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Modulating Foveal Representation can Influence Visual Discrimination in the Periphery

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A previous study by Williams et al. (2008) provided evidence for a novel form of feedback in the visual system, whereby peripheral information is contained in foveal retinotopic cortex. Beyond its possible implication for peripheral object recognition, few studies have examined the effect of a direct behavioral manipulation of the foveal feedback representation. To address this question, we measured participants' peripheral visual discrimination performance while modulating their foveal representation in a series of psychophysical experiments. On each trial, participants discriminated the identities of briefly presented novel, three-dimensional objects or the orientations of gratings in a peripheral location while fixating at the center. Besides the peripheral target, another stimulus (foil) was also presented and masked at the fovea. Our results showed that for objects, when the foveal foil that was identical to the peripheral target was presented 150 ms after the onset of the peripheral target, visual discrimination of the peripheral target was improved. This congruency effect occurred even though participants did not consciously perceive the foveal stimulus. No such effect was observed when the foveal foil was presented simultaneously with the peripheral target, or when the foil was presented in a parafoveal location. The foil effect in gratings was different from that in objects in terms of its effective timing and foveal specificity, suggesting that foveal feedback may be specific to high-level objects. These results indicate that modulating foveal information can affect individuals' ability to discriminate peripheral objects, suggesting a functional role of foveal representations in peripheral visual perception.

Introduction

It is widely accepted that the human visual system maintains a retinotopically organized structure, in which spatial locations in the visual field are mapped to corresponding cortical locations in a well-defined manner (Sereno et al., 1995; Wandell & Winawer, 2011). However, human visual cortical pathways are not merely constrained by feedforward projections, but also include a rich set of feedback connections. These feedback connections are believed to carry top-down information about behavioral context and thus modulate the response profiles of neurons in the earlier stages of visual processing accordingly (Bullier, 2001; Gilbert & Li, 2013; Lamme & Roelfsema, 2000).

Whereas earlier work examining feedback processing reported modulations of existing feedforward signals (Ress & Heeger, 2003; Roelfsema, Lamme, & Spekreijse, 1998), a more recent functional magnetic resonance imaging (fMRI) study using multi-voxel pattern analysis demonstrated a novel case of feedback in which information is generated where no feedforward input exists (Williams et al., 2008). They found that when participants performed a comparison task on two peripheral objects while fixating at the center, information about an object presented in the periphery was successfully decoded from spatial patterns of activation in the area of retinotopic cortex corresponding to the fovea, where no actual stimulus was presented. Chambers, Allen, Maizey, and Williams (2013) further showed that when participants' foveal cortex was temporarily deactivated using transcranial

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magnetic stimulation (TMS), their discrimination of peripheral objects was impaired. In particular, this impairment in peripheral target discrimination reached its peak when the TMS pulse was applied to the foveal cortex 350–400 ms after the stimulus onset, suggesting disruption may be specific to feedback rather than feedforward signals. These results have led to the "foveal feedback hypothesis," which proposes that, in order to enhance the processing of visual information in the periphery, foveal regions of retinotopic cortex receive feedback information about the content of the visual periphery from higher level cortical areas (Chambers et al., 2013; Williams et al., 2008).

Whereas these previous studies have examined the foveal feedback hypothesis at the cortical level and have provided evidence that foveal feedback representations are linked to discrimination performance in the periphery, to our knowledge, there is a lack of studies that examine the effect of a direct behavioral manipulation of this foveal feedback representation. Moreover, because previous studies on foveal feedback used novel, three-dimensional objects, which involve higher level visual areas such as lateral occipital and ventral temporal cortices (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Malach et al., 1995), the implications of the foveal feedback effect for the processing of low-level visual features remain unexplored.

Here, we conducted a series of psychophysical experiments using novel, three-dimensional objects and oriented gratings to investigate the behavioral relevance of foveal feedback representations for high-level objects and low-level visual features respectively. We hypothesized that the foveal representations of peripheral stimuli, if internally generated, should be able to interact with stimuli that are physically presented at the fovea. Therefore, to explore whether the foveal feedback representation plays a functional role in the processing of peripheral information, we presented a physical stimulus at the fovea to enhance or disrupt this internally generated foveal representation of the peripheral stimulus and examined possible effects on visual discrimination in the periphery. In the experiments, participants performed either an object or orientation discrimination task in the periphery while fixating at the center. Besides the peripheral target stimulus, an additional task-irrelevant stimulus was presented at the fovea (foveal foil). The foveal foil was either the same as the peripheral target stimulus, different from the peripheral stimulus, or a noise stimulus (scrambled object or plaid pattern) that did not contain any element of peripheral targets. Crucially, to prevent response bias that could occur if participants were able to consciously perceive the foveal stimulus, the stimulus at the fovea was made invisible through backward masking. In Experiments 1a, 1b, and 1c, we examined the effect of the foveal foil with novel, three-dimensional objects, and in Experiments 2a, 2b, and 2c, we tested the effect with oriented gratings.

General methods

Participants

Seventeen participants each participated in Experiments 1a, 1b, and 1c. Twenty participants participated in Experiment 2a, seventeen participants participated in Experiment 2b, and thirteen participants participated in Experiment 2c. All were between 18–32 years of age and had normal or corrected-to-normal vision. They participated in the experiment for partial course credit or monetary compensation. Participants were provided informed consent in accordance with the Institutional Review Board of Dartmouth College before the experiment.

Apparatus

Stimuli were presented on a 17-inch Mitsubishi CRT monitor. The screen resolution was 1024×768 and the refresh rate was 60 Hz. The viewing distance was 46 cm in Experiments 1a, 1b, and 1c; and it was 58.4 cm in Experiments 2a, 2b, and 2c. Stimuli were generated and presented using Matlab (The MathWorks, Natick, MA) and Psychtoolbox 3 extensions (Brainard, 1997; Pelli, 1997).

Experiment 1a

In Experiment 1a, we tested whether presenting a physical stimulus at the fovea can influence visual discrimination in the periphery. Cortical feedback processes are thought to be fast and immediate (Hupé et al., 2001; Lamme et al., 1998; Nowak, James, & Bullier, 1997), even as fast as feedforward processes that usually transmit object information to higher cortical areas (e.g., lateral occipital and ventro temporal cortices) in around 100 ms (Lamme & Roelfsema, 2000). Previous human TMS studies have also shown that cortical feedback can influence primary sensory cortex as early as 80–150 ms after stimulus presentation (Camprodon, Zohary, Brodbeck, & Pascual-Leone, 2010; Koivisto, Railo, Revonsuo, Vanni, & Salminen-Vaparanta, 2011). Based on these findings, we have chosen to present the foveal foil after the onset of the peripheral target with a 150-ms time interval. If feedback processing of object information through the

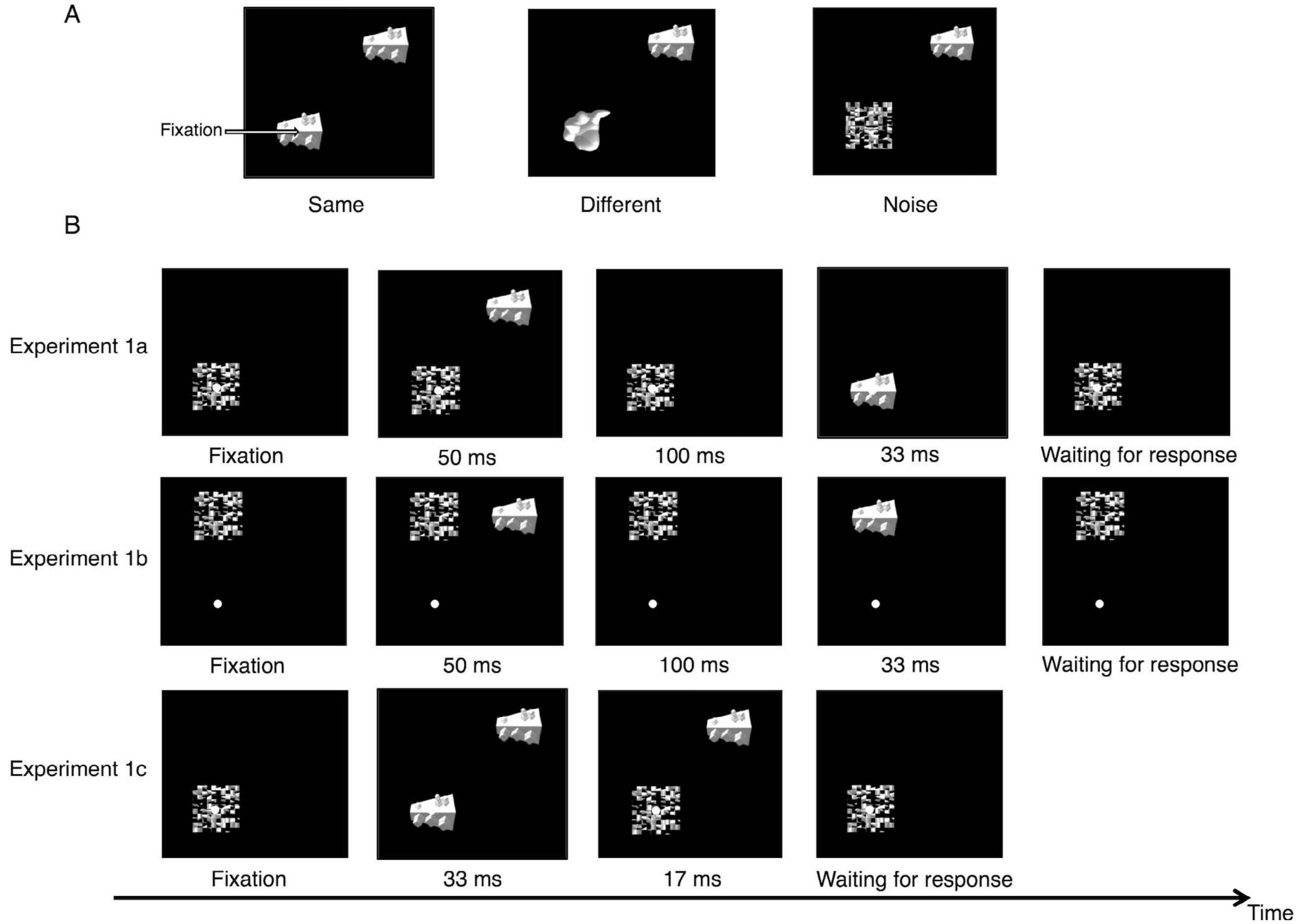

Figure 1. Stimuli and procedures in Experiments 1a, 1b, and 1c. All stimuli are shown in full contrast for demonstration purposes. (A) Examples of the three stimuli configurations (Same, Different, and Noise) in Experiments 1a and 1c. (B) A schematic diagram of a single trial in Experiment 1a (upper panel), Experiment 1b (middle panel), and Experiment 1c (lower panel).

visual hierarchy takes time to occur, we would expect to find a modulation effect by the foil when its onset was delayed compared to the peripheral target.

Methods

Stimuli and procedure

Two sets of novel, three-dimensional objects ("cubie" and "smoothie" respectively; see Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006; Williams et al., 2008) with eight exemplars each were used as stimulus sets. For each participant, one exemplar randomly chosen from each stimulus set (Cubie or Smoothie) was used as a target, while the other seven exemplars in each set served as nontargets. Another set of novel objects ("spikie") was used to create a scrambled object set. The scrambled objects were generated by superimposing a 10×10 grid on Spikie images and rearranging the squares randomly. One exemplar from this scrambled object set was used as a mask (contrast = 0.6) while the other eight exemplars were used as noise stimuli. All object images were 80×80 pixels in size. The contrast of the peripheral target image and the foveal foil image was 0.025 and 0.4, respectively.

Participants were required to fixate on the central fixation point throughout the experiment. On each trial, an object in the upper-right visual quadrant (eccentricity of 10°) was presented for 50 ms. One hundred fifty milliseconds after the onset of the peripheral target, a foveal foil stimulus was displayed at the center of the screen for 33 ms and masked. Each trial was followed by an 800 ms interval before the next trial began. Except for the time when the foveal foil was displayed, the mask stimulus remained on the screen throughout the experiment in order to minimize the influence of the stimulus onset at the fovea. There were three types of foveal foils (Figure 1A): a target exemplar (Same), a nontarget exemplar from a different stimulus set (Different), or an exemplar from a scrambled object set (Noise).

To obtain a quantitative measure of the conscious perception of the foveal stimulus, a dual task paradigm was used. First, participants judged whether the object

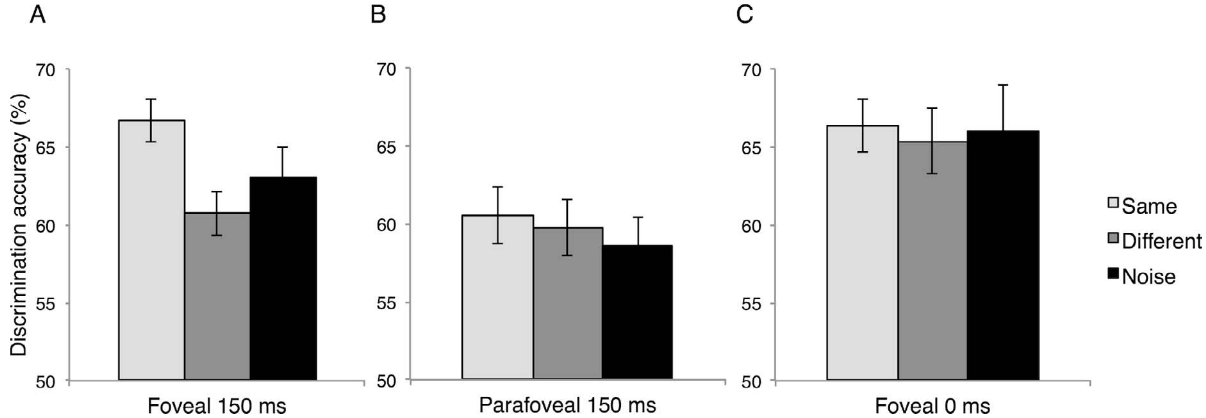

Figure 2. Average discrimination accuracies (%) of the peripheral object in the Same, Different, and Noise conditions in (A) Experiment 1a (foil delay = 150 ms, foveal foil), (B) Experiment 1b (foil delay = 150 ms, parafoveal foil), and (C) Experiment 1c (foil delay = 0 ms, foveal foil). Error bars show the ±1 standard error of the mean.

presented in the periphery was the target or a nontarget exemplar, and then they reported whether the object at the fovea was a Cubie or Smoothie (Figure 1B, upper panel). In each block, targets were selected exclusively from one object set (Cubie or Smoothie), and the order of each foil condition was randomized within a block. For a given block, nontarget exemplars in the periphery were chosen from the same stimulus set as the target exemplar. The experiment consisted of six to eight blocks (three to four blocks each for Cubie and Smoothie), and the order of blocks was randomized. Each block consisted of 60 trials, with 20 trials for each foil type. In total, participants performed 120 to 160 trials for each foil condition. Before the main experiment, participants completed a practice session of 32 trials with feedback for each stimulus set.

Results and discussion

In order to examine whether the foveal foil was consciously perceived, we first calculated the sensitivity index (d′) for the foil for each participant. Since participants performed a forced-choice task on whether the foil was a Cubie or Smoothie, no d′ results for the foil could be obtained in the Noise condition. Thus, we only analyzed the data in the Same and Different conditions. A one-sample t test showed that the d′ of the foveal foil ($M = 0.043$, $SD = 0.243$) was not significantly different from 0, $t(16) = 0.721$, $p = 0.481$. There was also no significant difference between the d′ for the Same and Different conditions, $t(16) = 1.198$, $p = 0.248$. These results confirmed that participants were not able to consciously identify an object presented at the fovea, suggesting that any difference in peripheral target discrimination across foil types was not likely to be caused by participants' conscious perception of the foil.

Next, we examined our main question of whether a foveally presented foil can influence visual discrimination of a peripheral object. Repeated measures Analysis of Variance (ANOVA) revealed that discrimination accuracies of the peripheral target were significantly different across different foil types, $F(2, 32) = 13.764$, $p < 0.001$. Subsequent pairwise t tests (Bonferroni corrected for all pairwise comparisons) between foil types revealed that the discrimination accuracy of the Same condition ($M = 0.667$, $SD = 0.060$) was significantly higher than that of the Different condition ($M = 0.607$, $SD = 0.060$), $t(16) = 5.673$, $p < 0.001$, as well as the Noise condition ($M = 0.631$, $SD = 0.079$), $t(16) = 3.046$, $p = 0.023$. However, no significant difference was found between the Noise and the Different conditions, $t(16) = 1.964$, $p = 0.202$ (Figure 2A). These results indicated that the foveal foil that consisted of high-level objects could facilitate peripheral object discrimination when it was identical to the peripheral target, even when this foil was not consciously perceived.

In the current experiment, the mask stimulus was a scrambled image of Spikie, which was a task-irrelevant object category that did not contain the features of either target category (Cubie and Smoothie). A follow-up experiment using mask stimuli that consisted of components from both target categories (Cubie and Smoothie) yielded qualitatively similar results to those obtained with the original Spikie mask, indicating that the differential effect between different foil conditions is unlikely to be caused by the specific type of mask.

In order to confirm participants' fixation during the experiment, we also collected the eye movement data from three additional participants. Whereas the same facilitative foveal foil effect was found, their eye movement results showed that participants' mean eye positions during the task were not significantly deviated from fixation, and that there was no substantial difference in the mean eye position between different foil conditions. Thus, the foveal foil effect on discrimination accuracy of a peripheral target was not likely to be accounted for by participants' eye position.

Experiment 1b

In Experiment 1a, we found that peripheral target discrimination was improved when a task-irrelevant foil that was identical to a target in the periphery appeared at the fovea. However, since the foil was presented only at the fovea, it is unclear whether this facilitation effect induced by the foil was specific to the foveal location as suggested by the foveal feedback hypothesis (Williams et al., 2008) or could also be generalized to other locations in the visual field. In Experiment 1b, in order to examine foveal specificity of the modulatory effect by an additional task-irrelevant stimulus, we tested the effect of a parafoveally presented foil.

Methods

The stimuli and procedure were identical to Experiment 1a, except that the foil was presented in a parafoveal location, which was on the upper vertical meridian at an eccentricity of 7.1°, horizontally aligned with the peripheral target (Figure 1B middle panel).

Results and discussion

Unlike Experiment 1a, no significant difference was found in discrimination accuracies of the peripheral target across the Same ($M = 0.605$, $SD = 0.074$), Different ($M = 0.598$, $SD = 0.075$), and Noise ($M = 0.586$, $SD = 0.078$) foil types, $F(2, 32) = 1.202$, $p = 0.314$ (Figure 2B). We further performed a 2 (foil location: foveal in Experiment 1a vs. parafoveal in Experiment 1b) × 3 (foil type) mixed-model ANOVA to compare the accuracies of peripheral target discrimination between the foveal and parafoveal foil conditions. The interaction effect between foil location and foil type was significant, $F(2, 64) = 4.816$, $p = 0.011$, indicating that the facilitative effect from an additional foil disappeared when the foil was moved to a parafoveal location. These results suggest that the effect of foil is specific to the fovea.

As in Experiment 1a, the d′ of the parafoveal foil ($M = 0.045$, $SD = 0.143$) was not significantly different from 0, $t(16) = 1.307$, $p = 0.210$, and there was no significant difference between the d′ for the Same and Different conditions, $t(16) = 0.209$, $p = 0.837$.

Experiment 1c

Experiment 1a showed that when a task-irrelevant foil that was identical to the peripheral target was foveally presented 150 ms after the onset of the target, peripheral target discrimination could be improved. A 150 ms delay of foil presentation is consistent with cortical delay of feedback input to early sensory cortex (Camprodon et al., 2010; Koivisto et al., 2011), supporting the involvement of foveal feedback in the foil effect in our experiment. However, there is a possibility that a similar effect may be observed even without a delay between the foil and the peripheral target. Thus, in Experiment 1c, we examined the effect of a delay of the foveal foil by presenting the foveal foil simultaneously with the peripheral target. If a delay from the onset of the peripheral target is required for the foveal foil to be effective, the foil effect would be diminished or absent when the foveal foil and the peripheral target are presented at the same time.

Methods

The stimuli and procedure were identical to those of Experiment 1a, except that the foveal foil was presented simultaneously with the peripheral target (Figure 1B lower panel).

Results and discussion

When the foveal foil and the peripheral target were simultaneously presented, no significant difference in discrimination accuracies of the peripheral target was found across the Same ($M = 0.664$, $SD = 0.069$), Different ($M = 0.654$, $SD = 0.078$), and Noise ($M = 0.660$, $SD = 0.105$) foil types, $F(2, 32) = 0.259$, $p = 0.773$ (Figure 2C). We then performed a 2 (foil delay: 150 ms in Experiment 1a vs. 0 ms in Experiment 1c) × 3 (foil type) mixed-model ANOVA to compare the accuracies of peripheral target discrimination between Experiment 1a and 1c. The main effect of foil delay was not significant, $F(1, 32) = 1.003$, $p = 0.324$, which indicated that overall task difficulty was not significantly different between when the foil was presented with a delay ($M = 0.635$, $SD = 0.061$) and when it was not ($M = 0.659$, $SD = 0.079$). However, there was a significant interaction effect between foil delay and foil type, $F(2, 64) = 3.982$, $p = 0.023$, and a significant effect of foil type, $F(2, 64) = 7.545$, $p = 0.001$. Consistent with the feedback hypothesis, these results suggest that the facilitation effect only occurs when the presentation of the foveal foil is delayed from the onset of the peripheral target.

Participants' d′ of the foveal foil ($M = -0.067$, $SD = 0.387$) was not significantly different from 0, $t(16) = 0.714$, $p = 0.485$. There was also no significant difference between the d′ for the Same and Different conditions, $t(16) = 0.886$, $p = 0.389$. To compare the performance in the foveal task between Experiment 1a and 1c, we conducted a 2 (foil delay: 150 ms in Experiment 1a vs. 0 ms in Experiment 1c) × 2 (foil type: Same vs. Different) mixed-model ANOVA. No significant interaction effect was found between foil delay and foil type, $F(1, 32) = 0.004$, $p = 0.947$. There was also no significant main effect of foil delay, $F(1, 32) = 1.822$, $p = 0.187$, or foil type, $F(1, 32) = 2.081$, $p = 0.159$. These results indicated that there was no difference between Experiment 1a and 1c in terms of task performance for the foveal foil.

Experiment 2a

In Experiments 1a, 1b, and 1c, we found that presenting a task-irrelevant foil identical to the peripheral target object can improve peripheral target discrimination. Consistent with previous studies on foveal feedback, this effect was specific to the fovea, and it only occurred when the foil appeared with some time interval after the onset of the target. However, this behavioral facilitation by the foveal foil was observed with high-level objects only, and it is unclear if low-level visual features, such as orientation, could also have a similar effect. Moreover, since previous fMRI and TMS studies have only tested novel objects to show foveal feedback (Chambers et al., 2013; Williams et al., 2008), it remains to be examined what information in the object stimuli is fed back. Is it high-level object information per se or low-level visual features that covary with object category, such as orientation? To address this question, in Experiment 2a, we examined if facilitation of peripheral target discrimination could also be found when basic visual feature stimuli, such as oriented gratings, were used as foveal foils and peripheral targets. As in Experiment 1a, the delay between the peripheral target and the foveal foil was 150 ms.

Methods

Stimuli and procedure

All stimuli were sinusoidal gratings (radius = 1.5°, spatial frequency = 2 cpd, phase angle randomized between 0° and 180°) or plaid patterns generated by combining the gratings. The target stimuli in the periphery were left- or right-tilted gratings (45° or 135°, contrast = 0.015). The stimuli at the fovea were the same left- or right-tilted gratings, or a plaid pattern composed of two superimposed gratings with 0° and 90° orientations (contrast = 0.15). The mask stimulus was created by superimposing two target gratings (contrast = 0.6).

Participants were required to discriminate the orientation of the grating presented in the periphery while fixating on the central fixation point. On each trial, a target grating in the upper-right visual quadrant (eccentricity of 10°) was presented for 50 ms. One hundred fifty milliseconds after the onset of the peripheral grating, a foveal foil stimulus was presented at the center of the screen for 33 ms and masked. Each trial was followed by an 800 ms interval before the next trial began. There were three types of foveal foils: a grating with the same orientation as the peripheral target (Same), a grating with an orientation that was orthogonal to the orientation of the target (Different), or a plaid that did not contain either target orientation (Noise). See Figure 3A.

As in Experiment 1, participants performed a dual task while fixating at the central fixation point. On each trial, participants first reported the orientation of the peripheral target (left- or right-tilted), and then indicated the orientation of the additional grating that appeared at the fovea (Figure 3B, upper panel). Each foil type was presented in separate blocks, and the order of foil types was randomized across blocks. The contrast of the peripheral target was adjusted on a trial-by-trial basis, and the discrimination contrast threshold of the peripheral target with 75% accuracy was obtained at the end of each block of 40 trials using a QUEST procedure (Watson & Pelli, 1983). The discrimination threshold for each foil type was estimated based on the results of two to three blocks.

Results and discussion

The d′ of the foil orientation ($M = -0.034$, $SD = 0.184$) was not significantly different from 0, $t(19) = 0.835$, $p = 0.414$. A paired t test showed that there was also no significant difference between the d′ for the Same and Different conditions, $t(19) = 0.941$, $p = 0.359$. These results indicate that participants were not consciously aware of the orientation of the additional foil regardless of its type.

We then compared the discrimination thresholds of the peripheral target across three foil types. Unlike Experiment 1a, the results showed that there was no significant difference across the Same ($M = 0.035$, $SD = 0.011$), Different ($M = 0.040$, $SD = 0.013$), and Noise ($M = 0.042$, $SD = 0.024$) conditions, $F(2, 38) = 1.328$, $p = 0.277$ (Figure 4A). This lack of the foveal foil effect in low-level visual features suggests that foveal feedback may be specific for high-level objects, and the information fed back in foveal feedback may be object information rather than low-level features that covary with object categories.

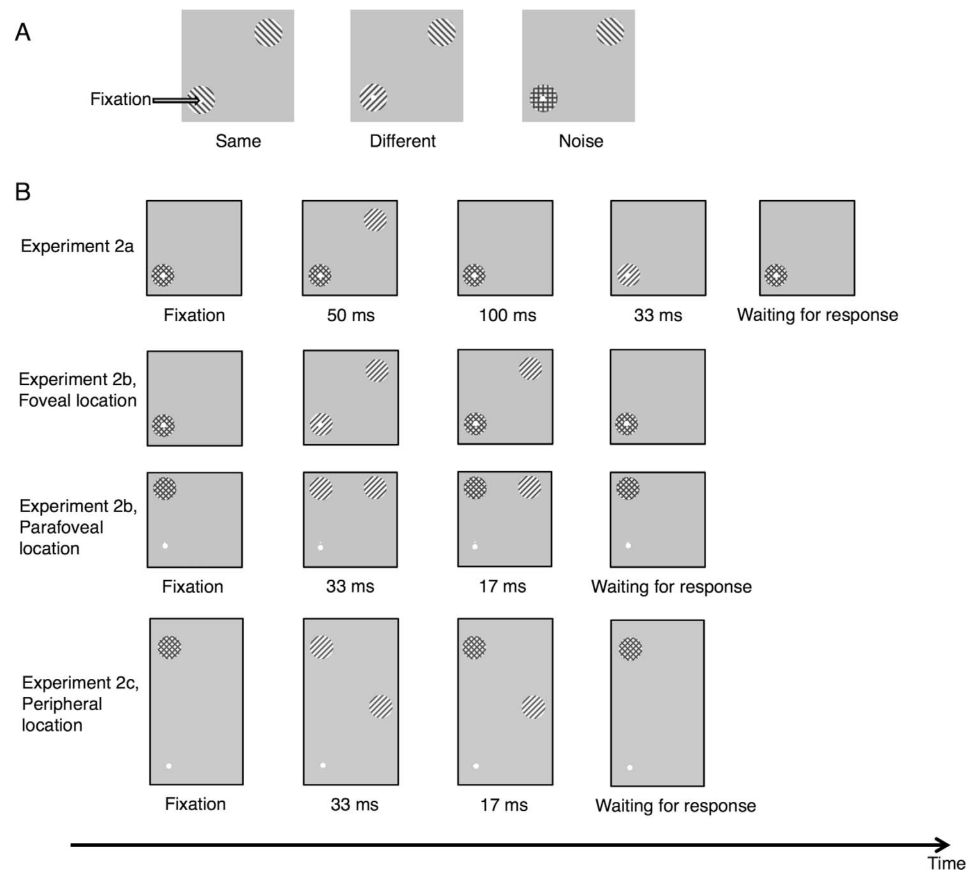

Figure 3. Stimuli and procedures in Experiments 2a, 2b, and 2c. All stimuli are shown in full contrast for demonstration purposes. (A) Examples of the three foil types (Same, Different, and Noise) used in Experiments 2a and 2b (foveal location condition). (B) A schematic diagram of a single trial in Experiment 2a, 2b, or 2c. Upper panel: a trial in Experiment 2a; Middle panel: a trial in the foveal location and in the parafoveal location conditions of Experiment 2b; Lower panel: a trial in Experiment 2c.

Experiment 2b

In Experiment 2a, using a similar paradigm as Experiment 1a, we failed to replicate the modulatory effect of the foveal foil for peripheral target discrimination in gratings. This result could occur if the foil effect in gratings follows a different time course from high-level objects. To test this possibility and examine potential differences in the foil effect between objects and visual features further, in Experiment 2b we presented the foveal foil simultaneously with the

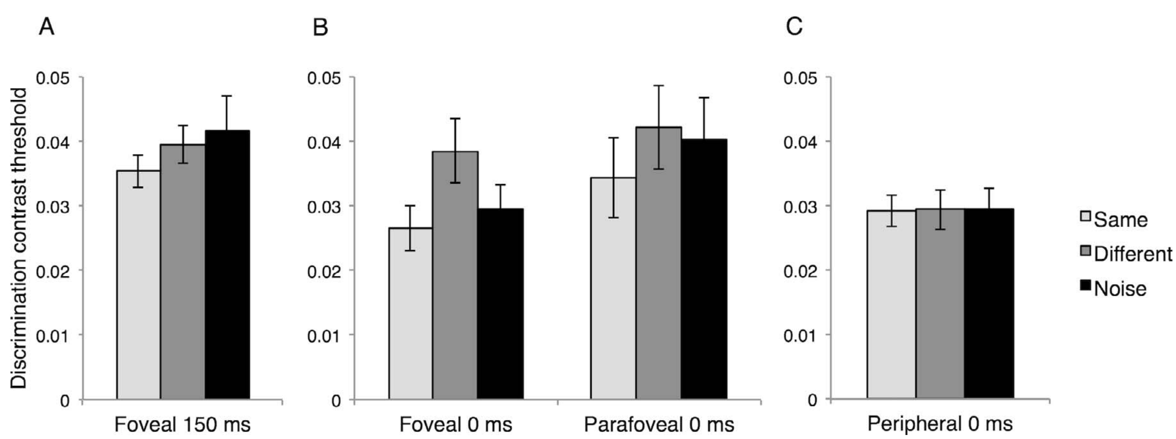

Figure 4. Average discrimination contrast thresholds measured for the Same, Different, and Noise conditions in (A) Experiment 2a, (B) Experiment 2b, and (C) Experiment 2c. Error bars show the ±1 standard error of the mean.

peripheral target without a delay. In order to examine foveal specificity of the foil effect in gratings, we also tested a parafoveal location.

Methods

The stimuli and procedure were identical to Experiment 2a except that the foil was presented simultaneously with the peripheral target (foil delay = 0 ms), and a parafoveal condition where a foil was presented parafoveally at an eccentricity of 7.1° (same as that in Experiment 1b) was also tested (Figure 3B middle panel). The order of the foil locations and foil types was randomized for each participant.

Results and discussion

One-sample t tests showed that the d′ of the foil orientation was not significantly different from 0 either in the foveal location condition ($M = -0.021$, $SD = 0.454$), $t(16) = 0.189$, $p = 0.852$, or in the parafoveal location condition ($M = 0.189$, $SD = 0.468$), $t(16) = 1.662$, $p = 0.116$. We further conducted a 2 (foil location) × 2 (foil type) repeated measures ANOVA to examine whether there was a significant difference in d′ between the Same and Different conditions in the two locations. There was no significant effect of foil location, $F(1, 16) = 0.052$, $p = 0.823$, of foil type, $F(1, 16) = 1.394$, $p = 0.255$, or significant interaction between foil location and foil type, $F(1, 16) = 1.473$, $p = 0.242$. As in Experiment 2a, these results indicate that participants were not consciously aware of the orientation of the additional foil regardless of its location and type.

We then conducted a 2 (foil location) × 3 (foil type) repeated measures ANOVA on the discrimination thresholds of the peripheral target. There were significant main effects of foil location, $F(1, 16) = 9.659$, $p = 0.007$, and foil type, $F(2, 32) = 5.457$, $p = 0.009$. However, the interaction effect between foil location and foil type was not significant, $F(2, 32) = 1.047$, $p = 0.363$ (Figure 4B). Pairwise comparisons across foil locations revealed that the discrimination threshold in the Different condition ($M = 0.040$, $SD = 0.023$) was significantly higher than the threshold in the Same condition ($M = 0.031$, $SD = 0.019$), $t(16) = 2.838$, $p = 0.036$, and was marginally significantly higher than that in the Noise condition ($M = 0.035$, $SD = 0.020$), $t(16) = 2.556$, $p = 0.063$. No significant difference was found between the Same and the Noise conditions, $t(16) = 1.401$, $p = 0.541$. Next, we performed a 2 (foil delay: 150 ms in Experiment 2a vs. 0 ms in the foveal location condition in Experiment 2b) × 3 (foil type) mixed ANOVA to compare the effect of foil delay between Experiment 2a and 2b. The interaction between the two foil delay conditions was marginally significant, $F(2, 70) = 2.798$, $p = 0.068$, suggesting that the foveal foil effect may be larger when the foil was presented simultaneously with the target grating than when it was delayed.

These results indicate that discrimination of the peripheral target was impaired when an additional foil with an orientation orthogonal to the peripheral target was presented. Unlike the foil effect in objects, the effect of the grating foil appears to be disruptive rather than facilitative. Besides this difference in the direction of the effect (disruptive vs. facilitative), the results in the current experiment and Experiment 1a illustrate two other important distinctions between the foil effect in objects and gratings. First, unlike high-level objects, the foil effect in gratings is not specific to the fovea, which is inconsistent with the foveal specificity characterized in the foveal feedback hypothesis. Second, the effective timing of the foveal foil for objects and gratings is different, such that a foil delay similar to the cortical processing delay of feedback input is required in the object foil effect, but simultaneous presentation of foil and target stimuli appears to be comparatively more effective than delayed presentation with grating foils. This discrepancy between objects and gratings suggest a possibility that different mechanisms might be involved in the foil effect of objects and gratings.

Experiment 2c

Experiment 2b demonstrated that discrimination of orientation in the periphery could be interfered with a simultaneously presented foil, although the foil interference effect was not specific to the fovea. To examine whether the effect induced by the foil diminishes or disappears when its distance from the fovea further increases, we conducted Experiment 2c, in which the foil was presented at a peripheral location with a larger eccentricity (14.2°).

Methods

The stimuli and procedure were identical to those of Experiment 2b, except that the foil was located on the upper vertical meridian at an eccentricity of 14.2° in the periphery, separated from the target by 10° (Figure 3B, lower panel). The distance between this peripheral foil and the target was equal to that between the foveal foil and the target in Experiment 2b. To fit the stimuli on the screen, the fixation point was moved down along the lower vertical meridian by 3°.

Results and discussion

As in the previous experiments, participants' d′ of the peripheral foil ($M = 0.017$, $SD = 0.240$) was not significantly different from 0, $t(12) = 0.251$, $p = 0.806$, confirming that the orientation of the peripheral foil was not consciously perceived. There was also no significant difference between the d′ for the Same and Different conditions, $t(12) = 0.848$, $p = 0.413$.

We then conducted a one-way, repeated measures ANOVA to compare the discrimination thresholds of the peripheral target across three foil types. The results showed that there was no significant difference across the Same ($M = 0.029$, $SD = 0.009$), Different ($M = 0.031$, $SD = 0.012$), and Noise ($M = 0.030$, $SD = 0.013$) conditions, $F(2, 24) = 0.017$, $p = 0.984$ (Figure 4C). A two-way mixed ANOVA comparing the discrimination thresholds in Experiment 2c and the foveal location condition in Experiment 2b revealed a significant effect of foil type, $F(2, 56) = 7.345$, $p = 0.001$, and significant interaction between foil type and foil location, $F(2, 56) = 6.873$, $p = 0.002$. Together with our finding from Experiment 2b, these results indicated that the impairment of peripheral target discrimination disappeared as the foil was moved farther away from the fovea into the periphery. However, unlike the foil effect in objects where only the foveal foil was effective, the effect of foil can be extended to a parafoveal location in gratings, suggesting that foveal specificity in low-level visual features may not be as apparent as in objects.

General discussion

Inspired by previous neuroimaging work demonstrating feedback of peripheral object information to foveal cortex (Williams et al., 2008), our goal in the current study was to examine the effect of direct behavioral modulation of the foveal feedback information on peripheral target discrimination. We conducted six experiments to investigate whether changing participants' foveal representation through the presentation of a task-irrelevant stimulus at the fovea could influence their discrimination of peripheral stimuli.

In Experiments 1a, 1b, and 1c, we tested the effect of the foveal foil on peripheral stimulus discrimination using novel, three-dimensional objects. Our result revealed that even when rendered invisible, the foveal foil could influence participants' ability to discriminate the identity of the peripheral object. This subthreshold presentation of the foveal stimuli excluded the possibility that observers responded to the peripheral target based on what they consciously perceived at the fovea. Critically, this modulatory effect was observed only when the foil object identical to the peripheral target was presented at the fovea 150 ms after the onset of the peripheral target (Experiment 1a), but not when the foveal foil and peripheral target objects were presented simultaneously (Experiment 1c). These results suggest that the foveal feedback effect takes some time to occur. Moreover, in Experiment 1b, the peripheral target discrimination was unaffected by the foil when the foil was presented parafoveally, confirming the foveal specificity of the effect. These results in the object experiments supported our hypothesis: Through the presentation of a physical stimulus at the fovea, we were able to modulate individuals' internally generated foveal representations and influence their ability to discriminate peripheral stimuli.

To examine whether this facilitation of peripheral target discrimination elicited by the foveal stimulus could also be found with low-level visual features, we tested orientation discrimination of sinusoidal gratings in Experiments 2a, 2b, and 2c using the same dual task paradigm. No modulatory effect was found when the foveal foil was presented at the fovea 150 ms after the onset of the peripheral target (Experiment 2a), and the interference effect was observed when the foil and peripheral target gratings were presented simultaneously (Experiment 2b). Participants' discrimination ability of peripheral target orientation was impaired when the orientation orthogonal to the peripheral target orientation was presented foveally or parafoveally, but this modulatory effect of the foil disappeared when the foil appeared in the periphery (Experiment 2c). These results in grating experiments indicate that the effect of the foil differed for orientations compared to high-level objects in terms of its effective timing and lack of foveal specificity. Thus, we suggest that our finding in grating experiments is more likely to 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 (Kanai, Tsuchiya, & Verstraten, 2006; Rossi & Paradiso, 1995; Serences & Boynton, 2007; Treue & Martinez-Trujillo, 1999) than by foveal feedback. Perhaps neural activities to the peripheral target were enhanced by the spreading of responses to the feature presented at the fovea. In Experiment 2b, the disruption effect of the parafoveal foil was not significantly different from that of the foveal foil. These results are consistent with the feature spreading account that attentional facilitation of the features displayed at the fovea can spread to other nonfoveal locations. It should be noted that this account is not suitable for explaining the results found in the object experiments. The modulatory effect of the foveal foil was shown when fine-scale discrimination of complex novel objects, rather than identification of simple visual features, was required. Such discriminations could not be made by attending to one of the objects' constituent features. Therefore, the foveal foil effects with gratings found in Experiments 2a, 2b, and 2c and with complex objects observed in Experiments 1a, 1b, and 1c may involve different underlying processes. Whereas foveal feedback contributes to discriminating complex objects in the periphery, feature spreading across the visual field caused by feature-based attention may contribute to the processing of low-level features.

Compared to the disruption by TMS which was shown to impair behavioral performance in the periphery when a TMS pulse was applied to the foveal cortex 350–400 ms after the onset of the peripheral target (Chambers et al., 2013), it appears that substantially less time was required to elicit a foveal foil effect (150 ms) in the present study. One explanation for this discrepancy can be found in a difference in tasks used in the current study and in the TMS study. In the previous TMS study, an object comparison task was used, where two objects were presented in the periphery and participants needed to make a comparison between the two. In contrast, we presented only one target object on each trial and the task was to judge whether the object was the target. Additional time needed to process and compare two objects compared to processing of a single object only may contribute to the difference in the effective timing. Furthermore, cortical feedback processes are thought to be fast and immediate, even as fast as feedforward processes (Hupé et al., 2001; Lamme, Supèr, & Spekreijse, 1998; Nowak et al., 1997). Given this neural evidence, behavioral disruption may closely follow the suggested time course for this cortical feedback. How this effect is systematically modulated by target-foil delays would be an interesting question for future studies to explore.

One alternative argument for the object results might be object-based priming (Bartram, 1976; Maljkovic & Nakayama, 1994). That is, the foveal foil could have primed processing of the peripheral target when the two stimuli were identical. However, in our experiments, the modulatory effect of the foil occurred only when the foveal foil was presented after the peripheral target with a lag (in Experiment 1a). Therefore, no prior information about the peripheral target could have been obtained before the peripheral object appeared, making the priming mechanism an unlikely explanation for our results.

Our result was also unlikely to be caused by eye movement from the foveal foil to the peripheral target because the foveal and the peripheral stimuli were presented with a 150-ms time interval. There was not enough time for participants to prepare and execute a full saccade, which usually takes 200 ms or longer (Robinson, 1964). Moreover, the additional eye movement data confirmed that participants maintained their fixation at the center throughout the experiment.

What underlying neural mechanisms can explain the modulation of peripheral target discrimination by task-irrelevant foveal stimuli? It is unlikely that such modulation is mediated by lateral interaction via horizontal connections within the primary visual cortex (V1) because the distance between the foveal and peripheral stimuli in our experiments (10°) exceeded the spatial range of typical monosynaptic, long-range horizontal connections in V1 (Angelucci et al., 2002; Das & Gilbert, 1995). Our results are instead more consistent with long-range cortical feedback from high-level visual areas. As we discussed previously, cortical recurrent pathways have been found to carry rich information about behavioral context to shape the responses in lower level cortical regions (Bullier, 2001; Gilbert & Li, 2013; Lamme & Roelfsema, 2000). Recent brain imaging studies have suggested that early visual cortex plays a unique role in maintaining the fine-grained information stored in working memory (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009) and in mental imagery (Albers, Kok, Toni, Dijkerman, & Lange, 2013). The fovea, which processes information at the center of the visual field with the highest spatial resolution, plays a critical role in fine-grained visual discrimination. Thus, foveal cortex may serve as an informational buffer that maintains and processes information about peripheral visual stimuli via feedback from higher cortical areas in order to enhance our visual responses to the periphery (Lee & Mumford, 2003; Rao & Ballard, 1999).

Conclusions

In conclusion, our study found that an additional task-irrelevant stimulus presented subconsciously at the fovea can significantly enhance the visual discrimination of a target stimulus in the periphery. Whether the task-irrelevant stimulus at the fovea enhances peripheral discrimination depends on its congruency with the peripheral target. Critically, a short latent period (e.g., 150 ms) may be needed for it to be effective. Furthermore, this effect was only observed for complex, novel, three-dimensional objects, but not for low-level visual features, such as orientation. Taken together, our results provide behavioral evidence that foveal feedback information plays a functional role in modulating visual perception in the periphery. It suggests an intriguing possibility that maintaining feedback representation at the fovea can aid fine-scale object discrimination in the periphery, presumably by uploading a high-resolution prototypical template of the peripheral target at that site (Williams et al., 2008).

Keywords: foveal feedback, visual periphery, object discrimination

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