 0 deg}, and (f) {8 c/deg, 45 deg}. Note that the images in the second row were generated using a higher signal-to-noise ratio than those used during the experiments for better visibility.

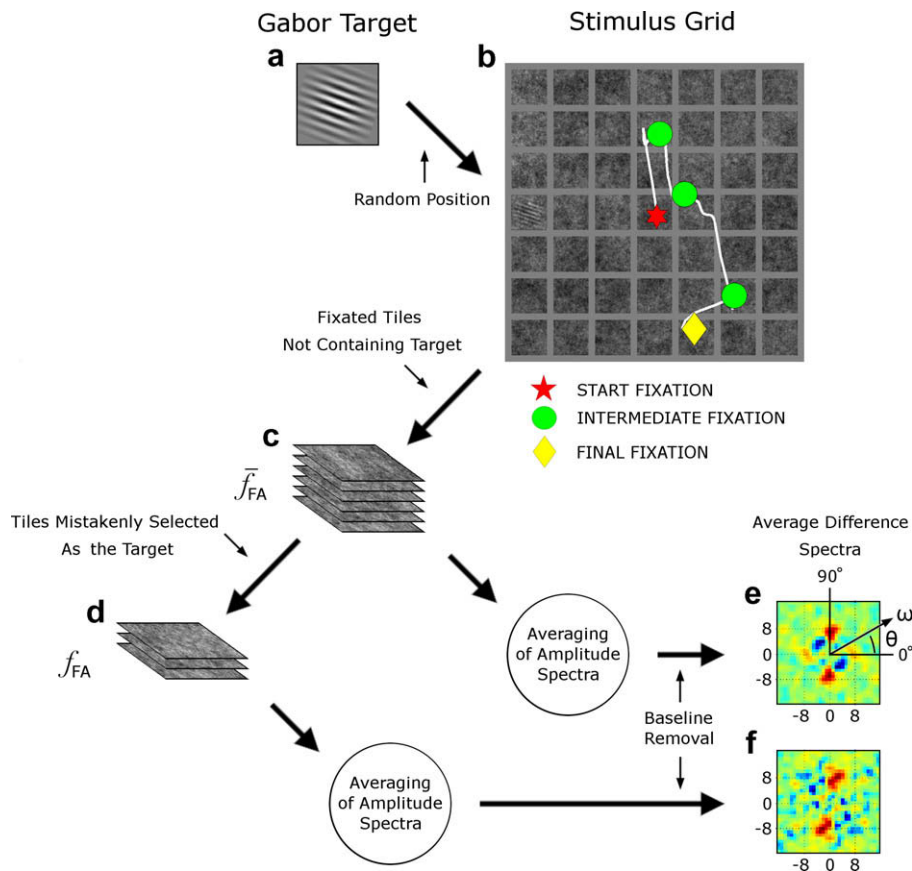


Fig. 2. Stimulus creation, data capture, and data analysis. (a) A Gabor patch used as a target (b) was added to a randomly selected tile of the $1/f$ noise grid. Observer eye movements were recorded while they searched for the target. A representative scan path is shown for a trial in which the observer did not find the target, located in the center of the leftmost column. (c) Fixated tiles that did not contain the target constitute our nonfoveal false alarm category, and (d) a subset of these tiles, which were mistakenly selected at the end of the trials as the target by the observer, constitute our foveal false alarm category. (e and f) Average difference spectra were computed by averaging the amplitude spectra of noise tiles in each category and subtracting the spectral baseline (see text). The x- and y-axis of the average difference spectra represent the horizontal and vertical components of frequency omega, respectively. For example, a sinusoidal grating of frequency 8 c/deg oriented at 90 deg would have an amplitude spectrum with two peaks at (0; 8) and (0; -8).

tiles not containing the target (i.e. noise-only tiles) and in some trials selecting one such tile as the target; an example stimulus grid with representative eye movements for a single observer is shown in Fig. 2b. We were therefore interested in examining why some noise-only tiles were fixated whereas others were not? And second, why, at the end of some trials, was a noise-only tile mistakenly selected as the tile containing the target?

To answer these questions, we assume that each fixation (excluding the initial fixation at stimulus onset) involves two decisions: the decision to fixate a certain tile (and not the others), and the subsequent decision to either remain on that tile or continue searching. We consider that the former is based primarily on nonfoveal information and the latter is based primarily on foveal information. We therefore stored noise-only tiles that were fixated

while en route to the target and labeled them as “nonfoveal false alarms” (f_{FA}) (Fig. 2c). Additionally, noise-only tiles that were mistakenly selected as the target at the end of a trial were labeled as “foveal false alarms” (f_{FA}) – these necessarily being a subset of the nonfoveal false alarms (Fig. 2d). These signal-absent categories better reflect observer behavior than signal present categories (those composed of tiles that contained the target), since only patterns in the noise, corresponding to visual information that the observer took to imply the presence of a target, are used (Eckstein, Shimozaki, & Abbey, 2002). Further information on the employed taxonomy may be found in our previous work (Tavassoli et al., 2007).

We computed the Fourier transform of each tile and averaged their amplitude spectra within category and observer. Because we used a finite number of $1/f$ noise tiles ($100 \times 7 \times 7 = 4900$) for the experiment, a spectral baseline is introduced in these averages, i.e. the expected amplitude spectrum that would be obtained by randomly sampling noise tiles would have a shape close to $1/f$. We therefore examined differences between the averages in our categories and the expected baseline. We obtained this baseline by averaging the amplitude spectra of all the 4900 noise tiles used to generate our stimuli. We then subtracted the baseline from the averages obtained in each category to form what we will refer to as *average difference spectra* (Fig. 2e and f); this process is similar to the amplitude spectrum correction method described by Willmore and Smyth (2003). These average difference spectra represent dominant (relative to the baseline) spatial frequencies (indicated by the distance from the origin, ω , see Fig. 2e) and orientations (indicated by the angle, θ , from vertical orientation, 0 deg, see Fig. 2e of the noise tiles within each category. Additionally, we zeroed the 0 and 1 c/deg components (only 0 c/deg was zeroed for the results with the 2 c/deg Gabors), then smoothed each image with a 3×3 pixel Gaussian mask with $\sigma = 0.9$ pixel to improve visualization. Setting the very low frequencies (0 and 1 c/deg) to zero simply allows the full color map to be used for the more interesting spectral structures in surrounding frequency components.

Note that directly averaging noise tiles (i.e. in the spatial domain) within each category and observer produced similar outcomes as those reported in earlier psychophysical detection studies (Beard & Ahumada, 1999; Solomon, 2002) whereby the average images contain some target-like structures in the case of search for lower frequency targets but no relevant structure for search for higher frequency targets. We therefore focused our study on the spectral analysis.

3. Results

Figs. 3 and 4 show the average difference spectra for the nonfoveal and foveal false alarm categories obtained for search experiments using Gabor targets of spatial frequency (a) 2, (b) 4, and (c) 8 c/deg, oriented anticlockwise from the vertical at 0 (first column), 20 (second column), 45 (third column), 70 (fourth column), and 90 deg (fifth column). For each observer and set of 700 trials, amplitude spectra were created using about 210 and 2800 noise tiles for the foveal and nonfoveal categories, respectively. A hue color map was used to visualize the data. The yellow-red and cyan-blue ranges of the color map indicate frequency components having amplitudes above (peaks) and below (valleys) the spectral baseline, respectively (i.e. above and below the expected amplitude spectrum for a random observer). Shades of green indicate frequency components close to the baseline.

Distinct local structures are obtained in all of the average difference spectra, i.e. the peaks cover regions of the spectrum close to the spatial frequency and orientation of the search target. We have fitted each average difference spectrum with the amplitude spectrum of a Gabor, using the MATLAB *fminsearch* function with spa-

tial frequency, bandwidth, orientation, and aspect ratio as input parameters (we have added a figure in the [Supplementary materials](#) showing the fits for data obtained for experiments using 8 c/deg Gabor targets). Note that this procedure is equivalent to Gaussian fitting the average difference spectra. Table 1 shows the spatial frequency (second main column), orientation (third main column), and bandwidth (fourth main column) characteristics of the obtained fits that we have used as estimates of the characteristics of the peak regions for the nonfoveal (left sub-column of each main column) and foveal (right sub-column of each main column) categories. The results across all observers for experiments using Gabor targets of spatial frequency 2 (first row), 4 (second row), and 8 c/deg (third row) are presented as Mean \pm Standard Deviation. Note that distances between the orientation of targets and the orientation of estimates are shown in the third main column of Table 1, instead of the actual orientation estimates of the peak regions. The results show that observers are selective for ranges of spatial frequencies (see Table 1, second and fourth main columns) and orientations (see Table 1, third and fourth main columns) that include the central frequency and orientation of the search target. However, the results also reveal that observers have inaccuracies in their estimates of target features during saccadic targeting and foveal target selection. These inaccuracies are in general worse in the nonfoveal compared to the foveal categories. Fig. 5 provides illustrated examples of some of these inaccuracies and biases. Examples of average difference spectra are shown illustrating (a) uncertainties (reflected by radial and rotational smearing) and (b) offsets (mostly occurring nonfoveally but corrected in the foveal category). The pink line indicates the orientation of the search target. For better visibility, the average difference spectra were halved perpendicularly to the pink line.

Furthermore, the peaks in the average difference spectra are flanked by well localized valleys present in the surround (more visible for the 4 and 8 c/deg target searches). To examine the location of the valleys relative to the peaks, we first rotated each average difference spectrum by the negative of the estimated orientation of its peak regions so as to align all the average difference spectra along the same axis (we picked the vertical axis as reference). Then, for each target spatial frequency condition, we averaged the aligned average difference spectra for all observers combined. The results are shown in Fig. 6a (see [Supplementary materials](#) for results obtained for each observer separately).

Interestingly, we also found that all three observers have strong peaks close to 0 deg in the nonfoveal categories for searches for the nonvertical Gabor targets, in addition to peaks close to that of the search targets. This vertical bias is present in observers' data for searches for Gabors of spatial frequency 8 c/deg oriented at 45, 70, and 90 deg (see last three columns of Fig. 3). The additional peaks appear to vanish in the foveal category, i.e. once observers fixated the noise tiles (see last three columns of Fig. 4). The effect is best illustrated for the 90 deg Gabors in Fig. 6b, where tightly tuned peaks close to 0 deg are present in the nonfoveal average difference spectra along with peaks close to 90 deg (second row), and then the additional peaks fade away in the foveal average difference spectra (first row). Note that the additional components are close to the spatial frequency of the search target.

Finally, we were curious to examine the effects of eccentricity and saccade order on saccadic targeting. We binned the noise tiles in the nonfoveal category by eccentricity and by order, separately (see [Supplementary materials](#) for examples). We found that the structures present in the average difference spectra in each bin, using either binning approaches, were generally similar to ones in the average difference spectra obtained without binning, although more trials would be needed to produce better convergence of the averages in some bins. When binning by saccade length, we noticed in the average difference spectra some instances

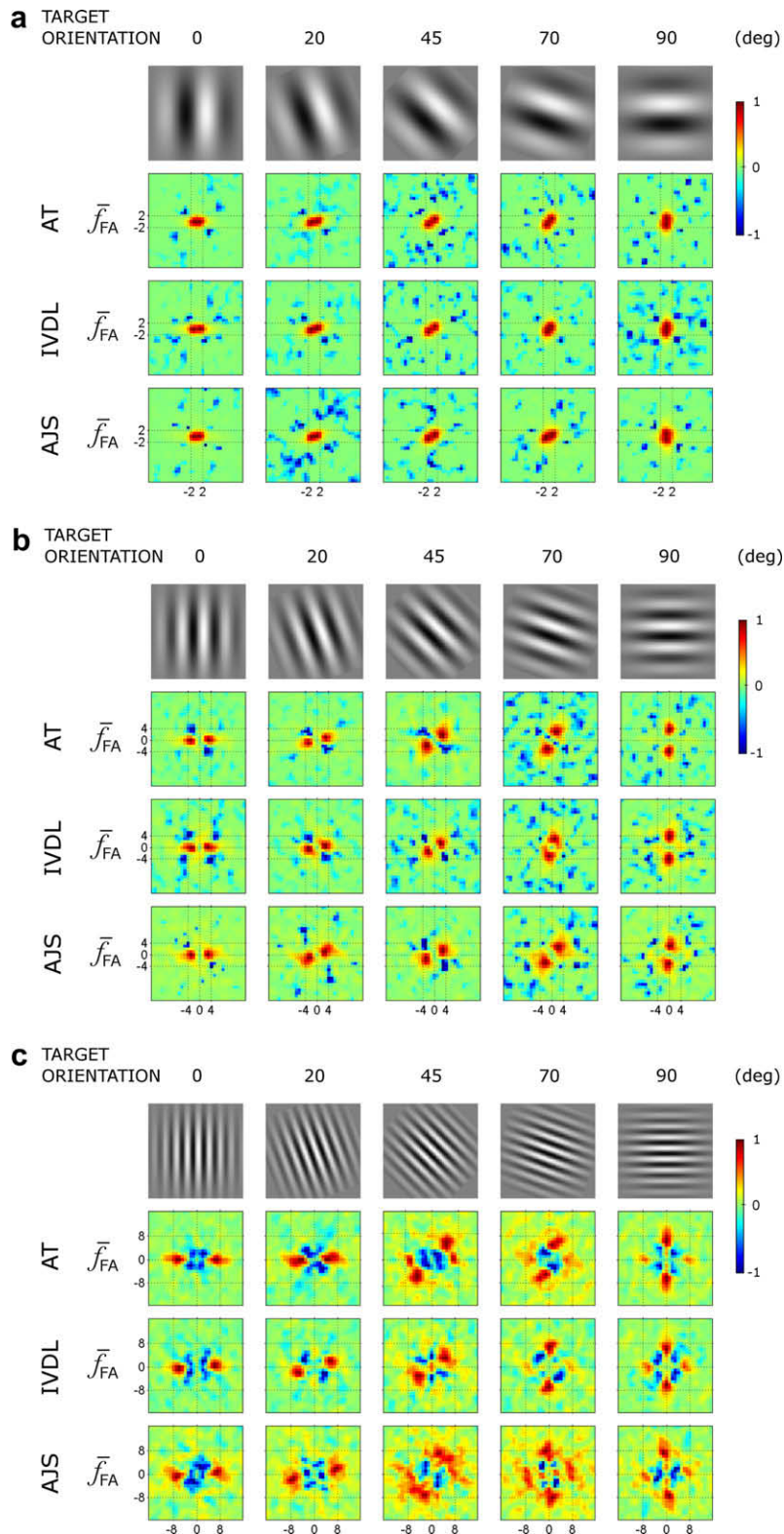


Fig. 3. Saccadic guidance. Nonfoveal average difference spectra, smoothed and contrast-stretched (between -1 and 1 , for visual enhancement), are shown for sets of 700 trials for visual searches for Gabor targets of spatial frequency (a) 2, (b) 4, and (c) 8 c/deg, oriented anticlockwise from the vertical at 0 (first column), 20 (second column), 45 (third column), 70 (fourth column), and 90 deg (fifth column). For each observer and each set of trials, the spectrum was created using about 2800 noise tiles. A hue color map was used to visualize the data. The yellow-red and cyan-blue ranges of the color map indicate frequency components having amplitudes above and below the spectral baseline, respectively (i.e. above and below the expected amplitude spectrum for a random observer). Shades of green indicate frequency components close to the baseline. The axes of the average difference spectra represent the horizontal and vertical projections of frequency components.

in which peaks for larger eccentricity bins were lower in spatial frequency than for smaller eccentricities. Although the latter effect may be expected due to the falloff of resolution in peripheral

vision, however, the effect was not reliable perhaps due to the limited number of noise tiles in each bin, especially for larger saccade lengths.

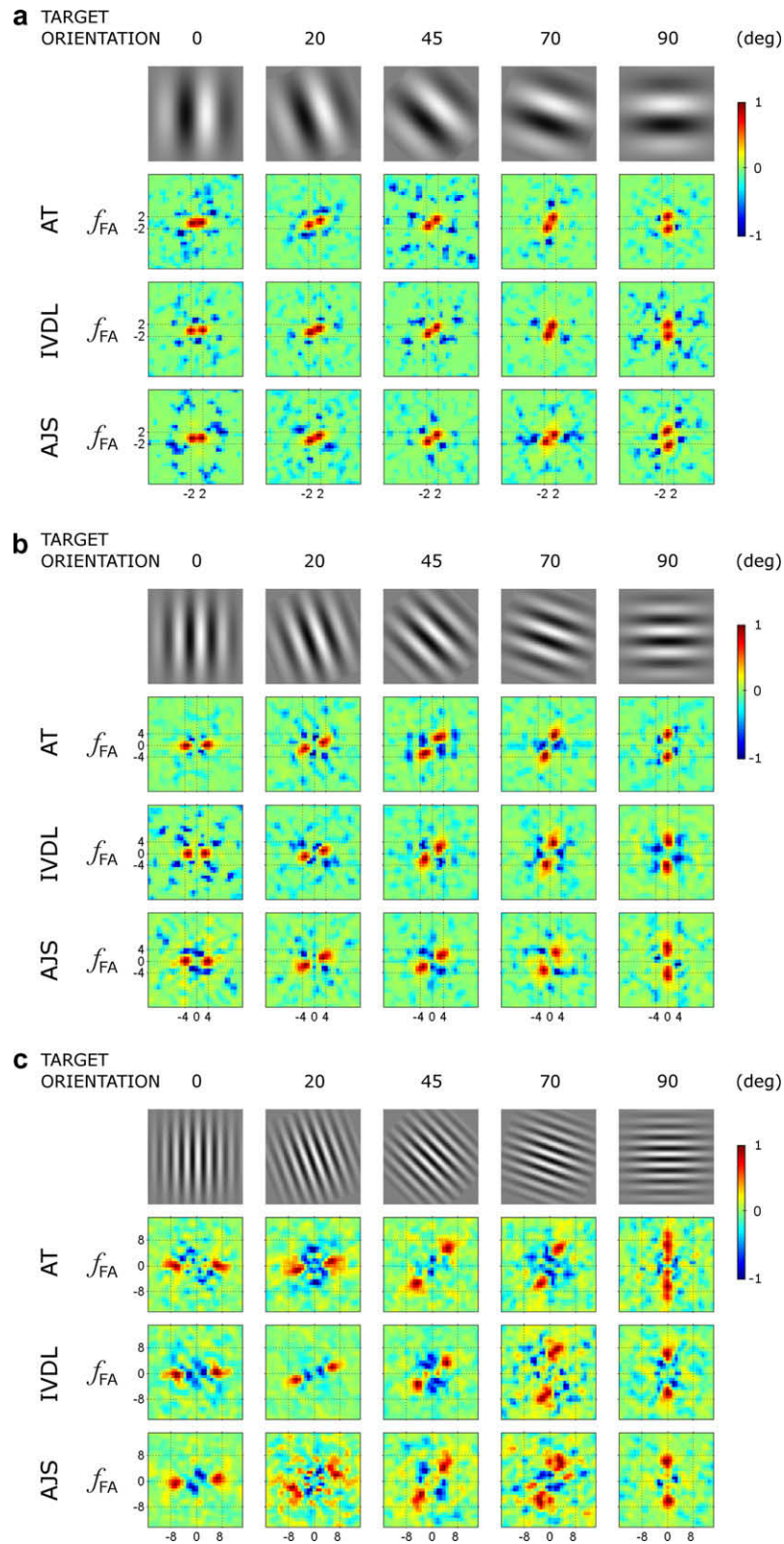


Fig. 4. Target Selection. Foveal average difference spectra, smoothed and contrast-stretched (between -1 and 1 , for visual enhancement), are shown for sets of 700 trials for visual searches for Gabor targets of spatial frequency (a) 2, (b) 4, and (c) 8 c/deg, oriented anticlockwise from the vertical at 0 (first column), 20 (second column), 45 (third column), 70 (fourth column), and 90 deg (fifth column). For each observer and each set of trials, the spectrum was created using about 210 noise tiles each.

4. Discussion

The aim of the current paper was primarily to explore saccadic targeting and target selection in naturalistic visual search

tasks, more precisely when human observers search for a Gabor target with known characteristics embedded in a grid of $1/f$ noise (which has a similar falloff in amplitude spectrum as natural images). We are interested in understanding what at-

Table 1

Estimated characteristics of peak regions. The average difference spectra were each fitted with the amplitude spectrum of a Gabor. Spatial frequency (second main column), orientation (third main column), and bandwidth (fourth main column) characteristics of the obtained Gabor fits were used as estimates of the characteristics of the peak regions for the nonfoveal (left sub-column of each main column) and foveal (right sub-column of each main column) categories. The results across all observers are presented as Mean ± Standard Deviation for the experiments in which the Gabor targets of spatial frequency 2 (first row), 4 (second row), and 8 c/deg (third row) were used. Note that instead of the actual orientation estimates of the peak regions, distances between the orientations of the target and the orientation estimates are presented (third main column).

Target frequency (c/deg)	Spatial frequency (c/deg)		ΔOrientation (deg)		Bandwidth (octaves)	
	Nonfoveal	Foveal	Nonfoveal	Foveal	Nonfoveal	Foveal
2	1.0 ± 0.2	1.5 ± 0.4	11.5 ± 9.7	7.3 ± 6.8	1.1 ± 0.6	1.3 ± 0.2
4	3.0 ± 0.4	3.4 ± 0.4	7.7 ± 6.2	4.0 ± 4.4	1.2 ± 0.3	0.8 ± 0.2
8	6.3 ± 0.6	6.5 ± 0.6	8.6 ± 7.2	3.9 ± 2.6	0.9 ± 0.4	0.6 ± 0.3

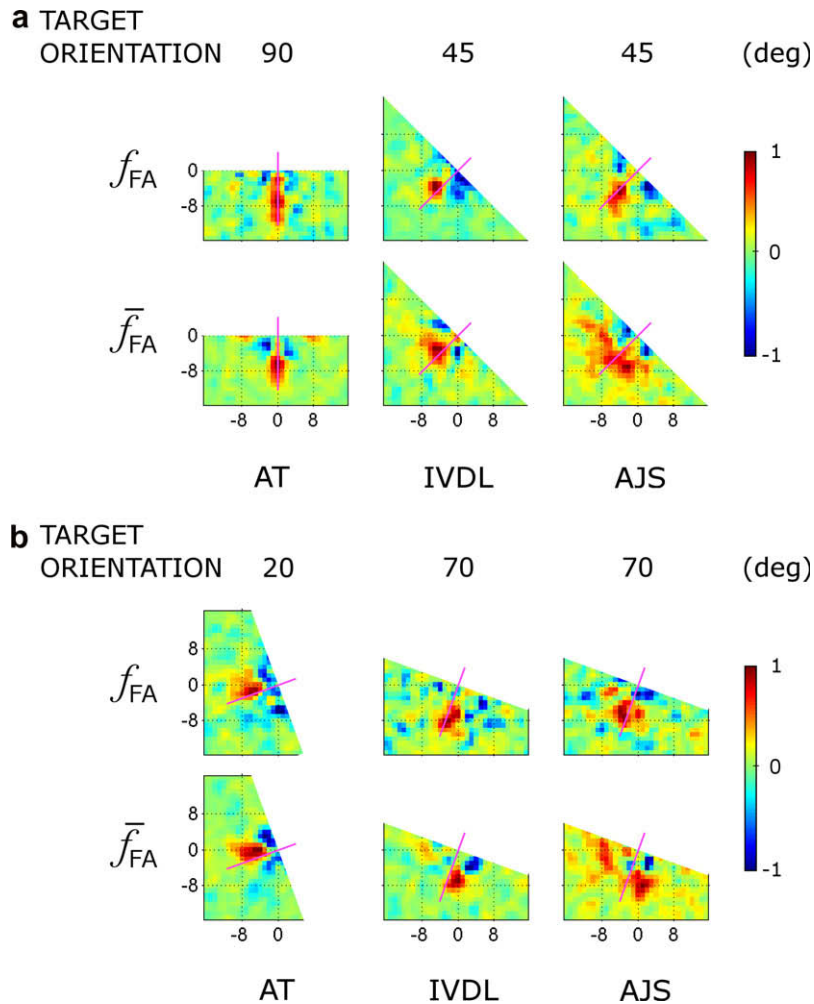


Fig. 5. Uncertainties and offsets. Observers exhibit inaccuracies in their estimates of target features. Examples of average difference spectra are shown illustrating (a) uncertainties (reflected by radial and rotational smearing) and (b) offsets (mostly occurring nonfoveally but corrected in the foveal category). The pink line indicates the orientation of the search target. For better visibility, the average difference spectra were halved perpendicularly to the pink line.

tracts fixations and how target candidates are selected upon fixation.

Our results clearly provide evidence of visual guidance in saccadic programming during search. A *similarity* effect (as defined by Findlay & Gilchrist, 2003) is revealed, showing that saccades are guided, on average, to distracters (here, noise tiles) presenting featural similarities to the Gabor target. In particular, we demonstrate saccadic selectivity for spatial frequencies and orientations close to the central frequency and orientation of the search target, i.e. the average difference spectra for fixated noise tiles show peaks localized in spatial frequency and orientation close to that of the target (Figs. 3 and 4; see also Table 1).

Furthermore, observers exhibit inaccuracies in their estimates of target attributes (see Table 1 and Fig. 5). These errors are revealed by the uncertainties and offsets in the average difference spectra, illustrated in the data by elongations in spatial frequency and orientation bandwidths; radial spread corresponding to less selectivity in spatial frequency and rotational smearing to less tuning in orientation. In many cases, offsets in estimates of target features occur nonfoveally but are corrected upon fixation, e.g. observers AJS and IVDL are attracted to noise tiles containing predominantly near-horizontal (close to 90 deg) structures when looking for a Gabor target of spatial frequency 8 c/deg oriented at 70 deg, then foveally select those with prevalent structures close

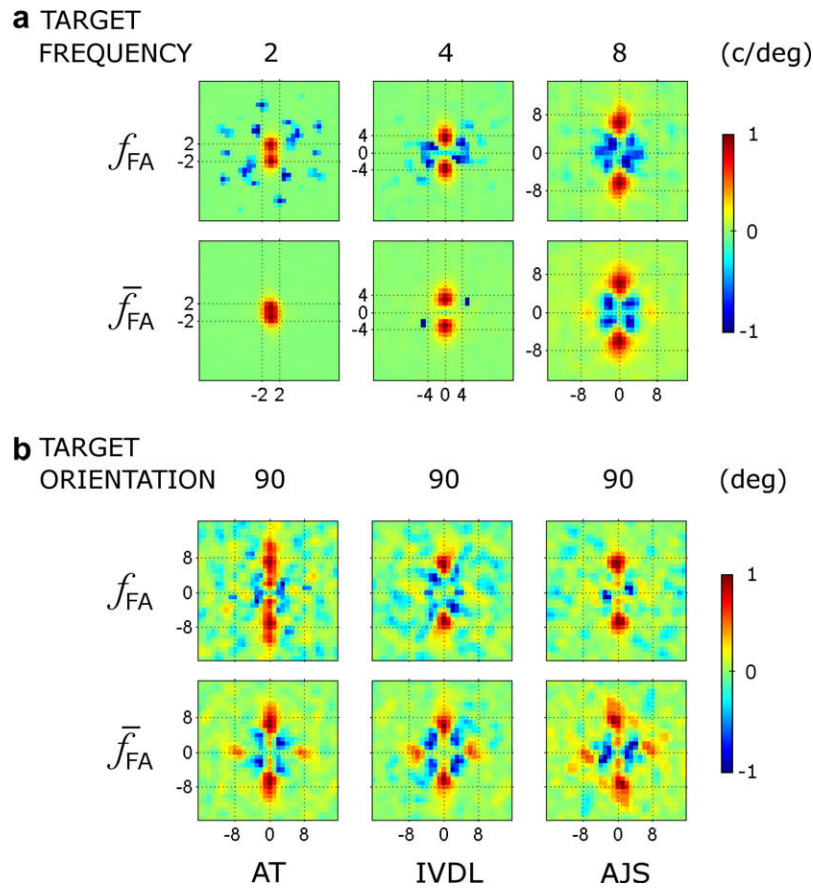


Fig. 6. Complementarity effect and unusual phenomenon. (a) Averages of aligned average difference spectra are shown for 2 c/deg, 4 c/deg, and 8 c/deg Gabor search experiments for observers combined. (b) Examples of an unusual phenomenon are illustrated whereby the average difference spectra show the presence of additional peaks close to 0 deg for the nonfoveal category (second row) but vanishing in the foveal category (first row).

to 70 deg (see second and third columns of Fig. 5b). Inaccuracies in observer estimates have been reported in psychophysical tasks (Ringach, 1998) and appear in psychophysical reverse-correlation data for detection tasks (Solomon, 2002).

Interestingly, a marked *complementarity* effect is found in much of our data; that is, the absence of various spatial frequencies and orientations appears to influence whether a noise tile is fixated and selected as target candidate upon fixation. In fact, the average difference spectra for fixated noise tiles contain valleys localized at spatial frequencies and orientations neighboring the peaks, more consistently for the 4 and 8 c/deg Gabor target experiments (Fig. 6a). The existence of valleys in the results may signify that observers are often disregarding noise tiles containing frequency components surrounding their estimates of the target's orientation and spatial frequency. Alternatively, it could reflect that a reduced presence of particular frequency components may have an enhancing effect in the detection of the components of interest. In general, it appears that the valleys in the average difference spectra tend to be at lower frequencies than the peaks for the higher frequency (8 c/deg) Gabor search experiments and that this tendency is reversed for lower frequency search experiments. This observation is consistent with findings in masking experiments where it was found that the most effective masks for low frequency test gratings were at higher frequencies and vice versa (Wilson et al., 1983); and, comparable to the “Mexican hat” orientation profiles found by Ringach (1998) in psychophysical experiments, although he reported that the effect disappeared for higher frequencies.

Curiously, there is, on average, an unusual presence of close-to-vertical structures in fixated noise tiles for visual searches for

nonvertical Gabors of spatial frequency 8 c/deg, i.e. the average difference spectra for the nonfoveal category present additional peaks close to the spatial frequency of the search target but at an orientation of close to 0 deg (Fig. 6b; see also last three columns of Figs. 3 and 4). This effect could be a simple bias for vertical structures during saccadic targeting. It could also reflect possible facilitation when vertical structures are present in the targeted noise tiles; as a comparison, Sillito, Grieve, Jones, Cudeiro, and Davis (1995) showed that responses of many neurons in V1 to their preferred orientation could be enhanced by introducing a surrounding field containing a pattern at significantly different orientation than the center. Alternatively, it could be the consequence of double-orientation tuning in nonfoveal detection; in analogy, Shevelev, Lazareva, Novikova, Tikhomirov, and Sharaev (1994) demonstrated the existence of neurons in V1 that have a main preferred orientation and an additional preferred orientation. The additional frequency components vanish once observers fixated the noise tiles.

5. Conclusions

Our results provide compelling evidence for band-pass mechanisms in saccadic targeting and target selection during visual search, in particular for grating-like targets. Furthermore, selectivity along feature dimensions (here, spatial frequency and orientation) shows inaccuracies, offsets, and curious biases. These errors are to some extent corrected during the foveal decision process. Furthermore, it appears that the presence or absence of various spectral components, other than those close to that of the search

target, influence the guidance of saccades. We find that the absence of certain surround frequency components or the presence of near-vertical structures (i.e. components close to 0 deg) in the noise tiles attracts observer fixations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2008.10.005.

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