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Different temporal dynamics of foveal and peripheral visual processing during fixation

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Humans explore visual scenes by alternating short fixations with saccades directing the fovea to points of interest. During fixation, the visual system not only examines the foveal stimulus at high resolution, but it also processes the extrafoveal input to plan the next saccade. Although foveal analysis and peripheral selection occur in parallel, little is known about the temporal dynamics of foveal and peripheral processing upon saccade landing, during fixation. Here we investigate whether the ability to localize changes across the visual field differs depending on when the change occurs during fixation, and on whether the change localization involves foveal, extrafoveal processing, or both. Our findings reveal that the ability to localize changes in peripheral areas of the visual field improves as a function of time after fixation onset, whereas localization accuracy for foveal stimuli remains approximately constant. Importantly, this pattern holds regardless of whether individuals monitor only foveal or peripheral stimuli, or both simultaneously. Altogether, these results show that the visual system is more attuned to the foveal input early on during fixation, whereas change localization for peripheral stimuli progressively improves throughout fixation, possibly as a consequence of an increased readiness to plan the next saccade.

temporal dynamics | peripheral processing | foveal processing | fixation

Picture yourself driving in a busy street. Skilled drivers generally perform this task effortlessly, but at each fixation the visual system not only focuses on what lies at the center of gaze (e.g., a car, a traffic light, or a pedestrian) but also monitors what happens across the rest of the visual field. Potential dangers can emerge from various locations at any given moment and, to react properly, localizing them accurately is essential.

Although previous work has shown that processing of foveal and peripheral stimuli proceeds in parallel (1, 2), there may be moments during fixation in which the visual system is more attuned to processing foveal vs. peripheral stimulation or vice-versa. Here we posit that the visual system is more attuned to foveal stimulation early on during fixation, whereas later on, when planning the next saccade usually becomes more pressing, it is more receptive to stimulation in the visual periphery. To address this issue, we examined humans' ability to localize brief orientation changes across the visual field during the course of fixation immediately following a saccade. In line with our expectation, our findings reveal an intrinsic advantage in processing foveal stimuli early on during fixation.

Results

Subjects (N = 8) performed a change localization task. Each trial started with subjects maintaining fixation on a marker presented in the lower part of the screen. After a few milliseconds, subjects were prompted to make a saccade toward a central fixation marker, and maintain their gaze steady until the trial ended. The central marker was surrounded by four vertical bars located either all in the fovea or all in the periphery (0.3° and 9° of eccentricity, respectively) or two in each region, requiring simultaneous monitoring of both areas (Fig. 1). Peripheral stimuli were enlarged to compensate for cortical magnification (3) and ensure comparable visual acuity (4). To mimic natural viewing conditions, the bars were shown throughout the trial, before and after saccade onset. To avoid unnatural fading due to the reduced retinal motion caused by head stabilization (5), especially in the periphery, a small jitter was added to each bar. Upon saccade landing, one of the four bars briefly (50 ms) changed orientation. The degree of orientation change was fixed for each stimulus and subject, and it was chosen to yield 79% of correct localizations when the change occurred ~490 ms after fixation onset. At the end of each trial subjects reported the location of the stimulus that changed orientation (see *SI Appendix* for details). Importantly, this task avoided the burden of a dual task (1); subjects always monitored the same number of items, focusing solely on localizing orientation changes regardless of stimulus location (fovea, periphery, or both).

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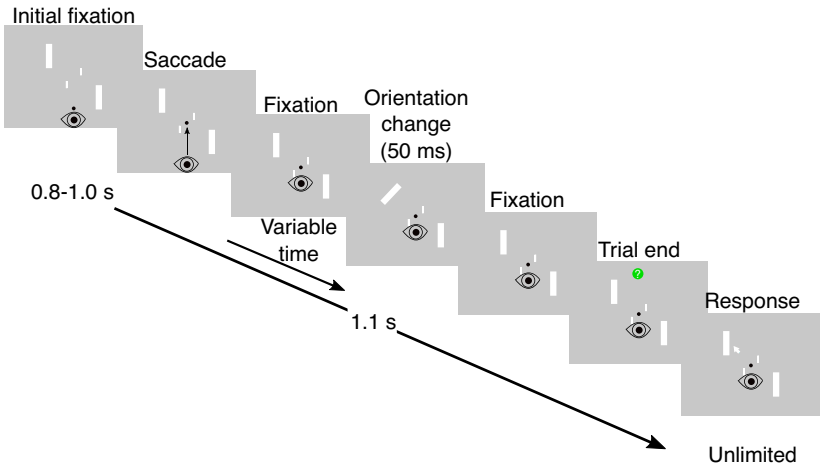

Fig. 1. Experimental paradigm. In the illustrated condition, targets were presented both foveally and peripherally. The probability of a stimulus changing in the periphery or in the fovea was the same, and both regions were monitored simultaneously. In the other conditions, all four bars appeared either in the fovea or in the periphery. See *SI Appendix* for details.

Our results show that the ability to correctly localize orientation changes depended both on the time and the location of the changes. When all the stimuli were displayed in the fovea (Fig. 2 *A* and *B*, *Left* panels), performance was statistically comparable when the changes happened 100 to 250 ms after fixation onset and when they happened 750 to 900 ms after fixation onset (68.7%, SD = 14 vs. 75.0%, SD = 15; post hoc using the Benjamini–Hochberg method to control for multiple comparisons: t-ratio = −2.00, P = 0.13). Instead, when stimuli were displayed in the periphery, performance improved over time, from 55% (SD = 15) when the changes occurred soon after fixation started (100 to 250 ms) to 76.7% (SD = 5) at 750 to 900 ms (t-ratio = −6.91, $P < 0.001$). These results indicate that early on during fixation there is an advantage in localizing changes in the foveal vs peripheral visual field (t-ratio = 2.98, P = 0.03). Yet, this advantage disappears when changes occur later on during fixation (t-ratio = −0.38, P = 0.81).

Similarly, when monitoring foveal and peripheral stimuli simultaneously (Fig. 2 *A* and *B*, *Right* panels), foveal performance remained constant throughout fixation (72.2%, SD = 17 vs. 72%, SD = 14 for changes occurring 100 to 250 ms and 750 to 900 ms after fixation onset; t-ratio = −0.01, P = 0.99). In the periphery, performance largely improved over time (60.8%, SD = 11 vs. 79.5%, SD = 8; t-ratio = −5.912, $P < 0.001$) reaching levels comparable to performance when changes occurred at the foveal level (t-ratio = −1.61, P = 0.26).

Discussion

Our findings reveal distinct temporal dynamics for foveal and peripheral visual processing during fixation. Upon fixation onset, there is an advantage for processing foveal vs extrafoveal stimuli. While performance for foveal stimuli remained relatively constant as fixation progressed, a gradual improvement was observed in localizing peripheral changes. This improvement unfolded within the first 250 to 350 ms of fixation, i.e., within the timeframe of typical fixations duration (6), showing significant variation in the ability to localize peripheral

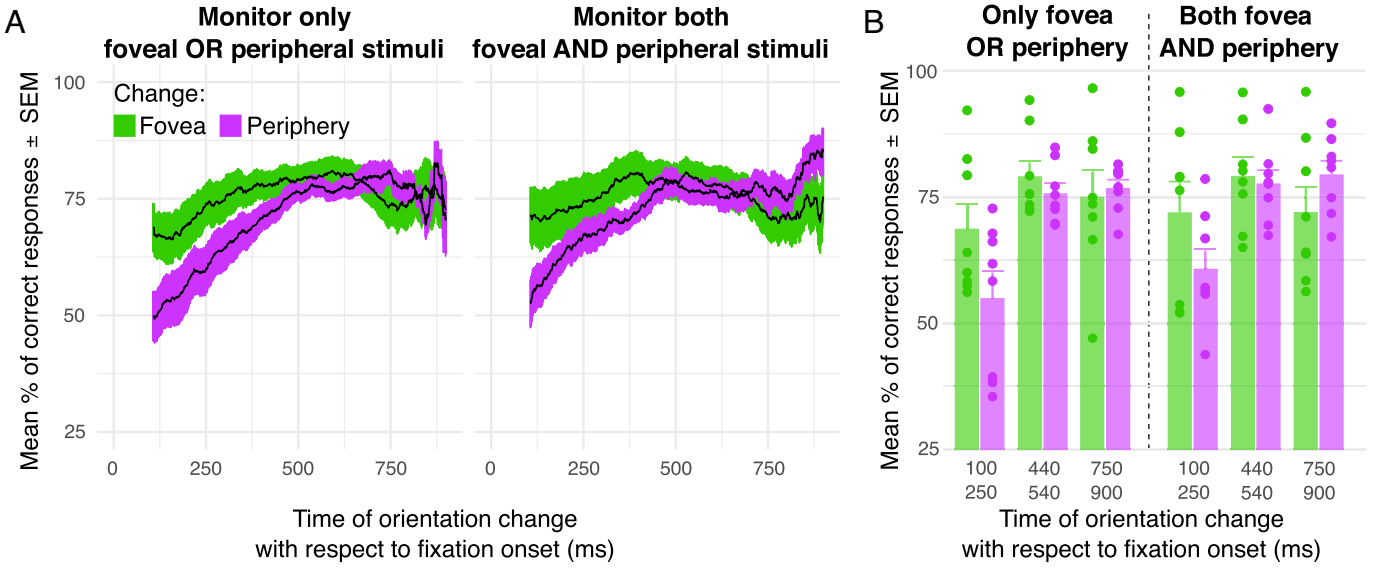

Fig. 2. Results. (*A*) Mean percentage of correct responses (sliding window of 100 ms) across subjects as a function of when the orientation change occurred with respect to fixation onset. Error bars are SEM. Performance during selective monitoring of foveal or peripheral stimuli (*Left* panel) and during simultaneous monitoring of both areas (*Right* panel). (*B*) Average performance across subjects for changes occurring 100 to 250 ms, 440 to 540 ms, and 750 to 900 ms after fixation onset. Error bars are SEM. Dots represent individual subjects' performance. Colors as in *A*.

changes over time even during brief fixations. Observers remained engaged in the task well after this period, so this trend was not due to saccade planning and execution. Yet, it may well be related to the typical fixation-saccade cycle and be so ingrained in the visual system that it unfolds even in the absence of an impending saccade. Further, this modus operandi seems to be obligatory as the same temporal course was observed regardless of whether the visual system monitored only foveal or peripheral stimuli or both simultaneously.

Attention research debates the ability to attend to multiple spatial locations concurrently (7, 8). Foveal tasks hinder peripheral processing (9, 10), and attempting to detect briefly flashed foveal targets while trying to simultaneously localize peripheral ones impairs both foveal detection and peripheral localization (11). Interestingly, we do not observe a compromise between foveal and peripheral performance, suggesting a simultaneous and independent monitoring of both areas, rather than a trade-off of attentional resources. Possibly, compared to a combined task, localization of changes is a rather parallel and automatic operation that does not require a significant amount of attentional resources, as the moving targets almost pop out from the display.

Our paradigm differs from previous work in that it examines the temporal evolution of visual perception during fixation rather than the overall subjects' performance for foveal and peripheral stimuli. Stimuli were continuously presented throughout the trial, and brought into the fovea via a saccade, which may allow processing the visual scene more naturally than when stimuli are flashed at fixation. Importantly, by measuring orientation change thresholds at each tested location, correcting for cortical magnification, and using the same number of stimuli in the fovea and in the periphery, and by not requiring subjects to perform a dual task, our paradigm ensured comparable task difficulty for foveal and peripheral stimuli, which was not always the case in previous work (e.g., ref. 11). It remains an open question whether temporal dynamics for foveal and peripheral processing differ in the same fashion for other visual functions (e.g., contrast sensitivity or acuity). Ultimately, these findings are consistent with the idea that later on during fixation the visuomotor system is more likely to execute a saccade to move the foveola toward its next target, and as a result, sensitivity increases for peripheral stimuli that can potentially become saccadic targets.

Materials and Methods

Details on methods and analyses are available as *SI Appendix*. The data to reproduce the figures are accessible through OSF.

Subjects provided written informed consent before participating. The study was part of a project approved by the Ethics Committee of the University of Barcelona (IRB00003099).

Data, Materials, and Software Availability. Anonymized (R data frame) data have been deposited in OSF (https://osf.io/7n5hd/) (12).

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Supporting Information for
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This PDF file includes:

Supporting Information Text

Participants. Eight subjects (1 author, 4 females, age range 23-40) took part in the study at the University of Barcelona. All except the author were naïve with respect to the purposes of the study. All participants had normal or corrected-to-normal (with contact lenses) vision, and none had evident motor abnormalities. All of them gave their written informed consent to take part in the study.

Apparatus. The experiments were conducted in a normally illuminated room. Experimental software was written using Python, controlled using a Mac Pro and presented on an ASUS monitor (24.5 in, 1920 × 1080 pixels, 240 Hz). We recorded both eyes' movements using an Eyelink II (SR Research) at 500 Hz. Participants bite a board with a dental imprint attached to a structure that was fixed on the table to keep their heads stabilized at 57 cm distance from the screen. At this distance 1 degree of visual angle approximates 1 cm. At the beginning of each experimental block, a standard nine-point calibration was used. The calibration was considered correct only when the precision was higher than 0.3º. Otherwise, the calibration was repeated.

Stimulus and procedure. Subjects performed a change localization task. To start each trial participants had to maintain their gaze on a fixation point that consisted of a combination of two white circles and a cross presented on a black background (Figure 1, details in the figure differ from the ones used in the experiment to facilitate visualization). Such a shape for the fixation point was chosen based on previous findings[1], showing that it eases a stable fixation. The initial fixation point was presented 10 cm below the screen center for a random period between 1 and 1.5 s. Then, the initial fixation point disappeared, and a second fixation point with the same characteristics as the first one appeared in the screen center. Participants had to make a saccade from the initial fixation point to the fixation point presented at the center of the screen. Subjects were then instructed to keep fixation until the end of the trial. We intentionally removed the initial fixation point before the central one appeared to facilitate fixation release and to shorten saccadic latencies[2-3].

At the same time as the initial fixation point appeared, four targets were also presented on the screen. These stimuli consisted of white vertical bars located around the screen center. The bars could be located all in the fovea, all in the periphery, or two in the fovea and two in the periphery (Figure 1). Bars that were presented at the fovea were located at an eccentricity of 20 arcmin away from the screen center. Bars located in the periphery were located at an eccentricity of 540 arcmin (9 deg) away from the screen center. The size of the bars depended on whether they were presented in the fovea or the periphery. The size of peripheral stimuli was scaled to compensate for cortical magnification[4,5]. Therefore, the foveally presented stimuli were 0.2 by 0.05 deg (height and width, respectively) and the ones presented in the periphery were 0.97 by 0.24 deg. To prevent visual fading[6] due to reduced retinal motion when the head is restrained compared to when it is free[7-8], we introduced a small amount of motion by jittering the stimuli. This small jitter was produced by moving the bars 1 pixel back and forth every 25 ms in a random direction. Within 1 s after the central fixation point appeared in the screen center, one of the four bars briefly (50 ms) tilted rightward. Each trial ended after 1.1 s, and a question mark appeared in the upper part of the display. Participants had to report which target changed its orientation by clicking on it with a computer mouse they controlled with their preferred hand. The extended fixation period of 1.1 s was chosen to eliminate any potential interference from saccade planning and execution, which would occur around 250-350 ms, the typical fixation duration[9]. Each experimental session included 128 trials. Within a session, there were 32 trials in which the four bars were presented foveally, 32 in which the four bars appeared in the periphery, and 64 in which there were two bars in the fovea and two in the periphery (32 in which the orientation change occurred in a foveal bar, and 32 in which the change occurred in a peripheral bar). The order in which each of these trials was presented was random. Each participant completed 40 sessions, yielding a total of 5120 trials per participant.

Prior to running the main experiment we assessed the orientation change for each target location yielding 79.4% of correct localizations in two different sessions, one for foveal stimuli and

one for peripheral stimuli. This ensured that task difficulty was matched for different stimulus locations, minimizing the potential confounding effect of asymmetries in performance between upper vs lower and horizontal vs vertical meridians[10-11]. In each of these sessions, four interleaved staircases[12] of 50 trials each were run (one for each target location). The procedure of the task to measure the thresholds was the same as the one used in the main experiment (Figure 1), but in this case stimuli were always presented either in the fovea or in the periphery. Which of the two sets of staircases was run first (fovea or periphery) was randomized across participants. Another difference with the main experiment was that in the staircase sessions the orientation change always occurred 800 ms after the central fixation point was presented. Note that the change in orientation was not contingent on the saccade execution. A change in stimulus orientation 800 ms after the central fixation location appeared, on average corresponded to 490 ms after fixation onset. Importantly, there were no differences in saccadic latencies between the two conditions (283±81 ms vs 277±65 ms, mean±sd for the foveal and peripheral tasks, respectively; paired t-test: t_7=0.255, p=0.81), so thresholds were estimated around the same time frame in both conditions. Consistent with this, in the main experiment, when the change in orientation occurred around 500 ms after saccade landing performance did not differ from 79.4% (the chosen threshold, tested using two-tailed t-tests) regardless of whether the change occurred in the fovea or in the periphery either in the condition where participants monitored only the fovea or the periphery (79.1%; t_7=-0.098, p=0.92 and 75.7%; t_7=-1.20, p=0.11) or both simultaneously (fovea: 79.2%; t_7=-0.06, p=0.95; periphery: 77.6%; t_7=-0.66, p=0.53).

Importantly, the aim of our study was to describe the temporal course of foveal and peripheral processing during fixation. To this end, we ensured that task difficulty was matched for foveal and peripheral stimuli within a specific time frame by presenting the same number of stimuli in the fovea and the periphery, by correcting for cortical magnification, and by measuring the thresholds separately at each tested location. Controlling for these factors eliminates the influence of potential confoundings (i.e., task difficulty, perceptual asymmetries across the visual field and cortical magnification of foveal stimuli) on the observed results.

Data analyses. Data were analyzed with RStudio[13]. We determined where participants were looking at each moment by averaging the estimated position of the two eyes. We used the Eyelink II algorithm to determine when saccades occurred. Saccades were detected when the eye velocity exceeded 30 deg/s velocity and there was an acceleration of 8000 deg/s^2. To remove small saccades that could escape this criterion, we also identified gaze velocity values above 1000 deg/s as saccades and identified their beginning and end based on acceleration. We removed all trials in which there was a saccade in the 100 ms preceding the change in orientation or in the 200 ms after the change in orientation (5512 trials). After removing these trials we were left with 35448 trials (87% of the total).

To evaluate how performance changed depending on when the change in orientation occurred with respect to fixation onset, we calculated a moving average of the percentage of correct responses with a 100 ms window. A one-way repeated measures ANOVA was used to examine the effect of where (fovea or periphery) and when (100-250 ms, 440-540 ms, and 750-900 ms after fixation onset) the change occurred on the percentage of correct responses and post-hoc pairwise comparisons were conducted using the Benjamini-Hochberg method to control for multiple comparisons.

Data availability. The data to reproduce the figures is available through the Open Science Framework.

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