The effect of retinal image slip on peripheral visual acuity

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Retinal image slip promoted by fixational eye movements prevents image fading in central vision. However, in the periphery a higher amount of movement is necessary to prevent this fading. We assessed the effect of different levels of retinal image slip in peripheral vision by measuring peripheral visual acuity (VA), with and without crowding, while modulating retinal image slip by using gaze-linked stimuli. Measurements were carried out at four isoeccentric positions at 5 and at 10 degrees eccentricity. Gaze position was monitored throughout using an infrared eyetracker. The target was presented for up to 500 msec, either with no retinal image slip, with reduced retinal slip, or with increased retinal image slip. Without crowding, peripheral visual acuity improved with increased retinal image slip compared with the other two conditions. In contrast to the previous result, under crowded conditions, peripheral visual acuity decreased markedly with increased retinal image slip. Therefore, the effects of increased retinal image slip are different for simple (noncrowded) and more complex (crowded) visual tasks. These results provide further evidence for the importance of fixation stability on complex visual tasks when using the peripheral retina.

Keywords: eye movements, visual acuity, peripheral retina, crowding, retinal image slip

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Introduction

Even when the eye is fixating a point target it is not totally motionless because fixational eye movements keep it moving incessantly. There are three types of fixational eye movements: tremor, drift, and microsaccades. Tremor is an aperiodic, wave-like motion with velocities of approximately 20 minutes of arc/sec and amplitude smaller than the diameter of a foveal cone. Drift movements occur simultaneously with tremor and are larger and slower than tremor, with velocities in the order of 4 minutes of arc/sec and mean amplitudes of around 2–5 minutes of arc. This amplitude corresponds to a movement of the retinal image across a dozen photoreceptors. Fixational microsaccades, also called 'flicks' in early studies, are small and fast eye movements that occur during voluntary fixation. Typically with peak velocities above 600 minutes of arc/sec, their amplitude ranges from 1 to 120 minutes of arc and they carry the retinal image across a width corresponding to several dozen to several hundred photoreceptors (Carpenter, 1988; Martinez-Conde, Macknik, & Hubel, 2004).

Despite this incessant retinal motion, images are perceived as static and clear. The visual system has mechanisms to deal with movement and the eventual blur resultant from the retinal image slip caused by fixational eye movements (Ahissar & Arieli, 2001). These mechanisms fail when the amount of movement is above their capacity of neutralization (Burr, 1980). In these conditions, the image is perceived as blurred due to motion smear. An immediate consequence of blur is a diminution of resolution (Burr & Ross, 1982; Morgan & Benton, 1989).

The highest resolution of the eye is obtained in the fovea where the density of receptors is very high. The limit of resolution depends on the target: different values are found for a single line, a Vernier target or a grating consisting of multiple parallel lines (Keesey, 1960). Even for gratings, the visual resolution is finer than the theoretical resolution predicted based on the number of receptors stimulated by the visual target (Keesey, 1960; Williams & Coletta, 1987). It has been proposed that this is due to the movement of the visual target caused by the fixational eye movements across groups of receptors on the retina. With fixational eye movements, the resulting

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signal is a mean of the combined activity of all receptors stimulated and not only those corresponding to the size of the visual target (Andersen & Weymouth, 1923; Keesey, 1960). This mechanism also explains why it is possible to discriminate Vernier offset of about 1 second of arc while the finest foveal receptors subtend about 24 seconds of arc (Berry, 1948; Keesey, 1960).

Another important function of the fixational eye movements is to counteract visual adaptation. Visual adaptation is a mechanism by which sensory neurons lose sensitivity when exposed to a constant high intensity stimulus, giving a response that declines with time. For example, if a bright target is kept steady on the retina the resultant neuronal response decreases with time, whereas it generates continuous strong responses if it moves about the retina causing abrupt changes in retinal receptor illumination (Barlow, 1952, 1997; Hubel & Wiesel, 1959; Martinez-Conde et al., 2004). The movement of the retinal image across receptors caused by fixational eye movements changes the illumination in retinal receptors generating "on" and "off" responses in the neural pathways associated with the stimulated retinal receptors preventing retinal image fading (Barlow, 1952; Coppola & Purves, 1996; Ditchburn, Fender, & Mayne, 1959; Hubel & Wiesel, 1959; Martinez-Conde et al., 2004; Rucci, Iovin, Poletti, & Santini, 2007; Sharpe, 1972; Tulunay-Keesey, 1982). Image fading in the central retina can only be demonstrated with sophisticated laboratory equipment. However, in the periphery image fading can be easily experienced during a relatively short period of careful fixation. This phenomenon, known as Troxler's fading, shows that in the peripheral retina fixational eye movements are insufficient to prevent retinal adaptation (Clarke, 1957, 1960, 1961).

From the center to the periphery of the retina, the interreceptor separation and the center-to-center separation of the receptive fields increases (Curcio & Allen, 1990; Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987; Drasdo, 1989; Hubel & Wiesel, 1960), and visual resolution decreases (Anderson, Mullen, & Hess, 1991; Green, 1970). Several studies have measured resolution in the peripheral retina with static (Banks, Sekuler, & Anderson, 1991; Green, 1970; Mandelbaum & Sloan, 1947; Toet & Levi, 1992) and moving targets (Bex, Dakin, & Simmers, 2003; Brown, 1972; Falkenberg, Rubin, & Bex, 2007). Brown found that in peripheral retina visual resolution can be improved when a target has a velocity of approximately 10 deg/sec. The linear or rotational movement used in these studies is likely to be less effective than the more random movement promoted by fixational eye movements (Ditchburn & Drysdale, 1977; Rucci et al., 2007; Sharpe, 1972).

A limitation of these previous studies is that retinal image movement has been simulated by asking subjects to fixate a central target while a peripheral target is jittered (Bex et al., 2003; Falkenberg et al., 2007), whereas fixational eye movements cover a large range of directions and velocities (Barlow, 1952; Ditchburn et al., 1959; Hubel & Wiesel, 1959) that cannot be accurately simulated by simple target jitter. Here, we measure peripheral visual acuity for crowded and noncrowded targets moving in synchrony with the fixational eye movements to determine the effect of different levels of retinal image slip on peripheral visual acuity.

Methods

Observers

Seven observers participated: two authors (AFM, MDC) and five subjects naive to the purpose of this study. Five observers participated in each experiment; three were common to both experiments. No participants had any eye or neurological disease. All had normal or corrected-to-normal vision. The study conformed to the Declaration of Helsinki and was approved by the UCL research ethics committee. Subjects gave their informed consent before data collection.

Apparatus

Programs for running the experiment were written in the Matlab programming environment using elements of the Psychophysics toolbox (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Pelli, 1997). Stimuli were displayed on a 21-inch computer monitor (Trinitron GDM-F500R, Sony, Japan), with peak luminance of 98 cd/m^2, resolution of 1280 × 1024 pixels, and 100-Hz refresh rate. The stimulus was displayed within a central square window of 30 × 30 cm with a black background. For all experiments, the stimulus was a Landolt "C" with 80% Michelson contrast. The size of the stimulus was controlled by multiple Quest staircases, applied to each position independently (Brainard, 1997; Watson & Pelli, 1983).

Eye position was measured with an eyetracker (Eyelink I, SR Research, Mississauga, Ontario, Canada) using Eyelink software (version 2.04). This eyetracker consists of two infrared cameras, which are mounted on a headband and record eye position using the "bright-pupil" technique. A further camera tracks head motion with respect to infrared emitters mounted in front of the observer at the corners of the video display. Compensation for head motion is made so that a real position of gaze can be calculated. Eye position is measured at a temporal frequency of 250 Hz and the manufacturers report a gaze position accuracy of <0.5 deg. Samples were collected on the computer controlling the eyetracker and sent through an Ethernet link to a second computer. In the beginning of each block, the eyetracker was calibrated using a nine-point calibration grid followed by a drift correction. Validation was performed prior to stimulus display using the algorithms

provided with the eyetracker for this purpose. During each block, drift correction was performed every five trials. The heuristic filter of the eyetracker was enabled.

During stimulus presentation, the velocity of the target was modulated by a gain factor, where gain = v_{eye} / v_{target}. Four gain factors were used: 0 (no compensation of eye movements corresponds to the baseline condition), 0.1 (reduced retinal image slip), 1.0 (null retinal image slip), and 10 (increased retinal image slip). For each frame, a circular artificial scotoma was centered on the point of gaze. This ensured that the target did not become closer to the fovea than the specified eccentricity. Figure 1A shows the target window. The distance between the scotoma boundary and the target, *d,* remained constant in relation to the size of the gap ($d = 2.5 \times g$). Responses were given via a response box.

Procedure—Experiment 1

Observers sat 60 cm from the monitor and a chin rest was used to minimize head movements and to maintain a constant viewing distance. Observers viewed the display monocularly with an eye patch covering their nondominant eye. The dominant eye was assessed by a pointing test. Participants practiced the task until they were able to finish an entire block of trials with fewer than 10% of trials having large saccades (defined below).

Visual acuity was measured at four isoeccentric positions: right, left, up, and down, at two eccentricities, 5 and 10 degrees. The minimum number of blocks for each subject for the gaze contingent conditions was: 2 (eccentricities) × 3 (gains) × 3 (repetitions[1]) = 18 blocks. Each position was tested 60 times per block. The gain and the order of positions tested in each block were selected randomly. Each block started with an observer's button press and the first trial for each position was preceded by an auditory signal. The orientation of the Landolt C was generated at random with the gap in one of four cardinal positions: up, down, right, or left. Participants were asked to report the orientation of the target by means of a button press. Observers were instructed to respond after the target disappeared to reduce the number of large saccades being made. The sequence of events during each trial is shown in Figure 1B. The cue, a gaze contingent gray circle with 33% contrast and the same size as the target, was present at the eccentricity being tested. This cue duration was selected to maximize discrimination in the periphery (Cheal & Lyon, 1991). The cue disappeared after 100 msec and was replaced by the gaze contingent Landolt C presented up to a maximum of 500 msec. If during target presentation no response was given, it was abruptly replaced by a mask (no gaze contingent) that remained visible until any response. The target was visible only during fixations; it was replaced by a black screen during saccades. During frames in which the monitor was blanked, the target position was updated based on the real eye movement (not modulated by gain), to avoid possible positional errors in the first frame after a saccade.

A saccade was defined when eye velocity was greater than 30 deg/sec and/or acceleration was greater than 8500 deg/sec^2. These saccade detection criteria were used to allow small microsaccades during the measurements,

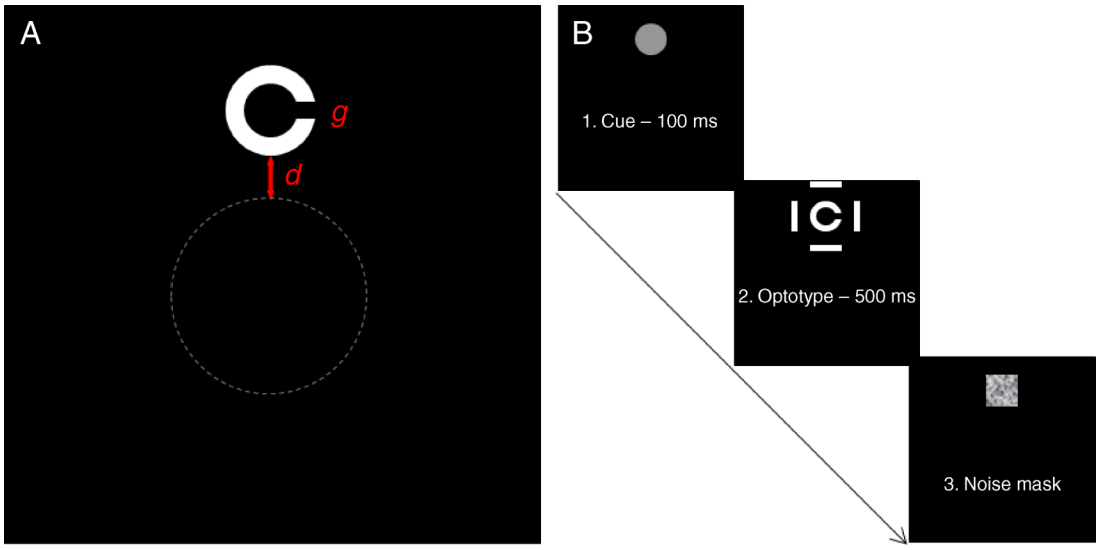

Figure 1. (A) Details of target window with the Landolt C (orientation—right). The dotted circle delimits the artificial scotoma; *g* represents the gap, equivalent to 1/5 of the Landolt C size; *d* represents the maximum distance that Landolt C could move before entering the area of the artificial scotoma. The size of the scotoma was varied such that: target size / *d* = 0.5. (B) Sequence of stimulus presentation; the Landolt C was presented with and without flankers.

given their useful role in central vision (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; Rucci et al., 2007).

The delay between eye movement and screen update is 20 msec or less (Cornelissen, Bruin, & Kooijman, 2005). This means that the distance between the eye and the target could be significantly reduced if a fast eye movement (large saccade) occurred during this period. Trials where a "large saccade" occurred were repeated. "Large saccades" were defined when the velocity was higher than 100 deg/sec, corresponding to a saccade of approximately 1-deg amplitude and 25-msec duration (van der Geest & Frens, 2002). An auditory alert was played to signal the occurrence of these saccades. Blocks were stopped if the number of trials repeated reached 10% of the total number of trials.

Eye velocity (v) and eye acceleration (a) were calculated by Equations 1 and 2 below, where i is the index of the ith sample collected from the eyetracker, and x and y are the horizontal and vertical positions of the eye; t represents time of sample collection.

$$v_i = \frac{\sqrt{(x_{i-1} - x_i)^2 + (y_{i-1} - y_i)^2}}{t_i - t_{i-1}}. \quad (1)$$

$$a_i = \frac{v_i - v_{i-1}}{t_i - t_{i-1}}. \quad (2)$$

For the baseline condition, observers were instructed to fixate a white dot (size 0.3 deg) presented in the center of the monitor. The eyetracker was used to monitor fixation. To avoid saccades toward the target (and therefore multiple repetitions of each trial), the optotype duration was reduced to 200 msec (Carpenter, 1988; Keesey, 1960).

Procedure—Experiment 2

Experiment 2 was similar to Experiment 1, but the target was presented with flankers. Four flankers (bars) were presented alongside the target, as shown in Figure 1B. The bar width was equal to g, length was equal to the Landolt C, and the distance from target to flankers was equal to 2 × g. The viewing distance for this experiment was 50 cm. The size of the target was adjusted for the viewing distance.

Statistical analysis

For statistical analysis, the mean value of visual acuity obtained for gain 0 (baseline visual acuity) was computed. Visual acuity for each eccentricity and position was normalized by the mean baseline visual acuity for each observer. Linear mixed models (using SPSS version 13.0) were used to determine the effects of gain, position and eccentricity, and their interactions, on peripheral visual acuity. Linear mixed models is an alternative to repeated measures ANOVA that is well suited for unbalanced experimental designs (e.g., different number of replications across subjects, as was the case in the present study).

Visual acuity values are expressed in logarithm base 10 of the minimum angle of resolution minutes of arc (logMAR), where 1.0 logMAR is equivalent to a minimum angle of resolution of 10 minutes of arc (20/200) and 0.0 logMAR is equivalent to a minimum angle of resolution of 1 minute of arc (20/20).

Results

Experiment 1—Peripheral visual acuity without crowding

Mean visual acuity results for each gain value at each position and eccentricity are summarized in Table 1 (individual means) and Figure 2 (variation of visual acuity with gain, means of all observers).

Visual acuity improves when the target was presented under gaze contingent conditions (gain: 0.1, 1.0, 10) compared with the no gaze contingent condition (gain 0). The mean improvement from gain 0 to gain 0.1 is 0.04 logMAR (p = 0.013). In the gaze contingent conditions, peripheral visual acuity improved slightly with increased retinal image slip: visual acuity with gain 10 was significantly better than that for gain 0.1 (mean improvement = 0.04 logMAR, $p < 0.001$). There was no improvement in VA from gain 0.1 to gain 1.0 (p = 1.00), but an improvement was seen for gain 10 compared to gain 1.0 (mean improvement = 0.03 logMAR, p = 0.01).

There was no interaction of gain × position or gain × eccentricity. These interactions are shown in Figures 3A and 3B, respectively. Thus, the effect of gain was the same for both eccentricities and for all four isoeccentric positions.

The interaction eccentricity × position is not significant, indicating that the variation in acuity with position was the same for both eccentricities.

Experiment 2—Peripheral visual acuity with crowding

Figure 4 and Table 2 summarize the results for Experiment 2. Gain, position, and eccentricity all had significant effects on peripheral visual acuity. The difference between gain 0, gain 0.1, and gain 1 is not statistically significant.

		5 degrees				10 degrees			
	Gain	Right	Up	Left	Down	Right	Up	Left	Down
S1	0	0.75	0.85	0.66	0.82	0.94	1.10	0.93	1.02
	0.1	0.60	0.79	0.56	0.73	0.87	1.04	0.84	0.98
	1	0.55	0.74	0.53	0.76	0.78	1.03	0.81	0.97
	10	0.57	0.70	0.57	0.70	0.76	0.97	0.77	0.88
S2	0	0.71	0.91	0.72	0.81	0.97	1.12	0.95	1.02
	0.1	0.62	0.83	0.64	0.72	0.91	1.06	0.92	1.04
	1	0.69	0.90	0.66	0.75	0.89	1.02	0.81	0.98
	10	0.66	0.87	0.70	0.80	0.88	1.03	0.98	0.98
S3	0	0.69	0.81	0.73	0.84	0.87	1.17	0.99	1.13
	0.1	0.77	0.93	0.72	0.93	0.89	1.19	0.96	1.12
	1	0.69	0.88	0.67	0.87	0.92	1.18	0.97	1.14
	10	0.72	0.84	0.71	0.91	0.92	1.13	0.93	1.07
S4	0	0.69	0.81	0.64	0.80	0.95	1.10	0.92	1.06
	0.1	0.61	0.76	0.61	0.75	0.91	1.08	0.89	1.12
	1	0.64	0.78	0.68	0.79	0.90	0.99	0.81	1.02
	10	0.61	0.68	0.58	0.72	0.86	0.93	0.81	1.05
S5	0	0.71	0.87	0.73	0.81	1.00	1.13	0.97	1.14
	0.1	0.72	0.92	0.64	0.86	0.96	1.11	0.91	1.12
	1	0.70	0.94	0.65	0.83	0.99	1.13	0.98	1.10
	10	0.67	0.85	0.58	0.79	0.91	1.07	0.90	1.08

Table 1. Individual mean values of peripheral visual acuity in logMAR for each observer (S), gain, and position for Experiment 1.

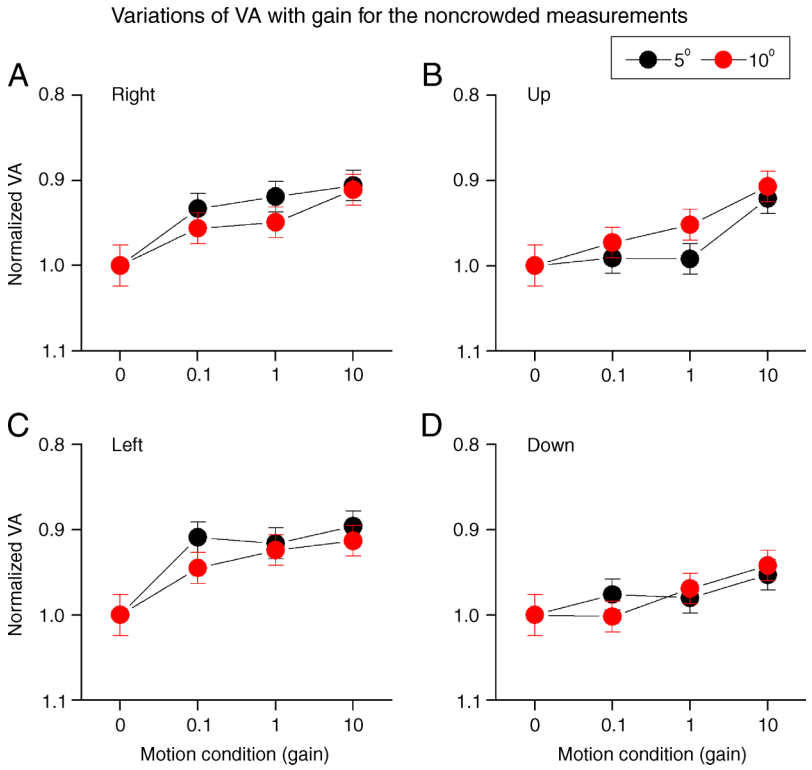

Figure 2. Variation of peripheral acuity, measured with a noncrowded Landolt C, for the four motion conditions of the target. Gain 0 corresponds to the nongaze contingent measurements. Each panel shows results for a different screen position. Black circles: 5 degrees eccentricity. Red circles: 10 degrees eccentricity. Error bars show one standard error.

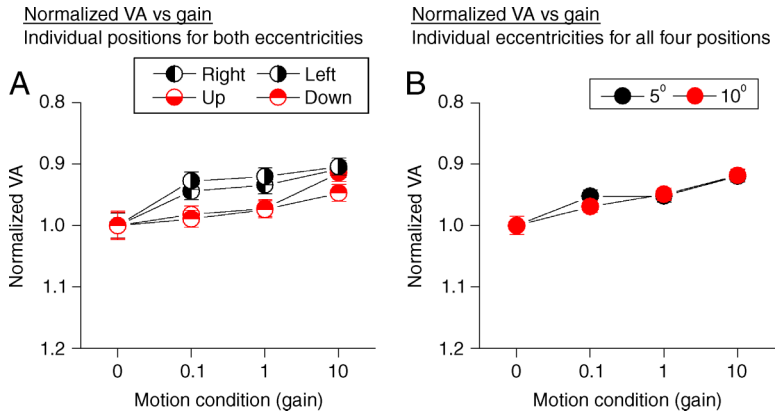

Figure 3. The interaction between (A) gain × position and (B) gain × eccentricity for Experiment 1. (A) Each curve corresponds to one position, mean values for positions in the horizontal meridian are shown in black and mean values for positions in the vertical meridian are shown in red. (B) Each curve corresponds to one eccentricity. Black circles: 5° eccentricity. Red circles: 10° eccentricity. Error bars show one standard error in (A) and (B).

In contrast with Experiment 1 for gain 10 visual acuity reduced significantly compared to all other gains.

The interaction of gain × position was significant (p = 0.002), indicating that the effect of gain was different depending on the position. This interaction is shown in Figure 5A. The interaction of gain × eccentricity was also significant ($p < 0.001$), indicating that the effect of gain was different for different eccentricities. This interaction is shown in Figure 5B.

Discussion

In these two experiments, we investigated the effect of increasing, reducing, and nullifying the retinal image slip generated by fixational eye movements on peripheral visual acuity. Visual acuity under these conditions was compared to visual acuity measured with no compensation for fixational eye movements.

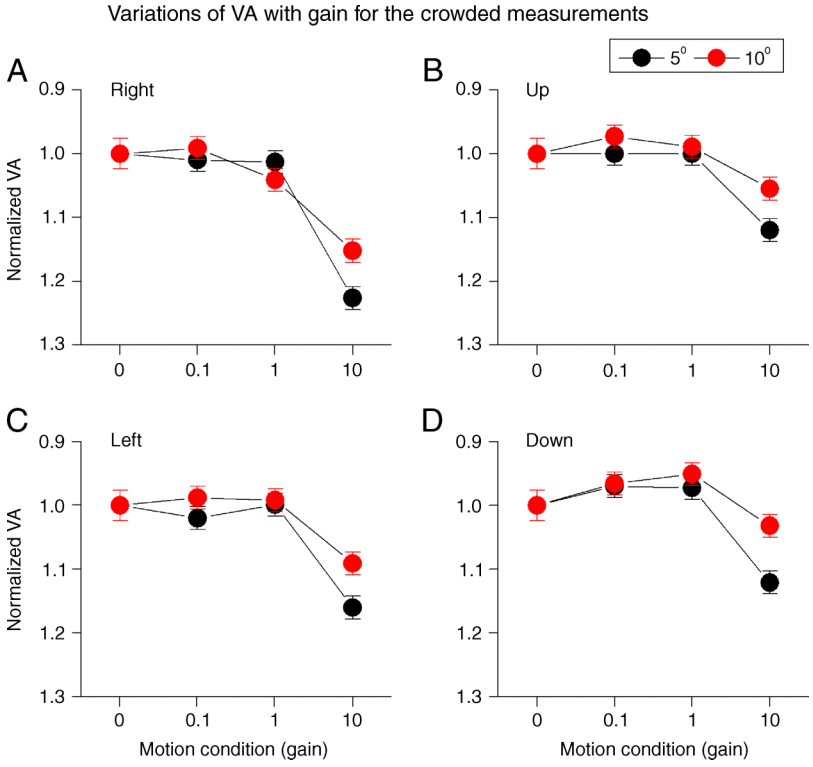

Figure 4. Variation of peripheral acuity, measured with a crowded Landolt C, for the four motion conditions of the target. Gain 0 corresponds to the nongaze contingent measurements. Each panel shows results for a different screen position. Black circles: 5 degrees eccentricity. Red circles: 10 degrees eccentricity. Error bars show one standard error.

		5 degrees				10 degrees			
	Gain	Right	Up	Left	Down	Right	Up	Left	Down
S1	0	0.80	1.00	0.83	1.08	1.16	1.29	1.06	1.40
	0.1	0.80	0.93	0.84	0.94	1.04	1.25	0.98	1.23
	1	0.83	0.97	0.84	0.97	1.05	1.24	0.98	1.25
	10	1.05	1.13	0.98	1.16	1.28	1.41	1.23	1.42
S6	0	0.90	1.12	0.99	1.02	1.09	1.35	1.24	1.24
	0.1	0.90	1.12	0.93	1.02	1.07	1.26	1.22	1.31
	1	0.87	1.12	0.88	0.96	1.13	1.35	1.17	1.28
	10	1.03	1.24	0.92	1.11	1.21	1.40	1.24	1.34
S7	0	0.91	1.10	0.89	0.96	1.11	1.40	1.26	1.32
	0.1	0.84	1.07	0.89	0.95	1.12	1.34	1.12	1.33
	1	0.84	1.06	0.86	1.03	1.29	1.39	1.15	1.25
	10	1.03	1.17	1.05	1.11	1.26	1.42	1.27	1.33
S4	0	0.73	0.83	0.75	0.94	0.91	1.17	0.97	1.29
	0.1	0.78	0.91	0.84	0.90	1.00	1.16	1.07	1.21
	1	0.79	0.92	0.83	0.90	1.02	1.19	1.09	1.17
	10	0.96	1.02	0.98	1.06	1.19	1.29	1.19	1.33
S5	0	0.88	1.12	0.87	0.91	1.11	1.40	1.15	1.33
	0.1	0.89	1.12	0.91	0.95	1.07	1.39	1.15	1.31
	1	0.88	1.13	0.86	0.92	1.10	1.36	1.17	1.33
	10	1.02	1.17	1.00	1.05	1.20	1.40	1.16	1.37

Table 2. Individual mean values of peripheral visual acuity in logMAR for each observer (S), gain, and position for Experiment 2.

We found that peripheral visual acuity measured without crowding (Experiment 1) improved slightly with increased retinal image slip, when compared with the other motion conditions. In contrast, under crowded conditions (Experiment 2), peripheral visual acuity decreased markedly with increased retinal image slip. Different effects of retinal image slip on crowded and noncrowded conditions have previously been reported in people with nystagmus (equivalent to an increased retinal image slip; Chung & Bedell, 1995; Pascal & Abadi, 1995).

We speculate that in both of our experiments increased retinal image slip caused blur due to motion smear. In the crowded condition, this would lead to superimposition of the flankers on the target, impairing the ability of observers to detect the gap position within the target. In the noncrowded condition, there are no flankers to interfere with target detection. Other authors investigating the effect of target motion on central visual acuity have found that the effect of motion depends on target configuration: a task that involves a component of localization, such as a Vernier task, is only minimally affected

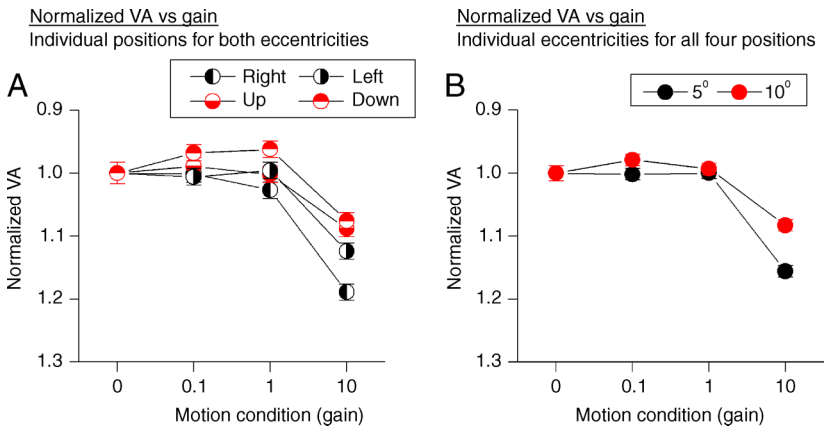

Figure 5. The interaction between (A) gain × position and (B) gain × eccentricity for Experiment 2. (A) Each curve corresponds to one position, mean values for positions in the horizontal meridian are shown in black and mean values for positions in the vertical meridian are shown in red. (B) Each curve corresponds to one eccentricity. Black circles: 5° eccentricity. Red circles: 10° eccentricity. Error bars show one standard error in (A) and (B).

by stimulus motion (Bedell, Chung, & Patel, 2000; Carpenter, 1988; Westheimer & McKee, 1975), whereas the ability to discriminate the spacing between two moving bars is greatly impaired by the same amount of motion (Burr & Ross, 1982; Morgan & Benton, 1989). Morgan and Benton (1989) suggested this happens because, unlike the Vernier targets, the two lines are very close and their trajectory falls in the same part of the retina reducing the luminance-valley cue to a single-peaked distribution that is no longer resolvable.

Peripheral visual acuity was worse when observers were instructed to fixate the central dot (baseline condition). VA for gain 0 might have been reduced due to the presence of two objects in the monitor compared with the other gains where only the peripheral target was visible. This has been reported by other authors comparing peripheral visual performance assessed with and without foveal vision (Posner, 1980).

In both experiments, peripheral visual acuity measured under reduced and null retinal image slip was similar. These results are in agreement with other authors who have measured central (Keesey, 1960) and peripheral (Millodot, 1966) visual acuity with nonstabilized and stabilized retinal images.

Increased retinal slip can improve peripheral vision. Previous studies have found a slight improvement in peripheral visual acuity for targets with velocities above the limit imposed by normal fixational eye movements (Bex et al., 2003; Brown, 1972). Recent research has reinforced the fundamental role of normal fixational eye movements in central vision (Martinez-Conde et al., 2006; Rucci et al., 2007) yet they cannot prevent visual adaptation in the peripheral retina (Clarke, 1960, 1961). Results from Experiment 1 are in agreement with these findings.

The effect of gain changed with eccentricity. It has previously been shown that the effect of image stabilization gets smaller with increasing eccentricity (Millodot, 1966). Our second experiment also shows that the change in visual acuity with different gains is more pronounced at 5 than 10 degrees eccentricity, suggesting that retinal image slip is better tolerated with eccentricity. This may be due to the increased size of more peripheral receptive fields (Drasdo, 1989; Hubel & Wiesel, 1960) and changes in the size of spatial interference zones (Bex et al., 2003; Toet & Levi, 1992; Tripathy & Cavanagh, 2002).

In both experiments, peripheral visual acuity was better in the horizontal meridian than in the vertical meridian. This asymmetry between positions is in agreement with other studies (Cameron, Tai, & Carrasco, 2002; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1999) and can be explained by anatomical properties of the human retina: the number of receptors in the vertical meridian decreases faster with eccentricity than in the horizontal meridian (Curcio & Allen, 1990). An offline analysis was performed to analyze the possible interaction between the orientation of the gap and the meridian of the position. These results showed no consistent relationship between these two variables.

A limitation of our experimental setup is that our stabilization system does not reduce retinal image slip to zero due to the imprecision of head-mounted video eyetrackers and the delay between the movement of the eye and the movement of the target in the screen. One indication of perfect stabilization is image fading, which was not reported under any of our conditions. However, image fading would have been unlikely given the very high target contrast: even with perfect stabilization it requires exposures far longer than 500 msec for the image to fade (Keesey, 1960; Tulunay-Keesey, 1982).

To quantify the error of our system, an offline analysis was performed to determine if the eye was moving toward or away from the target between each monitor retrace. In periods during which the eye moved away from the target, the value of gain would effectively be reduced, whereas when the eye moved toward the target the gain would effectively increase compared to the initially defined value. Despite some variance, for all three gains the value of the mean differed by no more than 1/10 of the defined value. For a typical set of 4 repetitions per gain for the same observer, the mean and 95% confidence interval was: 0.099 ± 0.0008 for gain 0.1; 0.99 ± 0.005 for gain 1.0; and 10.53 ± 0.5 for gain 10.

A further consequence of system delay would be a time lag between the onset of a saccade and screen blanking. The maximum distance the eye could travel during a saccade is approximately 0.12 deg every 4 msec. Thus, the maximum distance the eye could travel toward the target during a saccade before the blanking of the monitor was less than 0.5 deg. We retrospectively computed typical target amplitude, measured between monitor frames, for the nonzero gain conditions. The mean amplitudes of the target movements for 5 degrees eccentricity were 1.8 minutes of arc for gain 0.1, 18 minutes of arc for gain 1.0, and 33.6 minutes of arc for gain 10. The amplitude for gain 0.1 was many times below the limit of 1 pixel. Therefore, the difference in the mean amplitude of the target movement between gain 0.1 and gain 1.0 was not large enough to produce changes in peripheral visual acuity (Brown, 1972; Westheimer & McKee, 1975). However, performance differences between these two gains would exist if there was a systematic difference in the number of microsaccades due to different amounts of retinal image slip (Engbert & Mergenthaler, 2006). That was not the case: we did not find any systematic change in the number of microsaccades with increasing gain. At 5 degrees eccentricity, the mean number of microsaccades was 107.5 (range 272–53) at gain 0.1, 98.0 (range 289–13) at gain 1.0, and 110.1 (range 489–18) at gain 10.

A further potential limitation of our experimental technique is that our subjects wore the same refractive correction for 5 and 10 degrees eccentricity. While it is known that there are small differences in refractive error

with increasing eccentricity (Gustafsson & Unsbo, 2003; Millodot, Johnson, Lamont, & Leibowitz, 1975; Millodot & Lamont, 1974), this effect would have the same impact under each of our gain conditions and would not alter the pattern of our results.

Previous studies in people with macular scotomas caused by diseases such as age-related macular degeneration have shown that they have poor fixation stability (increased retinal image slip; Bellmann, Feely, Crossland, Kabanarou, & Rubin, 2004; Culham, Fitzke, Timberlake, & Marshall, 1993) and that their reading speed decreases if instability increases (Bellmann et al., 2004; Seiple, Szlyk, McMahon, Pulido, & Fishman, 2005). Our results confirm that fixation instability has a significant effect on peripheral visual acuity.

Conclusion

Increased retinal image slip improves peripheral visual acuity for isolated targets but worsens acuity when targets are crowded. These results have two important implications: first, measurements of peripheral visual acuity performed with isolated letters are not likely to be good predictors of visual function under normal crowded conditions; second, in real visual tasks poor fixation stability may be a limiting factor for visual function in the peripheral retina.

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Footnote

[1]For some observers, it was four repetitions.

References

Ahissar, E., & Arieli, A. (2001). Figuring space by time. *Neuron, 32,* 185–201. [PubMed] [Article]

Andersen, E. E., & Weymouth, F. W. (1923). Visual perception and the retinal mosaic: I. Retinal mean local sign—An explanation of the fineness of binocular perception of distance. *American Journal of Physiology, 64,* 561–594.

Anderson, S. J., Mullen, K. T., & Hess, R. F. (1991). Human peripheral spatial-resolution for achromatic and chromatic stimuli—Limits imposed by optical and retinal factors. *The Journal of Physiology, 442,* 47–64. [PubMed] [Article]

Banks, M. S., Sekuler, A. B., & Anderson, S. J. (1991). Peripheral spatial vision: Limits imposed by optics, photoreceptors, and receptor pooling. *Journal of the Optical Society of America A, Optics and Image Science, 8,* 1775–1787. [PubMed]

Barlow, H. B. (1952). Eye movements during fixation. *The Journal of Physiology, 116,* 290–306. [PubMed] [Article]

Barlow, H. B. (1997). Neuroscience: Adaptation by hyperpolarization. *Science, 276,* 913–914.

Bedell, H. E., Chung, S. T., & Patel, S. S. (2000). Elevation of Vernier thresholds during image motion depends on target configuration. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 17,* 947–954. [PubMed]

Bellmann, C., Feely, M., Crossland, M. D., Kabanarou, S. A., & Rubin, G. S. (2004). Fixation stability using central and pericentral fixation targets in patients with age-related macular degeneration. *Ophthalmology, 111,* 2265–2270. [PubMed]

Berry, R. N. (1948). Quantitative relations among Vernier, real depth, and stereoscopic depth acuities. *Journal of Experimental Psychology: General, 38,* 708–721.

Bex, P. J., Dakin, S. C., & Simmers, A. J. (2003). The shape and size of crowding for moving targets. *Vision Research, 43,* 2895–2904. [PubMed]

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436. [PubMed]

Brown, B. (1972). Resolution thresholds for moving targets at the fovea and in the peripheral retina. *Vision Research, 12,* 293–304. [PubMed]

Burr, D. (1980). Motion smear. *Nature, 284,* 164–165. [PubMed]

Burr, D. C., & Ross, J. (1982). Contrast sensitivity at high velocities. *Vision Research, 22,* 479–484. [PubMed]

Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research, 42,* 949–967. [PubMed]

Carpenter, R. (1988). *Movements of the eyes* (2nd ed.). London: Pion.

Cheal, M., & Lyon, D. R. (1991). Central and peripheral precuing of forced-choice discrimination. *Quarterly*

Journal of Experimental Psychology Section A: Human Experimental Psychology, 43, 859–880. [PubMed]

Chung, S. T., & Bedell, H. E. (1995). Effect of retinal image motion on visual acuity and contour interaction in congenital nystagmus. *Vision Research, 35,* 3071–3082. [PubMed]

Clarke, F. J. J. (1957). Rapid light adaptation of localised areas of the extra-foveal retina. *Journal of Modern Optics, 4,* 69–77.

Clarke, F. J. J. (1960). A study of Troxler's effect. *Journal of Modern Optics, 7,* 219–236.

Clarke, F. J. J. (1961). Visual recovery following local adaptation of the peripheral retina (Troxler's effect). *Journal of Modern Optics, 8,* 121–135.

Coppola, D., & Purves, D. (1996). The extraordinarily rapid disappearance of entoptic images. *Proceedings of the National Academy of Sciences of the United States of America, 93,* 8001–8004. [PubMed] [Article]

Cornelissen, F. W., Bruin, K. J., & Kooijman, A. C. (2005). The influence of artificial scotomas on eye movements during visual search. *Optometry and Vision Science, 82,* 27–35. [PubMed]

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods Instruments & Computers, 34,* 613–617. [PubMed]

Culham, L. E., Fitzke, F. W., Timberlake, G. T., & Marshall, J. (1993). Assessment of fixation stability in normal subjects and patients using a scanning laser ophthalmoscope. *Clinical Vision Science, 8,* 551–561.

Curcio, C. A., & Allen, K. A. (1990). Topography of ganglion cells in human retina. *Journal of Comparative Neurology, 300,* 5–25. [PubMed]

Curcio, C. A., Sloan, K. R., Jr., Packer, O., Hendrickson, A. E., & Kalina, R. E. (1987). Distribution of cones in human and monkey retina: Individual variability and radial asymmetry. *Science, 236,* 579–582. [PubMed]

Ditchburn, R. W., Fender, D. H., & Mayne, S. (1959). Vision with controlled movements of the retinal image. *The Journal of Physiology, 145,* 98–107. [PubMed] [Article]

Ditchburn, R. W., & Drysdale, A. E. (1977). Effect of retinal-image movements on vision. II. Oscillatory movements. *Proceedings of the Royal Society of London B: Biological Sciences, 197,* 385–406. [PubMed]

Drasdo, N. (1989). Receptive field densities of the ganglion cells of the human retina. *Vision Research, 29,* 985–988. [PubMed]

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences of the United States of America, 103,* 7192–7197. [PubMed] [Article]

Falkenberg, H. K., Rubin, G. S., & Bex, P. J. (2007). Acuity, crowding, reading and fixation stability. *Vision Research, 47,* 126–135. [PubMed]

Green, D. G. (1970). Regional variations in visual acuity for interference fringes on the retina. *The Journal of Physiology, 207,* 351–356. [PubMed] [Article]

Gustafsson, J., & Unsbo, P. (2003). Eccentric correction for off-axis vision in central visual field loss. *Optometry and Vision Science, 80,* 535–541. [PubMed]

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurons in the cats striate cortex. *The Journal of Physiology, 148,* 574–591. [PubMed] [Article]

Hubel, D. H., & Wiesel, T. N. (1960). Receptive fields of optic nerve fibres in the spider monkey. *The Journal of Physiology, 154,* 572–580. [PubMed] [Article]

Keesey, U. T. (1960). Effects of involuntary eye movements on visual acuity. *Journal of the Optical Society of America, 50,* 769–774. [PubMed]

Mandelbaum, J., & Sloan, L. L. (1947). Peripheral visual acuity—With special reference to scotopic illumination. *American Journal of Ophthalmology, 30,* 581–588.

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews, Neuroscience, 5,* 229–240. [PubMed]

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron, 49,* 297–305. [PubMed] [Article]

Millodot, M. (1966). Foveal and extra-foveal acuity with and without stabilized retinal images. *British Journal of Physiological Optics, 23,* 75–106. [PubMed]

Millodot, M., Johnson, C. A., Lamont, A., & Leibowitz, H. W. (1975). Effect of dioptrics on peripheral visual acuity. *Vision Research, 15,* 1357–1362. [PubMed]

Millodot, M., & Lamont, A. (1974). Letter: Refraction of the periphery of the eye. *Journal of the Optical Society of America, 64,* 110–111. [PubMed]

Morgan, M. J., & Benton, S. (1989). Motion-deblurring in human vision. *Nature, 340,* 385–386. [PubMed]

Pascal, E., & Abadi, R. V. (1995). Contour interaction in the presence of congenital nystagmus. *Vision Research, 35,* 1785–1789. [PubMed]

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442. [PubMed]

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32,* 3–25. [PubMed]

Rucci, M., Iovin, R., Poletti, M., & Santini, F. (2007). Miniature eye movements enhance fine spatial detail. *Nature, 447,* 851–854. [PubMed]

Seiple, W., Szlyk, J. P., McMahon, T., Pulido, J., & Fishman, G. A. (2005). Eye-movement training for reading in patients with age-related macular degeneration. *Investigative Ophthalmology & Visual Science, 46,* 2886–2896. [PubMed] [Article]

Sharpe, C. R. (1972). The visibility and fading of thin lines visualized by their controlled movement across the retina. *The Journal of Physiology, 222,* 113–134. [PubMed] [Article]

Talgar, C. P., & Carrasco, M. (2002). Vertical meridian asymmetry in spatial resolution: Visual and attentional factors. *Psychonomic Bulletin & Review, 9,* 714–722. [PubMed]

Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research, 32,* 1349–1357. [PubMed]

Tripathy, S. P., & Cavanagh, P. (2002). The extent of crowding in peripheral vision does not scale with target size. *Vision Research, 42,* 2357–2369. [PubMed]

Tulunay-Keesey, U. (1982). Fading of stabilized retinal images. *Journal of the Optical Society of America, 72,* 440–447. [PubMed]

van der Geest, J. N., & Frens, M. A. (2002). Recording eye movements with video-oculography and scleral search coils: A direct comparison of two methods. *Journal of Neuroscience Methods, 114,* 185–195. [PubMed]

Watson, A. B., & Pelli, D. G. (1983). Quest: A Bayesian adaptative psychometric method. *Perception & Psychophysics, 33,* 113–120. [PubMed]

Westheimer, G., & McKee, S. P. (1975). Visual acuity in presence of retinal-image motion. *Journal of the Optical Society of America, 65,* 847–850. [PubMed]

Williams, D. R., & Coletta, N. J. (1987). Cone spacing and the visual resolution limit. *Journal of the Optical Society of America A, Optics and Image Science, 4,* 1514–1523. [PubMed]

Yeshurun, Y., & Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Research, 39,* 293–306. [PubMed]