



UNIVERSITÀ DEGLI STUDI DI PADOVA

Dipartimento di Psicologia Generale

Corso di laurea in Scienze Psicologiche Cognitive e Psicobiologiche

Elaborato finale

**Feedback signal to foveal cortex for peripheral object
recognition**

Relatore

Prof. Marco Bertamini

Laureanda: Roberta Cessa

Matricola: 1190780

Anno Accademico 2020/2021

Contents

Introduction	4
CHAPTER 1	6
1.1 Visual processing in the fovea and in the periphery	6
1.2 Feed forward and feedback mechanisms involved in object recognition	7
1.3 The constructive role of feedback	8
1.4 Behavioural evidence of the constructive feedback effect	10
1.5 Temporally flexible feedback signal to foveal cortex for peripheral object recognition (Fan et al., 2016)	13
1.6 Theoretical interpretations	14
1.7 Conclusions	16
CHAPTER 2	18
2.1 Feedback signal to foveal cortex for peripheral object recognition	18
2.2 Method	19
2.2.1 Subject	19
2.2.2 Apparatus	20
2.2.3 Stimuli and procedure	20
2.3 Results	23
2.4 Discussion	25
Conclusion	28
References	30

Introduction

A recent study by Williams et al. (2008) has revolutionised the traditional beliefs about interactions between foveal and peripheral vision. The study showed that the two types of vision are intertwined, since a representation of what is present in the periphery has been found in the cortical areas that respond to the fovea. This phenomenon is known as “foveal feedback” and the explanation proposed by the researchers is innovative. They consider the foveal representation as the result of higher-level cortical areas feeding back visual information from the periphery to the foveal retinotopic cortex. The representation is task dependent and behaviourally relevant, suggesting that foveal vision is crucial for the processing of fine details of a stimulus during an object recognition task, while peripheral vision is only sufficient for superficial analysis.

Recent studies have focused on the behavioural consequences of the feedback effect. Overall, it has been demonstrated that a disruption of vision in the fovea during an object recognition task performed on stimuli in the periphery causes a drop in the performance. (Chambers et al., 2013; Weldon et al., 2016; Yu and Shin, 2016; Fan et al., 2016). The effectiveness of the foveal disruption has a variable time window: its effects have been recorded from +150 ms after peripheral stimulus onset (Yu and Shin, 2016) to even +350/400 ms after peripheral stimulus onset (Chambers et al., 2013).

This work intends to review the most recent findings concerning the foveal feedback hypothesis, including the results from a replication of the study by Fan et al. (2016), conducted under the supervision of Prof. Bertamini, Dr. Contemori, and Prof. Battaglini. In Chapter 1, a brief review of how visual processing works will be outlined, focusing on the mechanisms involved during object recognition tasks at the level of the retina. Then, it will be illustrated how the study by Williams et al. (2008) changed the perspective on the interactions between the fovea and the periphery and the foveal feedback hypothesis will be introduced. I will review a series of recent studies exploring the behavioural implications of the foveal feedback. Finally, I will illustrate the most accredited theoretical interpretations of the foveal feedback mechanism.

Chapter 2 will describe the methods and the results from the study we have conducted, a replication of one of the experiments by Fan et al. (2016). It investigates the effects of a dynamic noise patch presented in the fovea at five different stimulus onset asynchronies

(SOAs) while performing an object recognition task in the periphery. The dependent variable are the variations in the sensitivity index (d') (Macmillan & Creelman, 1991) at each of the SOAs.

CHAPTER 1

1.1 Visual processing in the fovea and in the periphery

According to the Cattell-Horn-Carroll (CHC) theory of cognitive abilities, visual processing is the ability to perceive, analyse, synthesise, and think with visual patterns (Schneider & McGrew, 2012, p. 129).

We experience a stable and continuous visual scene, and this experience emerges from processing within the visual system (Stewart et al., 2020). One important constraint can be found in the anatomical organisation of the human retina, which consists of two separate regions: the central region, called the fovea, and the periphery. The density of cone photoreceptors reaches its highest point in the fovea, which is free from rods, and drops in the periphery.

Further, photoreceptors in the fovea mainly have one-to-one connections with cells from the following layers, such as ganglion cells, while in the periphery, more receptors connect to a single cell (Stewart et al., 2020). This results in an over-representation of the fovea that is maintained through all the subsequent stages of visual processing, up to the visual cortex.

The way in which vision is affected by the architecture of the visual system provides evidence that foveal and peripheral vision perform different tasks. Vision in the fovea is responsible for detailed processing of central visual stimuli and it guarantees high spatial resolution, acuity and contrast sensitivity. Vision in the periphery lacks details and information about position and shape of objects, even though it processes the majority of the information in the visual field.

However, recent findings have shown that the impairment of foveal vision can severely compromise visual processing in the periphery (Williams et al., 2008). This suggests that, despite their different goals, the two areas are not as independent as previously assumed.

1.2 Feedforward and feedback mechanisms involved in object recognition

The study by Williams et al. (2008) introduced the innovative concept of a constructive feedback mechanism to explain the influence of foveal vision on peripheral visual processing. In order to better illustrate the findings of this and other recent studies, it is necessary to explain how visual object recognition works.

Traditionally, visual information processing in cortex is described as a system in which visual stimuli are processed by a hierarchy of cortical regions that reflects the functional organisation of the ventral visual stream (Riesenhuber and Poggio, 1999) (Figure 1.1). Earliest areas, such as V1, V2 and V3, detect simple features of the visual input, such as orientation and direction of motion. Areas beyond V3 create increasingly sophisticated representations, for instance the lateral occipital cortex (LOC) codes that something is part of an object and inferotemporal cortex (IT) can recognise a specific object (Kourtzi and Kanwisher, 2001).

The classical model considers visual processing as a mainly feed-forward mechanism, which means that the visual information coding only works unidirectionally and that influence of higher-level areas on lower-level areas is not considered essential.

However, stimulus-driven mechanisms do not fully explain human perception. Internally generated influences from attentional, emotional, or perceptual processes are crucial to guarantee that the representation of an input is as informative as possible (Panichello et al., 2013). Recent studies have examined in depth the role of feedback. The general idea is that when we experience something, we learn from it and we store at least part of what we learnt. The information stored through time will influence the way we perceive reality and guide us through the following events. Hence, feedback mechanisms create expectations around what is about to happen, shape the way we perceive it and make perception less ambiguous, more stable and faster. Overall, feedback is considered to have a modulating and anticipatory effect on feedforward responses and pre-activated representations of stimuli (Williams et al., 2008; Panichello et al., 2013).

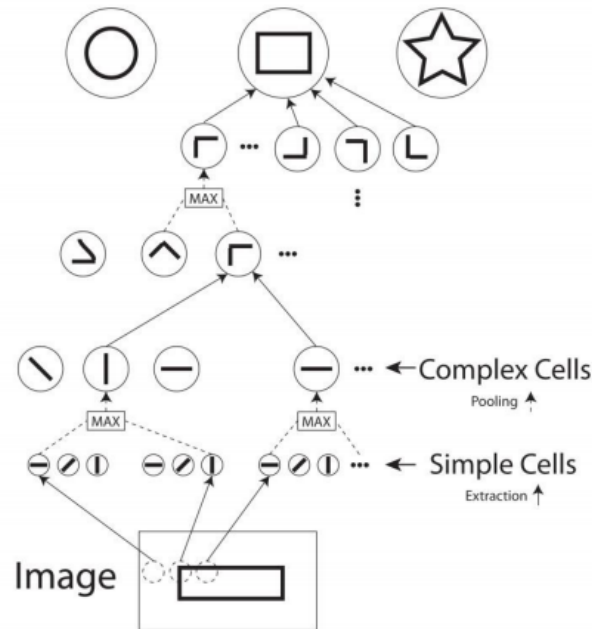


Figure 1.1: A sketch of the model by Riesenhuber and Poggio (1999). It is an extension of the models of simple cells that build up complex cells. The cells from each layer process different features of a stimulus, integrating the features from the lower stages. This procedure is repeated up to higher-level cortical areas, that can recognise sophisticated representations.

1.3 The constructive role of feedback

As anticipated earlier, the study by Williams et al. (2008) has brought to light a completely new role of visual feedback. It was first discovered through the pattern of functional magnetic resonance imaging (fMRI) response, and only later its behavioural effects were described. Brain imaging investigations showed that the foveal-retinotopic cortex contains a representation of the stimuli presented in the periphery of the retina. Researchers explained this with a constructive type of feedback responsible of creating a new representation of the peripheral stimuli in the retinal visual cortex, crucial for peripheral visual object processing.

In the study by Williams et al. (2008), participants maintained fixation while being presented two novel 3D objects in diagonally opposite locations of the peripheral visual field. They performed a perceptual comparison task: they were asked to state whether the two objects were slightly different or the same (Figure 1.2 (B) and (C)). Each pair of objects consisted in two abstract shapes that the subjects had never seen before, both from the same of three categories: spiky, smoothie, cubie (Op de Beeck et al., 2006) (Figure

1.2 (A)). In the meantime, their blood oxygenation level-dependent (BOLD) response was recorded through fMRI.

The study was originally designed to investigate how position-invariant stimuli are represented in higher-tier cortical areas. Not without surprise, a pattern of activation was instead found in the foveal-retinotopic cortex, even though the stimuli were only presented peripherally, more than five degrees outside of the fovea. The results showed that a representation of visual information can be found in a cortical area that is not involved in its feedforward processing. Further, the information was position-invariant, meaning that the accuracy of the representation in the foveal cortex was not affected by the position of the stimulus in the periphery. Before this study, there was no evidence that information in the retinotopic cortex could be position-invariant. In the light of these findings, researchers suggested that the effect was the result of higher-level cortical areas feeding back object information to foveal retinotopic cortex.

(A)

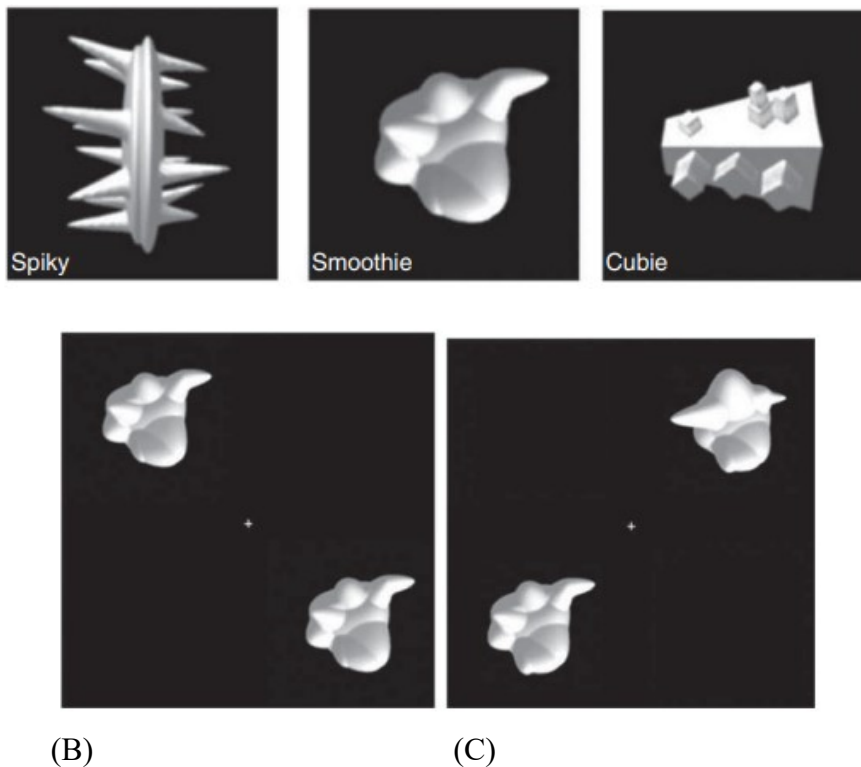


Figure 1.2: Typical examples of the stimuli used in the experiment by Williams et al. (2008), one from each category (A). An example of display with two identical smoothies on the left diagonal (B). An example of display with two different smoothies on the right diagonal.

1.4 Behavioural evidence of the constructive feedback effect

Williams et al. (2008) hypothesised that the foveal feedback effect was behaviourally relevant. They investigated two aspects of the phenomenon: (i) whether it could only be observed when performing a task relative to the shape and form of an object (ii) and whether a more robust information in the fovea would lead to an improvement in the task performance. Unusually, behavioural aspects were analysed only after finding neurobiological evidence of the effect through fMRI and have been extensively explored by following studies.

In a variation of the original study, Williams et al. (2008) found object information in the foveal-retinotopic cortex only when participants performed an object-comparison task. There was no effect with a colour-comparison task on the same stimuli and with the same level of difficulty. Further, when subjected to successive trials of the same stimulus category in lockstep, participants showed an increasing improvement in task performance. These results were interpreted as clear evidence of a behavioural relevance.

Chambers et al. (2013) used transcranial magnetic stimulation (TMS), a complementary technique to the fMRI, to extend the results from Williams et al. (2008) and try to answer some of the open questions they left. The matters included whether object information in the foveal retinotopic cortex has a causal role relating to perception or whether the pattern of activation is instead the result of nonessential activity elsewhere.

In the first experiment, participants performed a same or different task on peripheral stimuli, almost identically to Williams et al. (2008). The second experiment was the same as the first one, with the only difference that the targets could also be presented in the fovea. During both tasks, TMS was applied over the posterior termination of the calcarine sulcus (where the foveal representation is localised), or in a control non-calcarine area in the occipital lobe, between -150 and +400 ms relative to stimulus onset.

Results showed that (i) applying TMS on the calcarine site between +350/400 ms causes an impairment in object recognition in the periphery but not in the fovea, (ii) while stimulation at +50/150 ms (the time window when the feedforward system is expected to work) only disrupts foveal but not peripheral activity.

These findings are consistent with the initial hypothesis that foveal vision plays a causal role in peripheral object recognition. Also, the information is fed back during a specific time window that, if disturbed by interference, leads to a drop in performance.

More behavioural evidence comes from a study by Weldon et al. (2016), whose purpose was to investigate the consequences of displaying a visual distractor, at different timings and positions in the visual field, while performing an object recognition task in the periphery. The task used the same stimuli and was similar to the object discrimination task from the original study by Williams et al. (2008), with the only difference that a visual distractor was presented during part of the trials.

In the first experiment, the distractor was presented at fixation at five different stimulus onset asynchronies (SOAs) (-267, -117, 0, +117 or +276 ms) and was an object either from the same category of the targets or from a different category, spiky, smoothie and cubie (Op de Beeck et al., 2006). In the second experiment the distractor was presented in non-foveal locations of the visual field. The aim was to see if the performance could be altered due to an alerting effect, confusion in the display or influence from memory depending on whether the distractor was presented before, simultaneously or after the targets. Experiments 1 and 2 revealed that the effect is strongly dependent on time and location: the performance was most affected when the distractor appeared at +117 ms SOA and only when at fixation.

This specific paradigm made it possible to examine the consequences of competing feedback and feedforward systems. Unlike the study by Chambers et al. (2013), in which TMS had an immediate effect on the cortical areas of interest, a visual distractor needs to be processed by feedforward mechanisms first.

Further, Weldon et al. (2016) could also compare the impact of a distractor either consistent or inconsistent with the targeted objects category. Results showed that different types of distractors did not influence the performance in a significantly different way. Once again, the data were consistent with the idea that foveal vision is essential when performing complex tasks on peripheral stimuli.

In the same year, Yu and Shim (2016) conducted a series of experiments to find out the behavioural consequences of two different conditions that had never been investigated

before: direct manipulation of information in the fovea and processing of low-level visual information.

To recreate the first condition, they used a dual task paradigm that required participants to decide whether a stimulus presented in the periphery was the same as a previously shown target. Further, one of three types of distractors (foils) appeared in fovea at a subconscious level +150 ms after stimulus onset. The foil could be identical to the target, different from the target from a different stimulus set or different from the target from a scrambled object set. The higher-level stimuli were from the three abstract shape categories originally created by Op de Beeck et al. (2006). Results showed that, when the foil was a higher-level visual object identical to the target, peripheral object discrimination was facilitated. Consistent with previous studies, the effect only occurred in the fovea, and could only be observed some time after the presentation of the target.

To determine whether foveal low-level visual information affects peripheral object discrimination, Yu and Shim (2016) used a similar paradigm to the first set of experiments, except that the stimuli were gratings with different orientations. Unlike the foil effect in higher-level objects, it was found that a grating foil not only lacks foveal specificity, but it also has a different effective timing and direction of the effect. The performance is impaired (not facilitated) when the grating foil is presented simultaneously to target stimuli.

Taken together, these results indicate that two distinct mechanisms might be responsible for high- and low-level visual processing in fovea. Researchers suggested that the gratings effect could be explained by “the spread of bottom-up feature responses through feature-based attention, which can enhance the processing of a given visual feature across the visual field” (Yu & Shim, 2016, p. 19). On the other hand, the foil effect in objects is consistent with the foveal feedback explanation but it suggests a substantially reduced effective timing compared with previous studies. Chambers et al. (2013) reported an impairment in performance when applying TMS at 350-400 ms after stimulus onset, while Yu and Shim (2016) observed a similar effect at only 150 ms after the stimulus was presented. This could be explained by differences in the paradigms used in the two studies.

1.5 Temporally flexible feedback signal to foveal cortex for peripheral object recognition (Fan et al., 2016)

Finally, the study we decided to replicate is from the set of experiments carried out by Fan, Wang, Shao, Kersten and He (2016), who focused on investigating the temporal window in which the foveal feedback effect occurs. In the leading experiment, participants performed the same peripheral object discrimination task from the study by Williams et al. (2008): they fixated centrally while two stimuli were shown in diagonally opposite quadrants of the peripheral visual field. The stimuli were very similar to the ones from the “spiky” category by Op de Beeck et al. (2006). Further, a dynamic noise patch was presented at fovea at five different SOAs: 50, 150, 250, 350 and 450 ms, plus a no-noise condition. The data showed that the performance was significantly impaired 50 and 250 ms after stimulus onset. Fan et al. (2016) suggested different explanations for the two dips. The performance drop at 250 ms is consistent with the general idea of the foveal feedback effect, suggesting a time window during which the mechanism is effective. The performance drop at 50 ms was instead explained as the consequence of an attentional distraction caused by the partial overlap in time of the noise patch and the targets.

In the light of a clear proof of a foveal engagement limited to a specific time window, Fan et al. (2016) broadened their research to check whether this effect was both stimulus and task dependent. In the first condition, they used the same paradigm from the first experiment but with only stimuli with a low spatial frequency. In the second condition, the task involved patches of random dots moving at different speeds that participants had to discriminate. The effect was not found in either of the experiments, providing evidence that foveal feedback requires an object recognition task where detailed visual features must be detected in the periphery.

One more evidence that came from the study concerns the flexibility of the time window when the effect occurs. In a variation of the original experiment, Fan et al. (2016) made participants perform a discrimination task that also involved mental rotation. Thus, one of the two stimuli presented peripherally was in a horizontal position, while the other one was rotated clockwise at a certain angle. Subjects were prepared to mentally rotate the inverted stimulus and then compare it to the horizontal one. The same dynamic noise

patch from the main experiment was presented in fovea at five SOAs plus the no-noise condition.

As initially hypothesised, results still showed a drop in the performance, but it was observed at the SOA of 450 ms, with a clear delay compared to the SOA of the drop found in the main experiment (250 ms). Since the tasks were equally difficult, the results have been explained with a delay of the foveal engagement: the contribution of the foveal retinotopic cortex is not automatic; it starts as soon as detailed information is needed, which depends on the type of task performed and on the processes required by higher-tier cortical areas. This is consistent with the type of task used, where another process such as mental rotation needs to be implemented before the object discrimination.

Finally, Fan et al. (2016) used fMRI to investigate exactly what kind of information the foveal retinotopic representation contains. Multivoxel pattern analysis was applied to analyse the activity of three different regions of interest (ROIs): foveal cortex, peripheral cortex and LOC. The ROI relevant for the study was the foveal cortex, where sensitivity to orientation as well as to object category was found; however, the two types of information were independent. Therefore, the representation in the foveal cortex is greatly image based and contains much information about stimuli presented peripherally, especially regarding general shape and spatial details. These results support the hypothesis of the foveal retinotopic cortex containing different types of information at a both fine and coarse spatial scale. Thus, foveal feedback might be involved in tasks that require fine details processing as well as in tasks based on comparisons between more general features across different categories.

The performance impairment during peripheral object discrimination induced by a visual dynamic distractor is consistent with the results from the studies by Weldon et al. (2016) and Yu and Shim (2016). Taken together, results from the different sets of experiments from Fan et al. (2016) have added quite strong behavioural and psychophysical evidence to the foveal feedback hypothesis.

1.6 Theoretical interpretations

As illustrated above, in the last years several studies have shown empirical evidence of a foveal engagement in the processing of visual stimuli presented in the periphery of the

visual field. But what is the purpose of this phenomenon and what neural mechanisms can be underlying? Even though an unequivocal and final explanation is still to be found, a few theories have been suggested.

The results from the study by Williams et al. (2008) pointed that the influence of the foveal retinotopic cortex on peripheral object recognition is unlikely to be a product of monosynaptic lateral connections between low-level cortical areas, and this was confirmed by subsequent studies (Weldon et al., 2016; Yu and Shim, 2016; Fan et al., 2016). In all the studies reported, the distance between the foveal distractor and the peripheral targets goes beyond the typical spread of horizontal networks in V1, which does not exceed three degrees of visual field (Angelucci et al., 2002). Further, some data are difficult to explain without the support of a feedback mechanism. Passive transmission of information through the retinotopic cortex is not sufficient to justify why the information is propagated to no cortical areas other than the foveal retinotopic cortex, or why it is position invariant and task dependent while it is not in the peripheral retinotopic cortex (Williams et al., 2008).

Williams et al. (2008) and, later, also Fan et al. (2016) hypothesised that in peripheral object recognition tasks, such as the ones used in their studies, subjects might be influenced by the expectation that the image will eventually end up in the fovea, even though eye movements are not allowed. This might be driven by an innate mechanism resulting from our every-day experience, in which we normally foveate the objects of our interest so that we can process their finest details. In other words, subjects may perhaps unconsciously predict imminent saccades, thus providing anticipatory signals to the foveal retinotopic cortex. This phenomenon was found in other contexts and described as predictive remapping. For instance, Walker et al. (1995) observed that intermediate layer visuo-movement cells in monkeys anticipated their response to a visual stimulus before an imminent saccade would bring the stimulus in the receptive field. The results from the study by Fan et al. (2016) that the foveal noise did not influence the performance when subjects planned and completed a saccade support the predictive remapping hypothesis. However, this theory does not explain the finding from Williams et al. (2008) study that foveal information is nearly absent at the start of every series of trials from the same object category, but it eventually increases and accumulates by the end of the series.

Therefore, this might not be the final explanation of how feedback of object information to foveal cortex modulates task performance.

The most likely interpretation proposed so far suggests that V1 might work as a buffer or notepad and store high-resolution information for high-level cortical areas. This information is crucial in tasks that require visual details, such as object recognition. This theory was first discussed in a study by Lee et al. (1998) as an alternative to the classic model for the computation of image meaning. Overall, the results suggested that V1 benefits from intracortical and feedback connections to participate in many different stages of visual analysis. The primary visual cortex “is not just a module for computing local features, but possibly serves as a high-resolution buffer or visual computer to perform all computations that integrate global information with spatial precision” (Lee et al., 1998).

If this is the case, then it is possible that the foveal feedback effect implies higher-level abilities of foveal processing that enhance peripheral vision unidirectionally (Stewart et al., 2020).

1.7 Conclusions

Overall, there is a consensus that foveal vision is essential during tasks that involve peripheral object recognition. There also is joint evidence that this effect is the result of high-level cortical areas feeding back visual information to the foveal retinotopic cortex, where a representation of the peripheral stimuli was found through fMRI (Williams et al.). The disruption of the foveal representation was found to have clear behavioural consequences: it causes a performance impairment during peripheral object recognition tasks (Chambers et al., 2013; Weldon et al., 2016, Yu and Shim, 2016; Fan et al., 2016). The disruption can either be generated by TMS, as in Chambers et al. (2013), or by a visual distractor showed in fovea during the execution of the task. However, based on whether the effect is (i) caused by non-invasive brain stimulation or (ii) behaviourally induced, its effective time window shifts from +350/400 ms after stimulus onset in the first scenario to +250 ms in the second scenario. This is probably because TMS has an immediate effect on brain activity while a foveal distractor involves other feed-forward processing mechanisms before becoming effective (Fan et al., 2016).

Further, when the performance is modulated by a visual distractor, findings have shown that its effect is both location- and task-dependent, meaning that:

- the performance is only affected when a visual distractor is presented in the fovea, and not elsewhere (Weldon et al., 2016),
- the performance when completing tasks that do not involve object recognition, such as colour-comparison tasks, is not affected by impairment of foveal vision (Williams et al., 2008).

It seems likely that foveal vision, which has a very high spatial resolution, might give support to peripheral vision when the latter is involved in complex tasks that require visual details that would not be obtained otherwise.

Because foveal feedback typically occurs during fixation and is not observed when a saccade has been planned beforehand, there might be a connection between its effects and saccades (Stewart et al., 2020). It has been hypothesised that we anticipate the saccade during a peripheral object recognition task, even though it does not allow eye movement. Thus, we might be sending an anticipatory signal to the foveal retinotopic cortex. This might be due to a build in mechanism that originates from our tendency to look at visual stimuli with our fovea when we need detailed information about them. (Fan et al., 2016).

Another explanation might be that the primary visual cortex is capable of more complex activities than recognising position and orientation of visual stimuli (Lee et al., 1998). Its abilities might include storing detailed information that are later used by higher-level cortical areas for, in this specific case, peripheral object recognition tasks (Fan et al., 2016; Weldon et al., 2016).

Despite clear evidence of a foveal feedback mechanism that can influence peripheral object discrimination, the function of this effect remains unclear as well as its neurobiological explanation. Foveal feedback is a recent finding and it needs further analysis to explain the several questions that remain unanswered. Some of the aspects that could be examined in the future include the effect of foveal-feedback signals on learning how to recognise objects, the consequences of foveal scotomata on peripheral object recognition, or how foveal feedback works with different textures (Stewart et al., 2020).

CHAPTER 2

2.1 Feedback signal to foveal cortex for peripheral object recognition

As illustrated in Chapter 1, after the discovery of a foveal feedback mechanism by Williams et al. (2008), different studies have investigated the behavioural consequences when manipulating the foveal representation of peripheral stimuli (Weldon et al., 2016, Yu and Shim, 2016; Fan et al., 2016).

In particular, the first experiment from the study by Fan et al. (2016) investigated the effect of disrupting vision in the fovea while performing an object recognition task in the periphery. This was induced by the presentation of a foveal noise at five different stimulus onset asynchronies (SOAs) plus a condition where no noise appeared. The results revealed a significant drop in the mean object discrimination sensitivity (d') when the foveal noise was presented 250 ms after stimulus onset (Figure 2.1).

The effect found is very strong. Despite reasonable evidence that peripheral and foveal vision are not independent, the foveal feedback hypothesis is recent and it still lacks a comprehensive theory that describes how it operates.

The current study is an attempt to collect more data about how the foveal feedback works by replicating the first experiment from the study by Fan et al. (2016). We examined (i) whether there were any changes in the performance through the different levels of the SOAs; (ii) whether at some levels the performance was impaired and (iii) at what levels of the SOAs the drop occurs. The initial hypothesis was that we would replicate the pattern of results obtained in the original study in terms of changes in d' through the different levels of the SOAs.

The study was conducted during the Covid-19 pandemic which prevented the access to the laboratories. Therefore, this study represents an online replication of the original one. We tried to comply to the original paradigm as much as possible using the same stimuli and procedure. We had no direct control on participants position and distance from the

screen, or their eye movements. However, before starting the experiment, each subject received detailed information about how to position themselves and maintain fixation.

In the original Fan et al. (2016) experiment, 11 subjects participated, performing 2.688 trials each, excluding practice. Such a high number of trials per subject would cause a high drop rate in remote data collection. We decided to maintain the overall number of trials of the original study (29.568 trials) but distributed over a higher number of subjects. This ensures a similar statistical power to the original study. To keep the overall duration close to half an hour we decided to have 528 trials per subject (2 blocks of 264), resulting in a total number of required participants of 56.

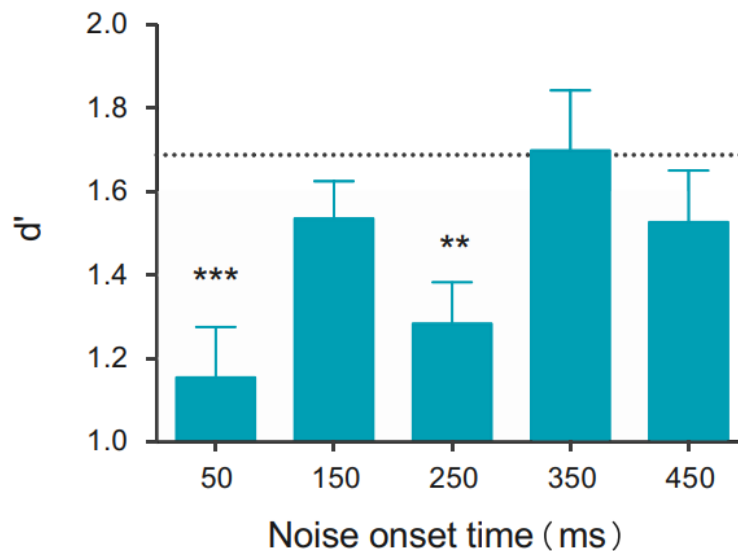


Figure 2.1: This is the pattern of results of the first experiment by Fan et al. (2016). The d' prime values revealed two dips, at 50 ms and 250 ms after stimulus onset. The 50 ms dip was explained by the authors in terms of an attentional distraction caused by the partial overlap in time of the noise patch and the targets. The 250 ms dip was consistent with the foveal feedback theory, suggesting a time window during which the mechanism is effective.

2.2 Method

2.2.1 Subjects

A total of 56 volunteers participated in the experiment (34 females). The age range was 16-63 years. All subjects had normal or corrected-to-normal vision. The criterion for the inclusion of a subject was a sensitivity index (d' prime) higher than 0.7, computed from correct and incorrect responses. This criterion was chosen because the task is difficult, and some participants may perform at chance.

2.2.2 Apparatus

The study was programmed using *PsychoPy*³ (Peirce, 2009) and carried out remotely using the Pavlovia server (https://run.pavlovia.org/GContemori/samedifferent_3blocks/html). This required the participants to perform the experiment on their own personal computer. They went through a preliminary step which involved resizing the picture of a credit card on the screen and matching it with the size of a real one. This was necessary to work out the screen dimensions for each device and adapt the stimuli each time. Further, the participants received the instruction to position themselves at a viewing distance of 57 cm. In this way, 1 degree of visual angle corresponds with 1 cm on the screen. All the screens had a refresh rate of 60 Hz.

2.2.3 Stimuli and procedure

Target objects were abstract 3D shapes from the spiky category used by Fan et al. (Figure 2.2 (B)). We thank the authors for providing the images.

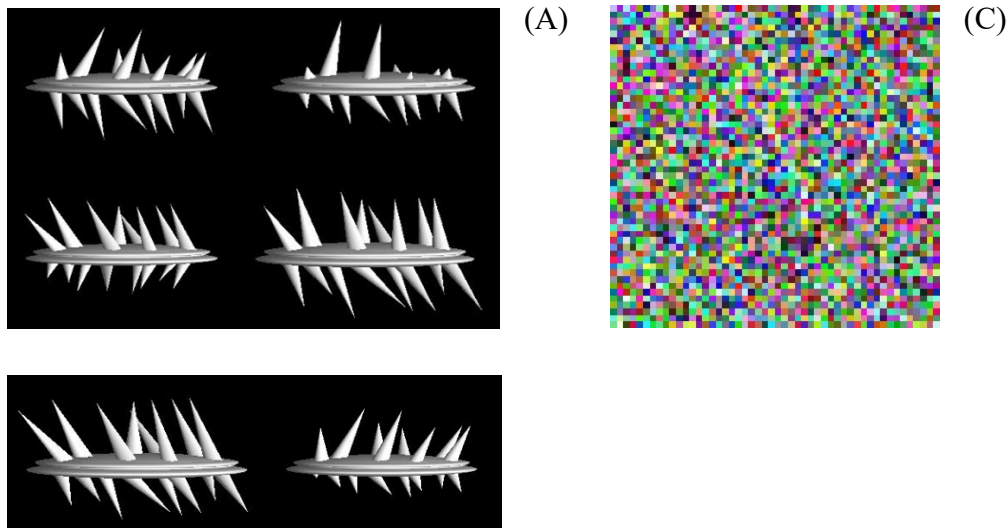
The average size of the stimuli was $3 \times 1.5^\circ$ and their eccentricity was 7° . The differences between the objects were represented by: (1) the length of upper spikes, (2) the length of lower spikes, (3) the orientation of upper spikes, (4) the orientation of lower spikes (Figure 2.2 (A)). In each trial two objects were randomly selected from the set of 1,296 so that they could either be different or the same. Some pairs of stimuli had clear differences, some had more subtle differences. They were presented on a black screen for 100 ms in diagonal quadrants on two sides of the fixation, switching during the trials from upper left and lower right (quadrants 1 and 3) (Figure 2.3 (A)) to upper right and lower left (quadrants 2 and 4) (Figure 2.3 (B)). This was made so that subjects did not have any expectations about where the targets will appear. Although we did not use eye-tracking, participants were instructed to maintain central fixation. Further, the presence of the targets on the screen was very short and it would have made eye-movements counterproductive (Weldon et al., 2016).

Participants performed a same-different task on the peripheral stimuli. They were asked to press one button for answering ‘different’ and another button for answering ‘same’ as fast as they could. A dynamic noise patch appeared in fovea for 83 ms at 5 stimulus onset asynchronies (SOAs) (50, 150, 250, 350, and 450 ms), plus a no-noise condition. The

patch was a $7 \times 7^\circ$ square, with centre at the fixation (Figure 2.2 (C)). The perception of movement was induced by the multiple smaller squares that the noise was made up of, whose colour changed repeatedly during the presentation of the patch.

Before starting, each subject watched a video of instruction on how to better detect the differences between the targets. The video showed some examples from the set of spikey objects and the characteristics to mainly focus on. The experiment consisted in one training block and two experimental blocks. This was necessary to make participants expert in the task and to replicate the condition from the original study where “subjects ran several training sessions before the experiment” (Fan et al., 2016, Supporting information, p. 1). The training block also included a feedback message after every trial to inform the subjects whether their answer was correct or not.

There were 24 stimulus conditions (2 [objects same vs. different] \times 2 [objects in quadrant 1/3 vs. 2/4] \times 6 [5 SOAs vs. no noise condition]). Each condition had 22 trials (total 528), and order of presentation was random. The practice block consisted in 24 x 11 trials.



(B)

Figure 2.2: These are the stimuli used in the experiment. Two samples of spikey objects chosen from the dataset to point out the differences between them: (1) the length of upper spikes, (2) the length of lower spikes, (3) the orientation of upper spikes, (4) the orientation of lower spikes (A). A random sample of four spikey objects extracted from the dataset (B). A frame of the dynamic foveal noise (C).

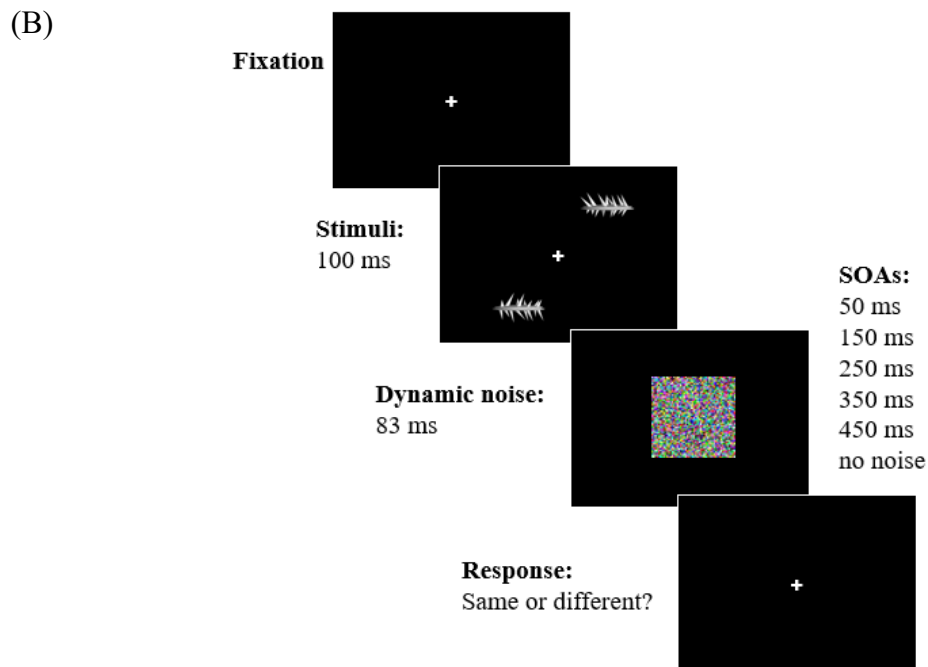
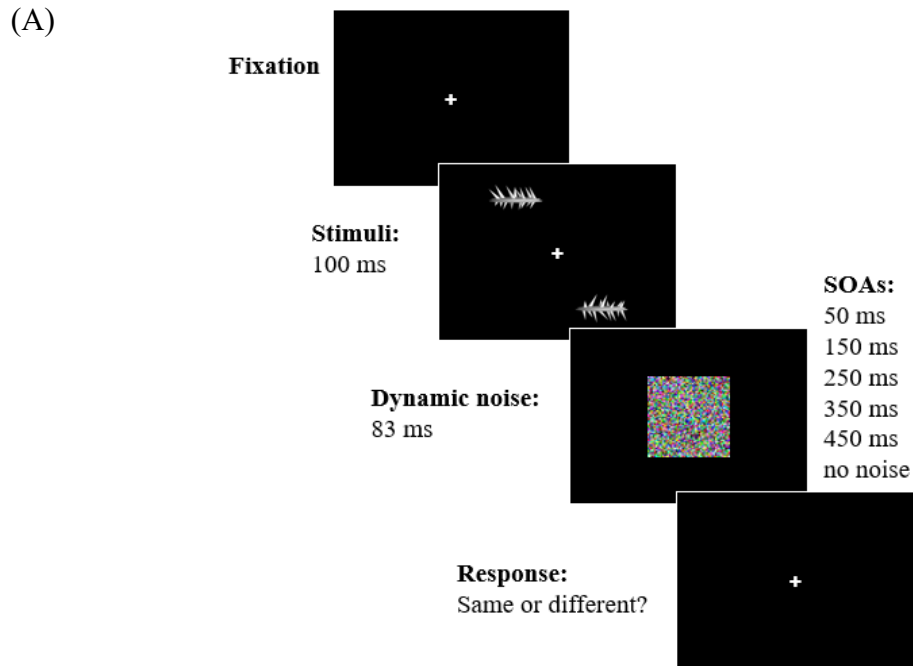


Figure 2.3: Schematic of a trial in the experiment. Two spiky objects were presented for 100 ms in the periphery of the visual field in diagonally opposite quadrants: quadrants 1 and 3 (A) or quadrants 2 and 4 (B). Then, a dynamic noise patch appeared in fovea for 83 ms at 5 different SOAs: 50, 150, 250, 350 and 450 ms. There also was a condition in which no noise appeared. Then, the participants had to make a “same or different” decision by pressing a button.

2.3 Results

The dependent variable was the d' prime for peripheral target discrimination computed from Hit and False Alarm Rates. The Hit rate corresponded to the proportion of correct “same” responses in “same” trials. The False Alarm rate corresponded to the proportion of wrong “same” responses in “different” trials. We computed overall d' prime as well as d' prime for each condition of the independent variable. We excluded 8 subjects due to an overall d' prime $< .7$. The independent variable was the SOA, which was treated as a discrete ordinal variable with six levels, where the first level corresponded to the absence of noise.

The analysis was conducted through the software *R*, using the packages *lme4* (Doran et al., 2007) and *lmerTest* (Kuznetsova et al., 2015) for the orthogonal polynomial contrasts.

A one-way repeated measures ANOVA, with the levels of the SOAs as the only within-subjects variable, revealed a significant main effect ($F(5, 275) = 5.78; p < .001$).

Therefore, we used orthogonal polynomial contrasts to identify the regression model that would best describe the data trend. A linear model did not adequately explain the variability of the data ($F(1, 279) = 1.29; p = 0.26$). So, we moved on to evaluating the goodness of fit of a non-linear regression. Using a quadratic model, SOAs levels were significant ($t = 3.88; p < .001$) as shown in Figure 2.5. Through a graphical representation we were able to locate a dip in the d' prime distribution at 150 ms SOA level (Figure 2.4).

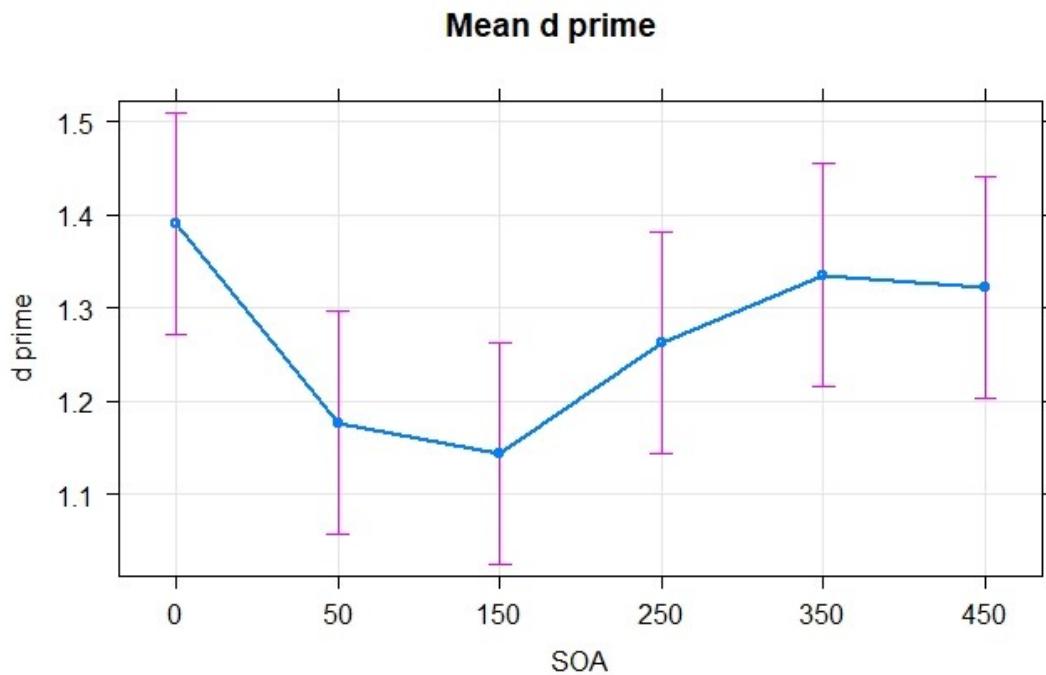


Figure 2.4: Mean values of d primes at each level of the SOAs (50, 150, 250, 350, 450 ms). The values at 0 (SOA) correspond to the condition in which no foveal noise was presented. The graph reveals a dip in d prime when the noise appears 150 ms after stimulus onset ($d' = 1.14$).

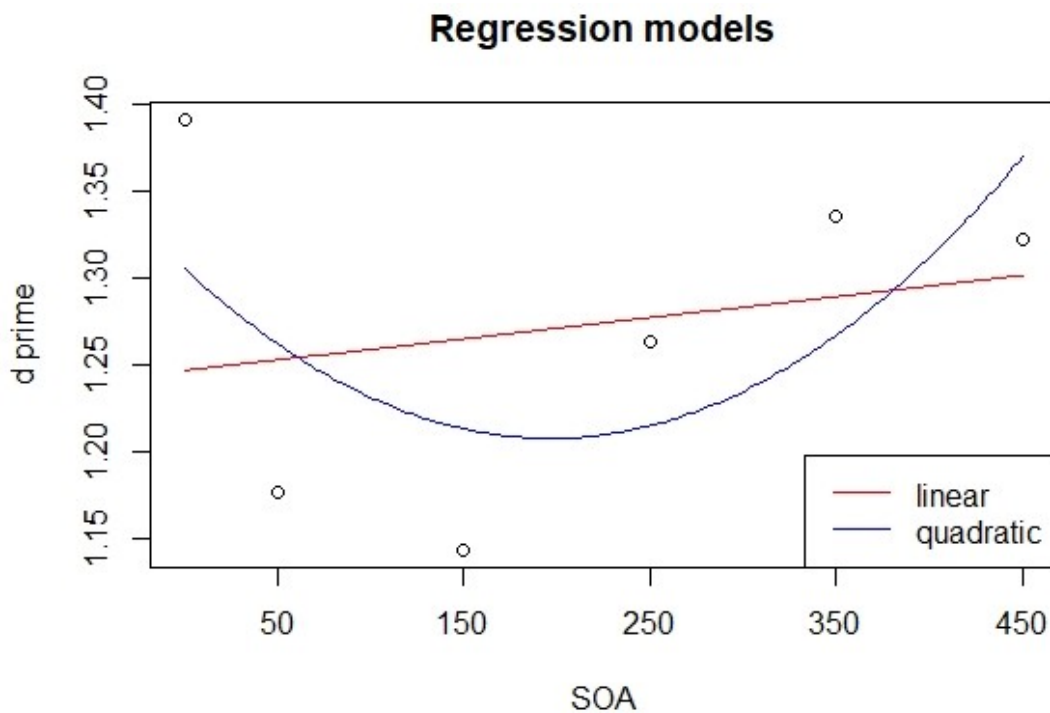


Figure 2.5: The regression models for the experiment results. The quadratic model is the one that best describes the data trend.

2.4 Discussion

The results from the experiment by Fan et al. (2016) revealed a dip in the performance at 250 ms after stimulus onset. With our replication we were able to obtain a similar pattern of results, but with a shift of the temporal window during which the dip occurs. The lowest d' prime level can be seen at 150 ms after stimulus onset (Figure 2.5). Overall, there is an interaction between the d' prime and the levels of the SOAs. We conclude that our findings are consistent with the foveal feedback hypothesis and that, in principle, they reproduce the non-monotonic function of SOA observed in the original experiment.

The location of the dip with respect to SOA was not consistent with the original study. This might have been caused by some changes to the original paradigm we were forced to make due to the Covid-19 pandemic. First, the experiment was entirely carried out online and to make the task less demanding we reduced the number of total trials per subject from 2,688 to 528, but we increased the number of subjects to balance the experimental design. Further, we did not have direct control on the subjects position and distance from the screen, or their eye movements. Despite these changes, it is interesting that we were still able to see the trend underlined in the literature in our data. This suggests that foveal feedback during object recognition tasks is a strong effect and is robust to various experimental conditions.

However, the literature indicates that the temporal window for interference is flexible rather than fixed. Fan et al. (2016) showed that, adding mental rotation to the task, the engagement of the foveal retinotopic cortex is delayed. Presumably, the timing changes depending on the amount of processing required by higher-tier cortical areas to properly distinguish the targets.

The foveal feedback effect is a recent discovery and there are questions that remain unanswered. The studies conducted so far have shown that foveal feedback is a strong and robust effect, and at the same time they suggest several promising paths for future investigations. One of these is identifying a more precise timing of the engagement of the foveal cortex processing. This could be achieved by making some changes to the classical paradigm, especially by considering more levels of the SOAs and a larger number of trials.

Further, Fan et al. (2016) also found a dip in the d' level 50 ms after stimulus onset. They identified the cause of this phenomenon as the partial overlap in time of the mask and the peripheral targets that provokes an attentional distraction. This may open the door to another line of research to understand the role of attention in the foveal feedback effect.

Conclusion

Starting with the study by Williams et al. (2008), an increasing amount of empirical research has underlined that foveal and peripheral vision are not as independent as it was previously believed. When performing a peripheral object recognition task, the foveal retinotopic cortex seems to be engaged in the processing at some point. When the foveal retinotopic cortex activity is impaired a drop in the quality of the overall performance has been observed. The time window of the drop is now believed to be flexible and to change together with the amount of pre-processing required for the stimuli.

Neuroimaging investigations have confirmed that a foveal feedback mechanism facilitates the processing of peripheral targets during object recognition tasks, especially when shape is a task-relevant characteristic (Weldon et al., 2016). The underlying processes might involve collecting high-resolution information from a foveal representation of the peripheral target, which will later be used by higher-level cortical areas to process the same stimuli at a finer scale.

The aim of the current experiment was to gather more evidence about how the foveal feedback mechanism works. Due to the restrictions imposed by the Covid-19 pandemic, it was only a partial replication of the study by Fan et al. (2016). However, it still revealed a drop in the performance of an object recognition task for the central values of the stimulus onset asynchronies (SOAs), our independent variable.

Taken together, all the latest findings suggest several promising paths that could be explored in the future to reveal more aspects of the fascinating foveal feedback effect.

References

1. Angelucci, A., Levitt, J. B., Walton, E. J., Hupe, J.-M., Bullier, J., and Lund, J. S. (2002). Circuits for local and global signal integration in primary visual cortex. *Journal of Neuroscience*, 22(19):8633–8646.
2. Chambers, C. D., Allen, C. P. G., Maizey, L., & Williams, M. A. (2013). Is delayed foveal feedback critical for extra-foveal perception? *Cortex*, 49, 327-335.
3. Doran, H., Bates, D., Bliese, P., & Dowling, M. (2007). Estimating the Multilevel Rasch Model: With the lme4 Package. *Journal of Statistical Software*, 20(2), 1 - 18. doi:<http://dx.doi.org/10.18637/jss.v020.i02>
4. Fan, X., Wang, L., Shao, H., Kersten, D., & He, S. (2016). Temporally flexible feedback signal to foveal cortex for peripheral object recognition. *Proceedings of the National Academy of Sciences*, 113 (41), 11627–11632.
5. Kourtzi Z, Kanwisher N. 2001. Representation of perceived object shape by the human lateral occipital complex. *Science* (New York, N.Y 293: 1506-9).
6. Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2015. Package ‘lmerTest’. RPackage Version, 2
7. Lee, T. S., Mumford, D., Romero, R., & Lamme, V. A. (1998). The role of the primary visual cortex in higher level vision. *Vision Research*, 38 (15-16), 2429-2454.
8. MacMillan, N., & Creelman, C. (1991). Detection theory: A user’s guide. Cambridge, UK: *Cambridge University Press*.
9. Op de Beeck, H. P., Baker, C. I., DiCarlo, J. J., & Kanwisher, N. G. (2006). Discrimination training alters object representations in human extrastriate cortex. *Journal of Neuroscience*, 26 (50), 13025-13036.
10. Panichello, M. F., Cheung, O. S., & Bar, M. (2013). Predictive feedback and conscious visual experience. *Frontiers in psychology*, 3, 620.
11. Peirce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, 2, 10. <https://doi.org/10.3389/neuro.11.010.2008>
12. Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature neuroscience*, 2 (11), 1019-1025.

13. Schneider, W. J., & McGrew, K. S. (2012). *The Cattell-Horn-Carroll model of intelligence*. In D. P. Flanagan & P. L. Harrison (Eds.), *Contemporary intellectual assessment: Theories, tests, and issues* (p. 99–144). The Guilford Press.
14. Stewart, E. E., Valsecchi, M., & Schütz, A. C. (2020). A review of interactions between peripheral and foveal vision. *Journal of Vision, 20* (12), 2-2.
15. Walker, M. F., Fitzgibbon, E. J., & Goldberg, M. E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *Journal of Neurophysiology, 73* (5), 1988-2003.
16. Weldon, K. B., Rich, A. N., Woolgar, A., & Williams, M. A. (2016). Disruption of foveal space impairs discrimination of peripheral objects. *Frontiers in Psychology, 7* :699, 1-8.
17. Weldon, K. B., Woolgar, A., Rich, A. N., & Williams, M. A. (2020). Late disruption of central visual field disrupts peripheral perception of form and color. *PloS One, 15*(1), e0219725. <https://doi.org/10/gjsn59>
18. Williams, M. A., Baker, C. I., Op de Beeck, H. P., Shim, W. M., Dang, S., Triantafyllou, C., & Kanwisher, N. (2008). Feedback of visual object information to foveal retinotopic cortex. *Nature Neuroscience, 11* (12), 1439–1445.
19. Yu, Q., & Shim, W. (2016). Modulating foveal representation can influence visual discrimination in the periphery. *Journal of Vision, 16* (3):15, 1–12