

# Temporally flexible feedback signal to foveal cortex for peripheral object recognition

Xiaoxu Fan<sup>a,b</sup>, Lan Wang<sup>a</sup>, Hanyu Shao<sup>a</sup>, Daniel Kersten<sup>c</sup>, and Sheng He<sup>a,c,1</sup>

<sup>a</sup>State Key Laboratory of Brain and Cognitive Science, Institute of Biophysics, Chinese Academy of Sciences, Beijing 100101, China; <sup>b</sup>University of Chinese Academy of Sciences, Beijing 100049, China; and <sup>c</sup>Department of Psychology, University of Minnesota, Minneapolis, MN 55455

Edited by David Mumford, Brown University, Providence, RI, and approved August 17, 2016 (received for review April 16, 2016)

Recent studies have shown that information from peripherally presented images is present in the human foveal retinotopic cortex, presumably because of feedback signals. We investigated this potential feedback signal by presenting noise in fovea at different object–noise stimulus onset asynchronies (SOAs), whereas subjects performed a discrimination task on peripheral objects. Results revealed a selective impairment of performance when foveal noise was presented at 250-ms SOA, but only for tasks that required comparing objects' spatial details, suggesting a task- and stimulus-dependent foveal processing mechanism. Critically, the temporal window of foveal processing was shifted when mental rotation was required for the peripheral objects, indicating that the foveal retinotopic processing is not automatically engaged at a fixed time following peripheral stimulation; rather, it occurs at a stage when detailed information is required. Moreover, fMRI measurements using multivoxel pattern analysis showed that both image and object category-relevant information of peripheral objects was represented in the foveal cortex. Taken together, our results support the hypothesis of a temporally flexible feedback signal to the foveal retinotopic cortex when discriminating objects in the visual periphery.

object recognition | feedback | visual cortex | fovea | periphery

Visual information processing involves feedforward and feedback interactions between different visual areas. Recent studies have identified a potential feedback signal specific to the foveal cortex (1, 2). Neuroimaging results have shown that object category information from peripherally presented images can be decoded from the foveal retinotopic cortex when subjects perform an object discrimination task (1). Further, subjects' behavioral performance is impaired when transcranial magnetic stimulation (TMS) is applied to the posterior foveal cortex at 350–400 ms after peripheral stimuli onset (2), consistent with the hypothesis of a feedback signal that directly affects behavior. Performance given a peripheral target can also be modulated psychophysically, by presenting information at the fovea (3, 4). These results support the idea that the foveal retinotopic cortex is engaged for object discrimination, even for peripherally presented objects. The current study addresses three key questions regarding the role of stimulus properties and task in modulating the foveal processing and the temporal properties of this event: Is foveal processing only engaged for high-resolution spatial tasks? Does it happen automatically, or only at the time a high-level task requires it? Does the foveal cortex contain information about retinotopic object properties, such as image orientation, in addition to object category-relevant information?

Presumably, foveal visual noise would disrupt subjects' performance in discriminating peripheral objects only when the noise and the potential feedback signal engage the foveal cortex at the same time. As predicted, we found a selective impairment of performance when a foveal noise was presented ~250 ms following the onset of the peripheral presentation of objects. We then tested whether this impairment is task and stimulus dependent by presenting moving dots or object images rendered in low spatial frequency in the periphery. Our results clearly show that foveal noise had no effect when performing peripheral

discrimination based on motion information and low spatial frequency information, suggesting that foveal processing is engaged only for peripheral tasks that involved spatial detail. Further, foveal noise was not effective when subjects made a saccade away from the peripheral objects, suggesting that saccade planning is a necessary condition for the foveal engagement. Third, we tested whether foveal processing is automatically engaged as soon as peripheral object information reaches higher levels of cortex; if so, we would predict a rather fixed temporal window for the foveal noise to be effective (i.e., ~250 ms); however, when the two peripheral objects were oriented differently and mental rotation was required for the discrimination task, the engagement of foveal processing was delayed as revealed by a systematic shift of the effective temporal window of foveal noise. Thus, during processing spatially detailed object information in the periphery, the foveal retinotopic cortical processing is engaged at a flexible time point when fine detail information is needed. Finally, to assess the information content in the foveal cortex, multivoxel pattern of activities from fMRI measurements showed that both image orientation and object category information could be decoded from the foveal cortex, suggesting that the information in the foveal cortex is more “image-like” in the sense of containing information about both image orientation and category-relevant spatial details.

The results from these three sets of experiments support the hypothesis of a temporally flexible feedback signal from higher-level cortex to lower-level foveal cortex, specifically for extra-foveal object tasks that benefit from analysis of detail.

## Results

**Delayed Foveal Noise Impairs Peripheral Object Discrimination.** Although the above-cited studies (3, 4) demonstrated that foveal stimulation affected peripheral object discrimination, it was unclear whether the foveal information was effective over a narrow or broad time window. In the current experiment, we investigated whether and when foveal noise could disrupt discrimination of objects presented in the periphery. Using stimuli similar to those in previous studies (1–3), two objects either the same or slightly

## Significance

When subjects were asked to discriminate objects in the periphery, foveal visual noise presented at precise time windows following the peripheral object onset disrupted their performance. Further, this effect of foveal noise depends on task demand and stimulus features and primarily occurs for object tasks that involve spatial details. The time window, during which the noise is effective, can be shifted based on the amount of preprocessing of the peripheral objects, revealing the operation of temporally flexible feedback processing in the foveal cortex for peripheral object recognition.

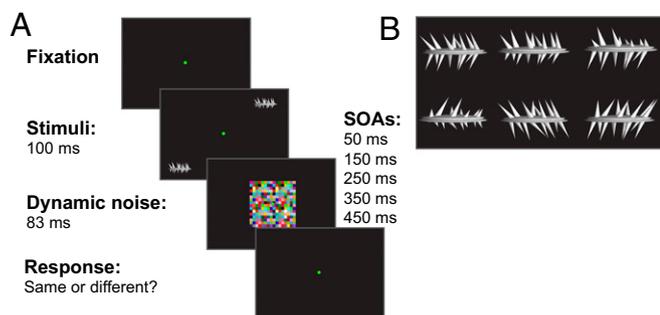
Author contributions: X.F. and S.H. designed research; X.F. performed research; X.F., L.W., and H.S. analyzed data; and X.F., D.K., and S.H. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

<sup>1</sup>To whom correspondence should be addressed. Email: sheng@umn.edu.

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1606137113/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1606137113/-DCSupplemental).



**Fig. 1.** Experimental paradigm. (A) Two objects (either the same or different) selected randomly from a set of stimuli were presented for 100 ms in diagonal quadrants on two sides of the fixation point. Subjects were asked to make a same or different decision by button press. A square patch of dynamic noise was presented for 83 ms in the fovea region at five different SOAs (50, 150, 250, 350, and 450 ms). (B) Six typical examples of objects selected from the spiky object set.

different were presented for 100 ms in diagonal quadrants on two sides of the fixation point (either in upper right and lower left or in lower right and upper left). Subjects were asked to make a same or different decision based on the detailed feature of objects. A dynamic noise patch was presented for 83 ms in the foveal region at stimulus onset asynchronies (SOAs) of 50, 150, 250, 350, and 450 ms after the onset of the object images (Fig. 1).

As shown in Fig. 2, subjects' performance (represented as  $d'$ ) clearly depended on the SOA of the foveal noise relative to the peripheral objects. One-way repeated ANOVA with Bonferroni multiple comparison correction revealed a significant main effect of SOA ( $F_{5,50} = 7.193$ ,  $P < 0.0001$ ; Fig. 2). More specifically, subjects' performance decreased when noise appeared at the SOA of 50 ms ( $d' = 1.155$ ,  $P < 0.001$ ) and 250 ms ( $d' = 1.284$ ,  $P = 0.005$ ), compared with a control condition without foveal noise (dashed line in Fig. 2). The current result showed that foveal processing is disrupted at 250 ms following the onset of the peripheral object images, consistent with the engagement of foveal cortical regions. For the performance drop at 50-ms SOA, the foveal noise overlapped with the peripheral objects in time, and presumably attracted attention away from the object images.

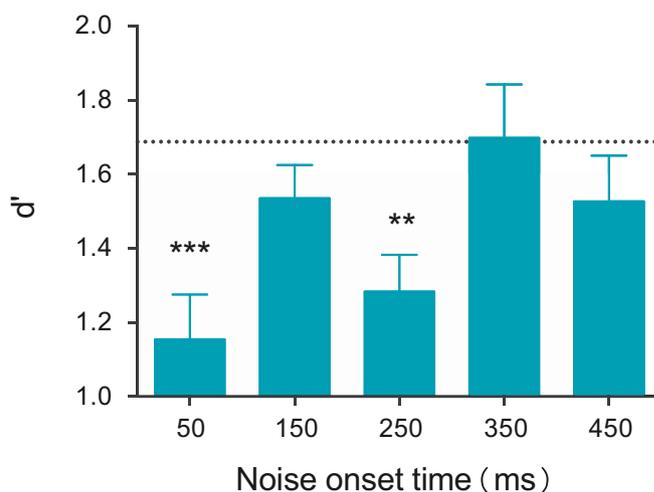
We then conducted three control experiments to rule out alternative explanations for the delayed interference effect. First, the size of the noise patch was reduced to  $4 \times 4^\circ$ . We found that the performance drops at 250-ms SOA remained robust (Fig. S1A). Thus, a noise patch more restricted to the foveal region was as effective in disrupting the peripheral object discrimination performance as the larger one, suggesting the involvement of foveal cortical areas rather than an area closer to the peripheral objects. Second, noise in the periphery failed to impact the peripheral object discrimination performance (Fig. S1B and SI Methods). Third, foveal noise was still effective in inducing the performance drop at 250-ms SOA, even when the two peripheral objects were both presented above the fixation and foveal noise was not in between the two peripheral objects (Fig. S1C).

In summary, we have firmly established that, within a narrow (FWHM: 132 ms  $\pm$  11 SEM, fit to a Gaussian function after normalization) and delayed temporal window, foveal interference produces an impairment in a peripheral object discrimination task, strongly implying that the foveal cortex is engaged for peripheral object discrimination at a specific time.

**Foveal Engagement for Peripheral Information Depends on Task and Stimulus Features.** Given the specializations of foveal vision, we hypothesized that the foveal cortex may not be automatically engaged for a peripheral task, but rather it depends on both the task and stimuli—specifically on object discrimination tasks that involve spatial details.

In the experiments described above, subjects had to analyze the fine details of the objects to complete the task. In this next experiment, we investigated whether foveal noise would still be effective if (i) the stimulus contains only low spatial frequency information (Fig. 3A) or (ii) the task is based on motion signals (Fig. 3C). In the first condition, subjects still performed the object discrimination task, but had to make judgments according to the general shapes of the objects which were spatially low-pass filtered. In the second condition the task was to discriminate the speeds of motion of two patches of random dots. Results show that, whereas a performance drop at 50-ms SOA was clearly observed [filtered objects:  $P = 0.022$  ( $F_{5,50} = 3.154$ ,  $P = 0.015$ ); moving dots:  $P = 0.002$  ( $F_{5,35} = 4.063$ ,  $P = 0.005$ )], as would be predicted by the general attentional distraction of the noise onset when the peripheral stimuli were still on the screen, there was no selective reduction in performance at later time points, including at the 250-ms SOA in either the blurred image condition ( $d' = 0.954$ ,  $P > 0.999$ ; Fig. 3B), or in the motion speed discrimination condition ( $d' = 1.364$ ,  $P = 0.796$ ; Fig. 3D). Thus, the results show that the temporally specific noise-induced performance reduction at 250 ms occurred when subjects performed an object discrimination task where fine spatial details of the peripheral objects were available.

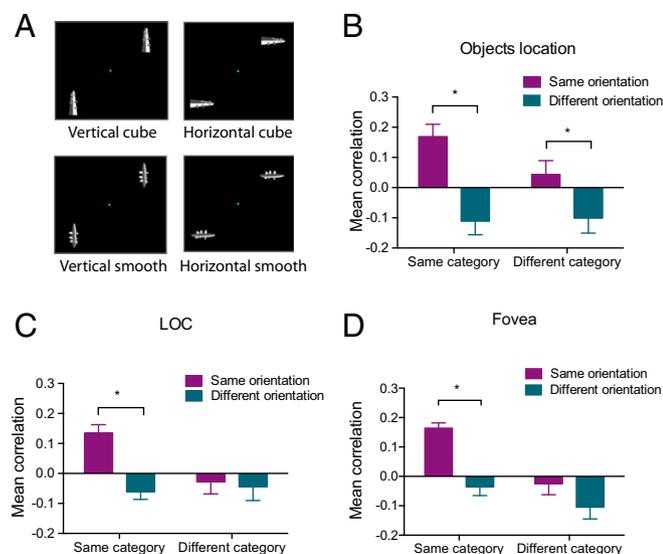
One possible reason for this foveal engagement is that there is a tendency to foveate peripheral objects, and thus the visual system may have built-in mechanisms to engage foveal cortical processing in anticipation of receiving object information at the fovea in the next moments, before the actual saccade. The following two-part experiment was designed to investigate the role of saccade planning in the observed effect of delayed foveal noise. The question was whether the delayed foveal noise could disrupt the peripheral object discrimination if a saccade was required away from the peripheral object, to the opposite side of the fixation. In the first part, subjects were asked to discriminate a single object in the periphery. At the beginning of the experiment, subjects learned the shape features of target objects; then during the experiment, their task was to report whether the object presented was a target based on the learned shape features. We found that performance was impaired by foveal noise presented at 150-ms SOA (Fig. 4A), which is consistent with the results of Yu and Shim (3), but goes beyond in showing that the foveal interference effect is temporally specific with a rather narrow window (FWHM: 86 ms).



**Fig. 2.** Mean object discrimination sensitivity ( $d'$ ) under different SOA conditions. Eleven subjects participated in this experiment. There was a significant decrease in  $d'$  when noise appeared at the SOA of 50 ms ( $d' = 1.155$ ,  $P < 0.001$ ) and 250 ms ( $d' = 1.284$ ,  $P = 0.005$ ), compared with control condition without the noise (dashed line). There was no significant drop in  $d'$  at the other SOAs. Error bars are  $\pm 1$  SEM.







**Fig. 6.** Example stimuli and results of the fMRI experiment. (A) Two sets of stimuli (elongated smoothie and cubie objects) were used in this experiment, generating four stimulus conditions (vertical cube, horizontal cube, vertical smooth, and horizontal smooth). A block design was adopted, and each block contained eight trials of same condition followed by 10 s blank. (B) Mean correlation between same or different orientation under same or different category for the peripheral objects location ROI. There was interaction between orientation and category ( $F_{1,5} = 9.234$ ,  $P = 0.029$ ), and correlation for same orientation was higher than correlation for different orientation under both same category ( $t_5 = 8.883$ ;  $P = 0.001$ ) and different category ( $t_5 = 4.586$ ,  $P = 0.012$ ). (C) For LOC, there was interaction between orientation and category ( $F_{1,5} = 7.209$ ,  $P = 0.044$ ), and correlation for same orientation was higher than correlation for different orientation only under same category condition ( $t_5 = 4.133$ ,  $P = 0.018$ ). (D) For the foveal cortex, there was no interaction between category and orientation ( $F_{1,5} = 2.365$ ,  $P = 0.185$ ), and correlation for same orientation was higher than correlation for different orientation only under same category condition ( $t_5 = 3.624$ ,  $P = 0.03$ ). Six subjects participated in this experiment. Error bars are  $\pm 1$  SEM.

showed that this temporally delayed engagement of the foveal cortex was specific for tasks that use spatial details (Fig. 3), which provided psychophysical evidence that the high-resolution specialization of the foveal cortex can be used for discriminating fine spatial details of peripheral objects. These results support the hypothesis of temporally flexible feedback signal from higher-level cortex to lower-level foveal cortex.

**The Temporal Window for Interference Is Flexible.** Remarkably, we found that the temporal window for the foveal engagement is flexible rather than fixed. When there was less or more processing of the peripheral objects, the timing of the noise-induced performance drop was either advanced or delayed; this can be seen in the comparison of the experiments that involve one vs. two objects (Fig. 2 vs. Fig. 4) and the mental rotation experiment (Fig. 5). The mental rotation experiment is highly suggestive of a feedback signal to early foveal cortex that is not automatically triggered by a peripheral stimulus, but instead is only engaged when the high level process is ready. In the case of mental rotation, the right superior posterior parietal lobe is believed to play a key role (12–14). It is possible that the delay in feedback signal to early visual cortex was due to the additional processing and interaction between, for example, LOC (11) and posterior parietal cortex.

Notice that there was a performance drop at 50-ms SOA in the object discrimination task, motion speed comparison task, and the low-spatial frequency object discrimination task (Figs. 2 and 3). At 50-ms SOA, the foveal noise overlapped with the peripheral objects in time, so it is likely that the observed performance drop in the peripheral tasks was due to attention distraction

caused by the onset of the foveal noise. Indeed, when both peripheral objects were presented above the fixation, the foveal noise presented at 50-ms SOA was no longer disruptive, presumably because subjects would shift their attention to the upper two quadrants in advance because the peripheral objects consistently appeared in the upper field (15); this voided the attentional distraction effect of the foveal noise at 50 ms (16, 17). For the other experiments, subjects' attention remained at the fixation point at the beginning of each trial because the two peripheral objects would appear either in the upper right/lower left or in the lower right/upper left locations, leading to a significant attention distraction effect at 50-ms SOA (18). This effect was also observed in the mental rotation experiments, though was not statistically significant.

The previous Chambers et al. (2) study using a similar behavioral task showed that disrupting the foveal cortex with TMS at 350–400 ms after stimuli onset impaired the object discrimination performance. Our psychophysical study revealed that foveal visual noise was effective when presented  $\sim 250$  ms following the onset of the peripheral objects. These estimates of the effective temporal window for the engagement of foveal retinotopic cortex are in fact consistent, considering that the TMS was applied to the posterior calcarine site directly, whereas the fovea visual noise takes 50 ms or more to arrive at the primary visual cortex (19–21).

**Category Information Is Available in Early Foveal Cortex.** Results from our fMRI experiment show that orientation information of peripheral objects was represented in the foveal cortex, as well as the object category information. This pattern of results (Fig. 6) suggests that the signal representation in the foveal cortex is more image-like than that in LOC, but more sensitive to object category information than that in the peripheral retinotopic cortex. In the peripheral retinotopic cortex, orientation information could be read out regardless of the object category; however, in the foveal cortex, orientation information could only be read out for objects in the same category. Moreover, the pattern correlation for orientation and object category information in the foveal cortex showed no interaction, unlike the LOC or peripheral retinotopic cortex. A possible scenario is that the foveal cortex represents the object category and orientation information at different spatial scales, with the object category and orientation information primarily supported at fine and coarse scales, respectively. Using multielectrode recordings from passively fixating macaques, Hong et al. (22) recently showed that “category-orthogonal” features of an object, such as orientation, could be linearly decoded from high-level object areas in the ventral stream, and that this information was likely available on a feedforward pass. At one level, our imaging results are consistent in that we found that LOC was sensitive to the category-orthogonal feature of image orientation; however, this was only for stimuli that were in the same category. Our results raise the possibility that feedback may be required for tasks that not only benefit from fine-grain comparisons, but also for comparisons of category-orthogonal features across categories.

**Theoretical Interpretations.** The delayed effect of foveal noise, as much as a few hundred milliseconds after the object onset, combined with the stimulus feature selectivity, makes it difficult to explain the observed effect in terms of attentional interruption (1). The large distance between the peripheral object and foveal noise makes it very unlikely that the effect was due to direct interaction between foveal noise and peripheral object through lateral horizontal connections within early cortical areas. Instead, two previous theoretical proposals are more relevant to our results. In 1998, Lee et al. (23) proposed a high-resolution spatial buffer hypothesis in which the primary visual cortex is used by the higher-level visual cortex for computations that requiring high-resolution detail (24). Likewise, in the reverse hierarchy theory proposed by Ahissar and Hochstein (25), initial feedforward processing provides a gist description of the input to the high-level cortex; then, at a later point in time, fine-detailed

information is queried through feedback interactions with lower areas (25–27). However, our study shows that in the case of the analysis of fine detail in the periphery, the important feedback interactions occurred between the high-level cortex and the foveal cortex, rather than the region occupied by stimuli in lower areas. A possible reason for this arrangement is that the fovea is normally used for processing fine details due to its high-resolution capacity, and normally we move our eyes to bring the image details into the fovea. In our experiment, eye movement was not allowed, yet the system may have built-in mechanisms to engage the foveal cortex in the feedback stage, maybe in anticipation that the input image would end up in the fovea, as is typically the case. Anticipatory activation before saccades has also been found in other cases; for instance, neurons in some brain areas become responsive to the visual stimuli that will be brought into their receptive field by an imminent saccade, described as predictive remapping (28–31). It is possible that the natural tendency to make a saccade when objects were presented in the periphery in our paradigm initiated the predictive remapping mechanism. The result that foveal noise was not effective when subjects planned and executed a saccade away from the peripheral object supports this possibility (Fig. 4B). However, our results show that this process was delayed with the added mental rotation operation, which would either suggest that the saccade planning itself was also delayed, or that a mechanism for predictive remapping also has a flexible and task-dependent timing. Thus, our results, on the one hand, provide further support and refinement for the high-resolution buffer hypothesis and reverse hierarchy theory, but on the other hand they also provide important constraints that theories of object recognition need to satisfy.

## Methods

**Subjects.** A total of 88 subjects (age range 18–26; 44 female) participated in these experiments, with some subjects participating in more than one experiment (see *SI Methods* for details). All subjects provided written informed consent before the experiments, and protocols were approved by the institutional review board of the Institute of Biophysics, Chinese Academy of Sciences.

## Stimuli and Procedures.

**Delayed foveal noise impairs peripheral object discrimination.** Two objects (either same or different) selected randomly from the set of stimuli were presented for 100 ms in diagonal quadrants on two sides of the fixation point (either in upper right and lower left or in lower right and upper left; *SI Methods*). Subjects were asked to make a same or different decision by pressing one or the other button as soon as possible, and to maintain fixation during that process. A dynamic noise patch ( $7 \times 7^\circ$ ), centered at the fixation, was presented for 83 ms at five different SOAs (50, 150, 250, 350, and 450 ms).

**Task and feature property dependency.** In the low-pass-filtered object comparison experiment, the spikey objects were low-pass filtered with a cutoff frequency of 0.64 cycles per degree (Fig. 3A). In the speed comparison experiment, target stimuli were replaced by two patches of moving dots located in the same area as spikey objects (Fig. 3C). The two patches of dots move in opposite directions ( $45$  or  $135^\circ$  with respect to horizontal). Each patch contained 10 dots of  $0.2 \times 0.2^\circ$  size, and their moving speed varied from 2.5 to 22.5°/s. All other aspects and procedures of these experiments were the same as in the main experiment. For the single-object experiment and the experiment with the additional saccade requirement, details are described in *SI Methods*.

**Flexible time window.** In this experiment, one of the two objects was presented in rotated orientation (measured counterclockwise from the horizontal), and the other remained horizontal. It was randomly determined which one would be rotated. Subjects were asked to mentally turn the tilted objects clockwise back to horizontal to see whether the two objects were the same or different as soon as possible, and they were discouraged from using any other strategy (32). In the first session of the mental rotation experiments, conditions with mental rotation (rotation angles  $30$ ,  $40$ , or  $50^\circ$ ) and without mental rotation were interleaved. In the second session, rotation angle was set to  $0$ ,  $40$ , or  $80^\circ$  and were run separately.

**fMRI experiment.** Scanning was performed on a 3T Siemens Trio scanner in the Beijing MRI Center for Brain Research using a gradient echo-planar sequence [20-channel head coil, repetition time (TR) = 2 s, echo time (TE) = 30 ms, resolution  $2.0 \times 2.0 \times 2.0$  mm, 31 slices, matrix =  $96 \times 96$ ]. Information about the experimental design and data analysis can be found in *SI Methods*.

**ACKNOWLEDGMENTS.** This work was supported by Chinese Academy of Science Grant XDB02050001; National Nature Science Foundation of China Grants 81123002 and 31300937; National Key Basic Research Program of China Grants 2012CB825500 and 2015CB351701; and Office of Naval Research Grant 000141210883.

- Williams MA, et al. (2008) Feedback of visual object information to foveal retinotopic cortex. *Nat Neurosci* 11(12):1439–1445.
- Chambers CD, Allen CPG, Maizey L, Williams MA (2013) Is delayed foveal feedback critical for extra-foveal perception? *Cortex* 49(1):327–335.
- Yu Q, Shim WM (2016) Modulating foveal representation can influence visual discrimination in the periphery. *J Vis* 16(3):15.
- Weldon KB, Rich AN, Woolgar A, Williams MA (2006) Disruption of foveal space impairs discrimination of peripheral objects. *Front Psychol* 7:699.
- Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. *Science* 171(3972):701–703.
- Cooperau LA, Shepard RN (1973) The time required to prepare for a rotated stimulus. *Mem Cognit* 1(3):246–250.
- Hochberg J, Gellman L (1977) The effect of landmark features on mental rotation times. *Mem Cognit* 5(1):23–26.
- Haxby JV, et al. (2001) Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293(5539):2425–2430.
- Norman KA, Polyn SM, Detre GJ, Haxby JV (2006) Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. *Trends Cogn Sci* 10(9):424–430.
- Cox DD, Savoy RL (2003) Functional magnetic resonance imaging (fMRI) “brain reading”: Detecting and classifying distributed patterns of fMRI activity in human visual cortex. *Neuroimage* 19(2 Pt 1):261–270.
- Malach R, et al. (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc Natl Acad Sci USA* 92(18):8135–8139.
- Harris IM, et al. (2000) Selective right parietal lobe activation during mental rotation: A parametric PET study. *Brain* 123(Pt 1):65–73.
- Harris IM, Miniussi C (2003) Parietal lobe contribution to mental rotation demonstrated with rTMS. *J Cogn Neurosci* 15(3):315–323.
- Tagaris GA, et al. (1997) Mental rotation studied by functional magnetic resonance imaging at high field (4 tesla): Performance and cortical activation. *J Cogn Neurosci* 9(4):419–432.
- Klein R, McCormick P (1989) Covert visual orienting: Hemifield-activation can be mimicked by zoom lens and midlocation placement strategies. *Acta Psychol (Amst)* 70(3):235–250.
- Yantis S, Jonides J (1984) Abrupt visual onsets and selective attention: Evidence from visual search. *J Exp Psychol Hum Percept Perform* 10(5):601–621.
- Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3(3):201–215.
- Beck DM, Lavie N (2005) Look here but ignore what you see: Effects of distractors at fixation. *J Exp Psychol Hum Percept Perform* 31(3):592–607.
- Martinez A, et al. (1999) Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nat Neurosci* 2(4):364–369.
- Foxe JJ, Simpson GV (2002) Flow of activation from V1 to frontal cortex in humans. A framework for defining “early” visual processing. *Exp Brain Res* 142(1):139–150.
- Cottaris NP, De Valois RL (1998) Temporal dynamics of chromatic tuning in macaque primary visual cortex. *Nature* 395(6705):896–900.
- Hong H, Yamins DLK, Majaj NJ, DiCarlo JJ (2016) Explicit information for category-orthogonal object properties increases along the ventral stream. *Nat Neurosci* 19(4):613–622.
- Lee TS, Mumford D, Romero R, Lammie VA (1998) The role of the primary visual cortex in higher level vision. *Vision Res* 38(15–16):2429–2454.
- Lee TS, Mumford D (2003) Hierarchical Bayesian inference in the visual cortex. *J Opt Soc Am A Opt Image Sci Vis* 20(7):1434–1448.
- Ahissar M, Hochstein S (2004) The reverse hierarchy theory of visual perceptual learning. *Trends Cogn Sci* 8(10):457–464.
- Hochstein S, Ahissar M (2002) View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron* 36(5):791–804.
- Ahissar M, Nahum M, Nelken I, Hochstein S (2009) Reverse hierarchies and sensory learning. *Philos Trans R Soc Lond B Biol Sci* 364(1515):285–299.
- Walker MF, Fitzgibbon EJ, Goldberg ME (1995) Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J Neurophysiol* 73(5):1988–2003.
- Duhamel JR, Colby CL, Goldberg ME (1992) The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255(5040):90–92.
- Melcher D (2007) Predictive remapping of visual features precedes saccadic eye movements. *Nat Neurosci* 10(7):903–907.
- Cavanagh P, Hunt AR, Afraz A, Rolfs M (2010) Visual stability based on remapping of attention pointers. *Trends Cogn Sci* 14(4):147–153.
- Cooper LA (1975) Mental rotation of random two-dimensional shapes. *Cognit Psychol* 7(1):20–43.
- Duncan RO, Boynton GM (2003) Cortical magnification within human primary visual cortex correlates with acuity thresholds. *Neuron* 38(4):659–671.