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The contribution of foveal activation to the oculomotor gap effect

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HIGHLIGHTS

- We investigated the origin of the gap effect.
- Previous research has suggested the gap effect to be foveal specific.
- We used a gaze-contingent fixation adaptation of the fixation offset task.
- The gap effect is mediated by more than foveal specific factors alone.
- Lateral interactions in the superior colliculus also contribute to the gap effect.

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ABSTRACT

Saccade initiation is facilitated when there is no physical stimulus at the start position of the saccade. There have been numerous explanations for this 'gap effect', the most prominent one being the facilitated release from active fixation when no visual information is present. Attributed to potential fixation sensitive neurons in the superior colliculus, previous research has suggested the gap effect to be a foveal specific effect. The aim of the present study was to investigate whether the gap effect is strictly a foveal effect by using a gaze-contingent eccentric fixation adaptation of the fixation offset paradigm. Results show that, although the gap effect is diminished under eccentric viewing conditions, it is still significantly present. This suggests that the gap effect is mediated by more than foveal specific factors alone. We argue that lateral interactions in the superior colliculus may also contribute to the gap effect.
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1. Introduction

Saccades are the rapid movements of the eyeball to direct the fovea onto an object or region of interest. In many situations in daily life a saccade will depart from a location at which a visual object is presented. It is, however, also possible to start a saccade from an 'empty' location, i.e., a location without any strong visual information, like an empty spot on a wall. When these two situations are simulated in an experimental situation, results have shown that saccade initiation is facilitated in the condition in which the saccade is initiated from an empty location [6,18]. This has been termed the 'gap effect' and reflects the shortening of saccade latencies if a fixation point disappears before a target appears (gap condition) compared to when the fixation point is still present at target presentation (overlap condition). This reduction in saccade latency is maximum when the fixation point disappears 200–300 ms before target presentation, but is also observed when the fixation point disappears simultaneously with the presentation of the target [18].

It has been hypothesized that the gap effect involves two components [7]: one involving generalized response preparation due to the warning effect evoked by the offset of the fixation point [16,17] and one involving a facilitated release from active fixation. This facilitated release is caused by the lack of any visual presentation at fixation, making it easier to end the current fixation and initiate the saccade [3,5,11,15]. Support for the facilitated release was provided by neurophysiological recordings in the superior colliculus (SC), an area in the midbrain strongly associated with oculomotor programming [3,11]. Before a saccade can be initiated, fixation related neurons in the rostral pole of the SC are deactivated. The offset of the fixation point prior to a saccade facilitates this deactivation, resulting in a reduced saccade latency [3,11]. Indeed, the fixation offset causes the discharge of fixation related neurons to drop to about 65% of their initial rate. Furthermore, the changes in the discharge rate of rostral pole fixation neurons which occur

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when a fixation point is turned off are known to reflect the time course of the gap effect [3], providing further evidence for a colliculus driven explanation of the gap effect [although for a different explanation of the functioning of rostral neurons, see [9]].

Assuming that the gap effect is indeed mediated by SC fixation cells, Fendrich and colleagues [4] hypothesized that the effect should be reduced or eliminated by the use of an eccentric (non-foveal) fixation anchor, especially when there is no generalized response preparation. With such an anchor, there is no visual stimulation of the fixation cells in the SC, so any offset of the fixation anchor should not evoke a gap effect. To exclude the influence of any generalized response preparation, they also included a zero gap condition, in which the fixation anchor disappeared simultaneously with the target presentation. Indeed, when subjects fixated the empty centre of a square formed by four points with an eccentricity of more than 2°, saccade latencies were similar between the zero gap condition and the overlap condition. In contrast, a reduction was observed with a foveal fixation area (i.e., the corners of the square forming the eccentric fixation point were only 1° from the fovea). Based on these results, they reasoned that the gap effect could be attributed to the facilitated shutdown of colliculus rostral pole fixation neurons.

To verify the conclusion that foveal stimulation is indeed crucial to observe the gap effect, we employed a gaze-contingent eccentric fixation in which fixation was controlled peripherally and there was a zero ms gap between the offset of the fixation point and the onset of the target. So, although the fixation anchor was presented at the centre of the screen, the fovea was pointing to a peripheral location. Therefore, it should not matter whether the corners of the square forming the eccentric fixation point were 1° or 3° from the centre of this fixation anchor, because in both conditions there was no foveal activation as the fovea was pointed to an empty location. We compared the results of participants performing this 'peripheral' condition to the results of participants performing a 'central' condition in which the fixation anchors were presented at the centre of the screen and participants were required to look directly at it. For the central group, the 1° condition reflected foveal activation whereas the 3° did not. We therefore expected to replicate the findings of the zero gap manipulation of Fendrich and colleagues [4] for the central group in that a gap effect should only be observed for the condition with foveal activation. However, if foveal activation is indeed crucial to observe the gap effect, there should be no gap effect for both conditions in the peripheral group.

2. Method

2.1. Participants

For this study we recruited a total of 20 healthy participants with normal or corrected to normal vision (mean age: 27 years; 9 males). Ten participants performed the standard fixation offset paradigm and the other ten performed the gaze contingent version.

2.2. Fixation offset paradigm

To test fixation characteristics we used a fixation-offset paradigm [14]. All trials started with a drift check to ensure that calibration was still accurate. Participants viewed a display containing an eccentric anchor surrounding an *unmarked* centre (located at the centre of the display) with a background luminance of 32.07 cd/m^2. The eccentric fixation anchors consisted of four black crosses (0.64° × 0.64°) and were presented on the corners of an unmarked square. The distance from the crosses to the centre of the screen was either 3° or 1°. This way, participants viewed a fixation stimulus in which there is either foveal stimulation (1° fixation anchor) or no foveal stimulation (3° fixation anchor). After a pseudo-random interval (between 550 and 950 ms.), a black target circle appeared (diameter of 1.43°). Simultaneously, the fixation stimulus disappeared (zero gap condition) or remained on the screen (overlap condition). See Fig. 1 for an overview. Participants were instructed to fixate at the *unmarked* centre until the target dot appeared, and subsequently were to move their eyes as fast as possible to the target circle. The target display was presented for 1500 ms. Afterwards all objects were removed from the display. The experiment consisted of 240 experimental trials and 24 practice trials.

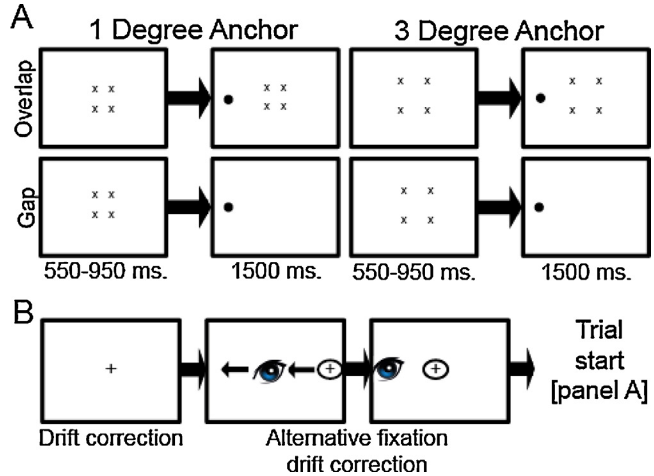

Fig. 1. Schematic overview of the two fixation offset paradigms used. Panel A shows the regular fixation offset paradigm. Prior to the start of each trial a drift check is performed after which the eccentric anchors are presented at either 1° or 3° of eccentricity. Next, a target is presented whereby in the gap condition the anchors disappear at target onset and in the overlap condition they remain visible. Panel B shows the adaptation made to the original paradigm. After the initial drift check a peripheral gaze-contingent fixation cross is shown and participants are instructed to align this cross with a central fixation cross using their eye movements. After stable alignment of these fixation the regular fixation offset paradigm is initiated with the only difference that targets are presented above, below or to the left of the true eye position as opposed to relative to the central fixation.

2.3. Fixation offset gaze contingent paradigm

In the adapted peripheral paradigm, a para-foveal fixation cross was presented at 8° to the right side of the true fixation. This eccentric fixation was an offset of the eye-position as measured with the eye-tracker and was thus controlled by participants' eye-movement (e.g., gaze-contingent). Participants were instructed to move this alternative fixation point over a centrally located fixation cross, hold their fixation steady and press the spacebar. When this alternative fixation was stable within 2° of the central fixation cross, the trial started by removal of the central fixation point. Participants were instructed to keep their para-foveal fixation cross steady at moment the fixation cross disappeared. See Fig. 1B for a graphical overview. At the same time as the central fixation cross disappeared, fixation anchors were presented at either 1° or 3° eccentricity from the centre of the screen. These were exactly the same as in the original paradigm and were presented for the same pseudorandom interval (550–950 ms). After this a target was presented above, below or to the left of the true fixation and participants were instructed to move the eyes there as fast as possible and press the spacebar once they had done so. Also here, there was a zero gap and an overlap condition. Size of the target dots, fixation crosses and fixation anchors as well as all luminance ratios was kept the same as in the original paradigm. This task was programmed using PyGaze [2].

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