

# Feedback of visual object information to foveal retinotopic cortex

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The mammalian visual system contains an extensive web of feedback connections projecting from higher cortical areas to lower areas, including primary visual cortex. Although multiple theories have been proposed, the role of these connections in perceptual processing is not understood. We found that the pattern of functional magnetic resonance imaging response in human foveal retinotopic cortex contained information about objects presented in the periphery, far away from the fovea, which has not been predicted by prior theories of feedback. This information was position invariant, correlated with perceptual discrimination accuracy and was found only in foveal, but not peripheral, retinotopic cortex. Our data cannot be explained by differential eye movements, activation from the fixation cross, or spillover activation from peripheral retinotopic cortex or from lateral occipital complex. Instead, our findings indicate that position-invariant object information from higher cortical areas is fed back to foveal retinotopic cortex, enhancing task performance.

Virtually all theories of visual feedback share the central idea that feedback exerts its effect on perception by modulating or anticipating representations that are generated by feedforward responses to stimuli. In predictive coding models<sup>1</sup>, feedback from high-level visual areas serves to ‘explain away’, and hence reduce, activity in lower areas<sup>2,3</sup>, simplifying the description of the stimulus. In figure-ground segregation, feedback putatively increases V1 responses to image regions corresponding to figure relative to those corresponding to ground<sup>4–7</sup>. Attentional models posit that feedback to primary visual cortex modulates, tunes or anticipates<sup>8</sup> the feedforward response to visual stimuli. Other theories argue that feedback sharpens perceptual representations<sup>9</sup> or enhances consciously available representations<sup>10</sup>. In contrast with all of these theories in which feedback modifies or anticipates a feedforward representation, we found a case in which feedback apparently constructed a totally new representation in a different cortical region from the feedforward representation. Because the feedback and feedforward representations arise in non-overlapping parts of retinotopic cortex, the two representations can be clearly distinguished and studied separately.

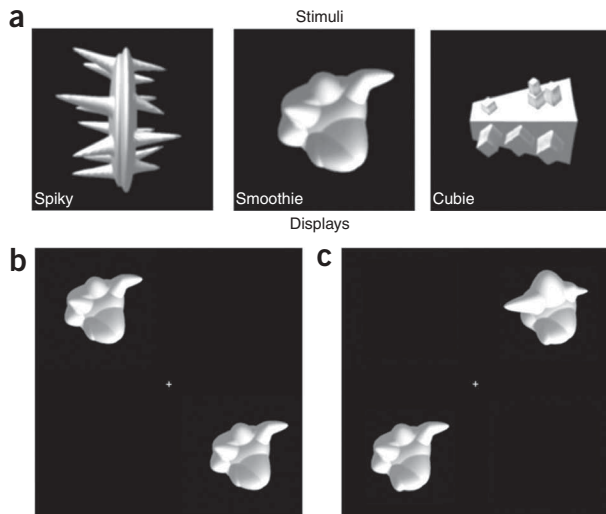
The form of feedback reported here was discovered unexpectedly in a procedure designed to investigate position-invariant object representations in higher-level cortex. Subjects fixated centrally while viewing three categories of novel objects (Fig. 1a) in the periphery<sup>11</sup>. In each trial, we presented two objects simultaneously in diagonally opposite

peripheral retinal locations (Fig. 1b,c). These two objects were always from the same object category and subjects were asked whether the two objects were identical (Fig. 1b) or subtly different (Fig. 1c) exemplars of that category. We then used multivariate pattern-analysis methods<sup>12,13</sup> to determine whether information about object category was present in the pattern of response across voxels in each of several cortical regions of interest (ROIs).

Our results indicate that the pattern of the functional magnetic resonance imaging (fMRI) response in foveal retinotopic cortex contains information about the category of objects presented more than 5° outside of the fovea, in the visual periphery. This object information had two properties that were unexpected for retinotopic cortex: it was in a part of the retinotopic map (the fovea) that does not correspond to the stimulus location (the periphery) and it was position invariant (that is, the pattern in foveal cortex is similar across different peripheral stimulus locations). Furthermore, we found that the object information in foveal retinotopic cortex was behaviorally relevant: it was present during a discrimination task on objects presented in the periphery, but not during a color-discrimination task performed on the same stimuli, and stronger object information in foveal cortex was correlated with higher performance on the object-discrimination tasks. These findings suggest a phenomenon that is not predicted by prior theories of feedback, in which position-invariant object information is fed back from high-level object areas to foveal retinotopic cortex, enhancing task performance.

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**Figure 1** Example displays from Experiment 1. (a) A typical example from each of the three stimulus categories (for information on the slight variations across exemplars in each category see ref. 11). (b) Example of the presentation display with identical 'smoothies' present in the top left and bottom right quadrants (left diagonal). (c) Example of the presentation display with different 'smoothies' present in the top right and bottom left quadrants (right diagonal). Objects had a mean width of  $1.8^\circ$  visual angle and were presented  $7^\circ$  from fixation.

## RESULTS

We applied correlation analyses to investigate the information contained in the spatial patterns of fMRI responses, as described previously<sup>12–14</sup>. Specifically, the data were split in half (even versus odd runs), separately for each subject, and the spatial pattern of the fMRI response to each object category was extracted from each half of the data independently<sup>15</sup>. The presence of category information in a given ROI is indicated by a greater similarity or correlation between two activation patterns when they are generated by the same stimulus category than when they are generated by two different categories.

Specifically, in each ROI, we computed the correlation between independent pairs of activation patterns from the same object category (for example, 'smoothies' correlated with 'smoothies'; see Fig. 1a) versus different object categories (for example, smoothies correlated with 'spikies'). This allowed us to determine which brain regions contain information that can discriminate one category from another (for example, smoothies versus spikies). A higher correlation for same object category than for different object category indicates the presence of information in that ROI that can discriminate between those object categories. To test whether the category information is tolerant to changes in object location, we compared correlations across pairs of activation patterns in which the objects were presented at the same retinotopic locations (for example, both datasets from the left diagonal locations shown in Fig. 1b) with data in which objects were presented in different locations (for example, correlation of the activation pattern from left diagonal locations in Fig. 1b with the activation pattern from right diagonal locations in Fig. 1c). If category information is specific to object location, correlations should be substantially higher for same versus different category only when the two activation patterns come from the same locations, and not when the patterns come from different locations.

These analyses were computed separately for each subject on each of several ROIs. One ROI was in the lateral occipital complex (LOC ROI), a region with a well-established role in shape representation<sup>16</sup>, and the

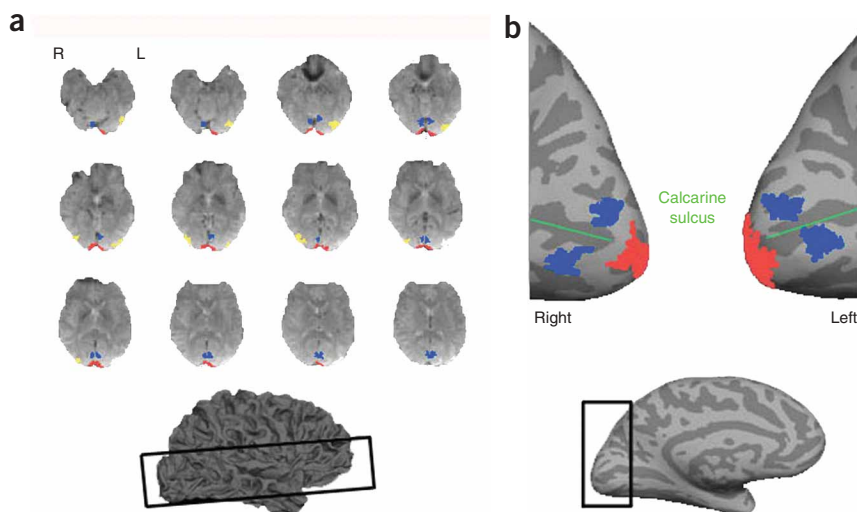
other three were in retinotopic cortex; the object location ROI was the part of retinotopic cortex that responded to the stimuli, the between objects ROI was a retinotopic region representing the space between the peripheral objects along the vertical or horizontal meridian, and the foveal ROI was the foveal region of retinotopic cortex (see Fig. 2 and Supplementary Fig. 1 online).

In Experiment 1, we scanned six subjects during the object discrimination task. In the analysis, we examined the object category information (same versus different category) present in each ROI under conditions in which the objects were in the same versus different locations (same versus different location). An omnibus ANOVA across subjects on the correlations found a significant three-way interaction of ROI  $\times$  same/different category  $\times$  same/different location ( $F_{1,5} = 5.52$ ,  $P = 0.009$ ), indicating that the pattern of correlations differed significantly across ROIs. We therefore analyzed each ROI separately. Same category correlations were higher than different category correlations in the LOC ( $F_{1,5} = 13.32$ ,  $P = 0.015$ ), indicating the presence of object category information in this region, consistent with previous results<sup>11,15</sup>. Furthermore, we found no significant interaction of same/different location  $\times$  same/different category ( $F_{1,5} = 2.53$ ,  $P = 0.173$ ; see Fig. 3a), indicating that the information about object category in LOC is largely position invariant, which is also consistent with prior results<sup>17</sup>.

In the object location ROI, which corresponded to the parts of retinotopic cortex that are activated directly by the stimuli, object categories could be distinguished on the basis of their activation patterns. However, as we would expect given the nature of retinotopic cortex, this was only true for the same location condition (that is, when the objects were presented on the same diagonal in both datasets;  $t_5 = 3.61$ ,  $P = 0.015$ ) and was not true when they were presented in different locations ( $t_5 = 1.27$ ,  $P = 0.261$ ); this difference between same versus different locations was significant (interaction of same/different location  $\times$  same/different category,  $F_{1,5} = 10.34$ ,  $P = 0.024$ ; see Fig. 3b). The between objects ROI showed no significant object information for either the same location or different location analyses. There was no main effect of same/different category ( $F_{1,5} < 1$ , n.s.) and no interaction of same/different category by same/different location ( $F_{1,5} = 1.17$ ,  $P = 0.330$ ; Fig. 3c). These results are consistent with expected location specificity of retinotopic cortex.

Notably, we found that the foveal retinotopic cortex ROI contained object category information (see Fig. 3d). Correlations in the foveal region of retinotopic cortex were higher for same category than for different category pairs in the same location condition ( $t_5 = 3.609$ ,  $P = 0.015$ ), demonstrating that activity in this region of cortex can distinguish among these three object categories, even though no stimuli were presented in the foveal retinotopic location. This object information was invariant to changes in stimulus location; that is, correlations were significantly higher for same category than for different category in the different location conditions ( $t_5 = 2.660$ ,  $P = 0.045$ ) and object category information was not significantly stronger in the same location than in the different location conditions (see Fig. 3d). Indeed, the invariance to stimulus location was as strong in the foveal ROI as it was in LOC (interactions were not significant for foveal ROI  $\times$  same/different location  $\times$  same/different category,  $F_{1,5} = 0.79$ ,  $P = 0.414$ , or for same/different location  $\times$  same/different category,  $F_{1,5} = 2.49$ ,  $P = 0.175$ ). Notably, mean percentage signal change in the foveal ROI was very low and did not differ significantly across object categories, indicating that it is the spatial pattern of response across voxels, not the mean response, that carries the object information ( $F_{1,5} = 0.37$ ,  $P = 0.70$ ; see Supplementary Fig. 2 online).

The presence of object information in foveal retinotopic cortex is surprising because the stimuli were presented in the periphery



**Figure 2** ROIs in one example subject. **(a)** Native functional slices 4–15 (see Methods), with this subject's functionally defined ROIs in color: LOC (objects > scrambled from localizer experiment) in yellow, foveal retinotopic cortex (all > rest from the localizer runs, including active voxels only at the occipital poles) in red and peripheral retinotopic ROIs (smoothies, spikies and cubies > rest from half the experimental runs) in blue. In each analysis, the union of two peripheral (blue) regions constituted the same location ROI (the cortical region corresponding to the location where the stimuli occurred; for example, in the upper right and lower left visual field) and the union of the two other peripheral (blue) regions constituted the different location ROI (the cortical region corresponding to the location where stimuli occur in the other stimulus location condition; for example, upper left and lower right). **(b)** Inflated cortical surface from the same subject showing the location of these retinotopic ROIs on the cortical surface (inflation was performed using Freesurfer<sup>35</sup>).

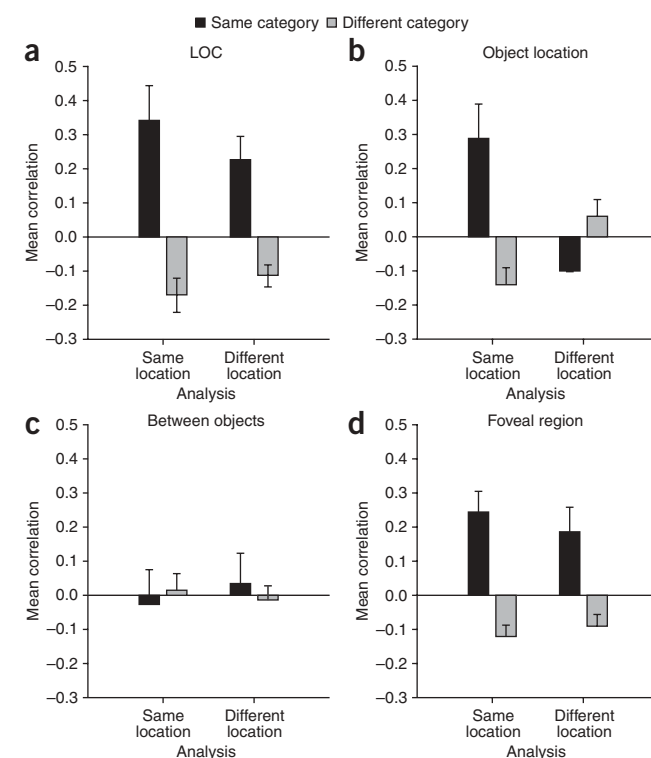
only. This object information is therefore present in a cortical region that is not involved in the feedforward processing of the stimuli. In addition, the information is position invariant, a phenomenon that has not, to the best of our knowledge, been reported previously in retinotopic cortex. The most parsimonious account of these findings is that object information from higher cortical areas (possibly including LOC) is fed back to foveal retinotopic cortex. However, before this hypothesis can be accepted, several alternatives must be considered.

### Testing alternatives to the feedback hypothesis

First, might the foveal ROI show response properties that should have been attributed to the object location ROI, but that somehow got spuriously attributed to the foveal ROI? This could occur if either some voxels that should have been assigned to the object location ROI were wrongly assigned to the foveal ROI or functional signals from the object location ROI were displaced to the foveal region by veins<sup>18</sup> or ghosting artifacts. This hypothesis cannot account for the fact that the foveal ROI showed position-invariant category information, whereas the peripheral ROIs did not.

Second, could category information in the foveal ROI result from participants actually foveating the stimuli? This is unlikely because it

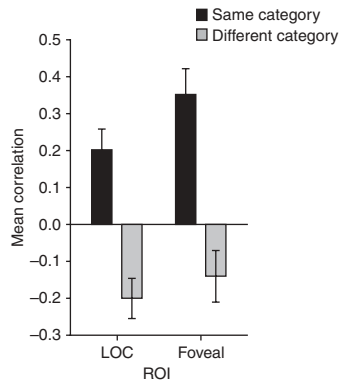
**Figure 3** Mean correlations ( $\pm 1$  s.e.) for same (black bars) versus different (gray bars) categories and for same versus different locations for the four ROIs in Experiment 1. **(a)** LOC (objects > scrambled objects). **(b)** The object location ROI is the region of the peripheral retinotopic cortex corresponding to the location where the stimuli occurred. **(c)** The between locations ROI is a peripheral retinotopic region corresponding to the gap between stimulus locations. **(d)** The foveal region in retinotopic cortex (foveal; central object presentation > fixation).



would place the other stimulus so far in the periphery that task performance would be nearly impossible. More subtly, might subjects have made consistently different eye movements for each object class? This hypothesis seems unlikely, as such category-specific eye-movement patterns would have to be the same across stimulus location to produce the observed position-invariant information. Nonetheless, we tested both possibilities by analyzing the eye movement data from Experiment 1. There was no significant difference in eye movements or pupil diameter between the object categories (horizontal:  $F_{1,4} = 0.62$ ,  $P = 0.473$ ; vertical:  $F_{1,4} = 0.26$ ,  $P = 0.632$ ; pupil:  $F_{1,4} = 0.66$ ,  $P = 0.540$ ; see **Supplementary Fig. 3** online).

Finally, even if eye movements are too small to reach significance in our eye tracker data, could they nonetheless produce systematically different patterns of activation in the foveal ROI because of their effect on the cortical response to the fixation cross itself? To test this hypothesis, we repeated the experiment on well-trained subjects without the central fixation cross (Experiment 2). Instead, four crosses were placed permanently in the location of the objects and the subjects were asked to fixate at the implied central intersection of the crosses. The significant object information

in the foveal ROI remained under these conditions ( $F_{1,15} = 32.83$ ,  $P = 0.029$ , Experiment 2; **Fig. 4**), thus ruling out the possibility that the phenomenon occurred because of a response to the foveal fixation cross.



**Figure 4** Mean correlations ( $\pm 1$  s.e.) within and between categories (always between locations) for two ROIs in Experiment 2. Three subjects participated in this experiment, which was identical to Experiment 1, except that no central fixation was presented. (a) LOC (objects > scrambled objects). (b) The foveal representation in retinotopic cortex (foveal; central object presentation > fixation).

Taken together, these considerations provide compelling evidence that position-invariant object information from higher cortical areas (possibly including LOC) is fed back to foveal retinotopic cortex. We considered further the spatial specificity of the effect and its relevance to perception.

#### Is the object information restricted to the foveal region?

Could the effect that we observed here reflect feature-based attention<sup>19,20</sup>? Although feature-based attention effects can spread beyond the attended object<sup>21</sup>, with one recent study finding feature-based attention effects across the entire visual field<sup>20</sup>, no prior data or theory would predict that feature-based attention effects should be restricted to foveal retinotopic cortex. Given this apparently critical difference between our results and feature-based attention, we revisited this question in Experiment 3, which more precisely tested the spatial specificity of our effects by including an eccentricity-mapping localizer scan. Specifically, our localizer included three concentric disc or ring-shaped stimuli that were composed of a flashing checkerboard texture (see Methods for stimuli details). We measured position-invariant object information in each of these ROIs in a manner that was otherwise identical to Experiment 1 (Fig. 5). An omnibus ANOVA across subjects on the correlations found a significant two-way interaction of ROI (foveal/outer ring)  $\times$  same/different category ( $F_{1,4} = 8.941$ ,  $P = 0.040$ ), indicating that the pattern of correlations differed significantly across ROIs. We therefore analyzed each ROI separately and found significantly higher correlations for same than for different categories only in the foveal ROI ( $t = 3.840$ ,  $P = 0.018$ ), but not in the outer ring ROI ( $t = 1.611$ ,  $P = 0.183$ ) or the middle ring ROI ( $t = 0.975$ ,  $P = 0.385$ ). The same pattern of results was observed when linear SVMs were used to analyze the data instead of correlations (Supplementary Fig. 4 online). These results confirm the spatial specificity of object information to foveal retinotopic cortex and render our findings difficult to explain in terms of feature-based attention.

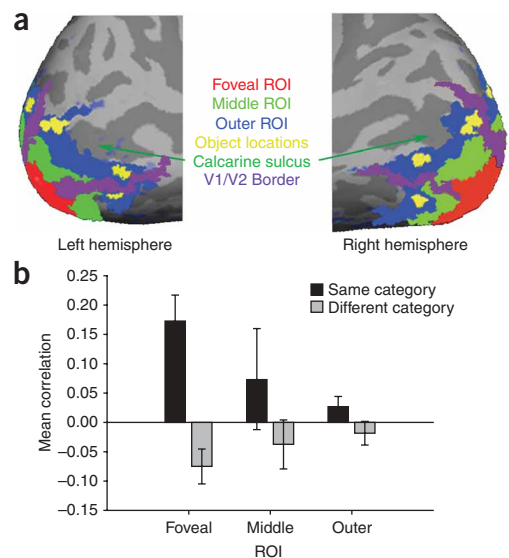
According to a second alternative hypothesis, the object information is not restricted to the fovea *per se*, but rather is found at retinotopic positions corresponding to the spatial midpoint between the two simultaneously presented stimuli, which happened to coincide with the fovea in our previous experiments. In a fourth experiment, we tested this hypothesis by presenting the two stimuli in either the two upper positions or the two lower positions, rather than along diagonals.

We again found position-invariant object information in the foveal ROI: that is, a significantly higher correlation for within object category than for between object category ( $t_4 = 6.13$ ,  $P < 0.005$ ) for the between-location analysis, even though the fovea was not between the two simultaneously presented stimuli in this experiment. Furthermore, we found no significant object information in ROIs positioned at the midpoint between the two stimuli ( $t_4 = 1.523$ ,  $P = 0.202$ , upper and lower ROIs separately calculated and averaged), providing no evidence for an additional effect of the midpoint position. This experiment generalizes our result to a new stimulus configuration and shows that the foveal specificity of our effect is not an artifact of stimulus configurations that straddle the foveal region.

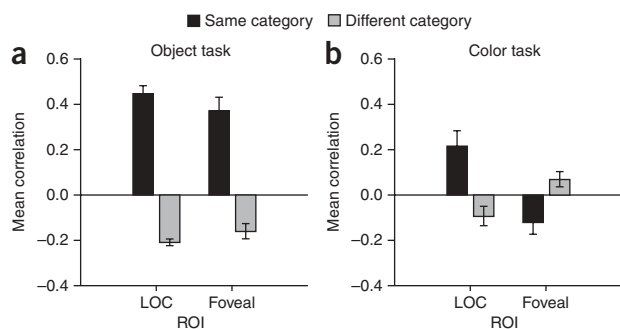
#### Behavioral relevance of category information

Is the object information that we found in foveal retinotopic cortex epiphenomenal (that is, unrelated to task performance), as has been seen in several prior studies of pattern information in retinotopic cortex<sup>15,20,22,23</sup>, or does it reflect a behaviorally relevant process that improves task performance? In Experiment 5, we addressed this question by asking whether foveal cortex contains category information whenever objects are presented or only when the participant performs an object-discrimination task.

We found object information in the foveal retinotopic ROI only when subjects performed an object-comparison task ( $t_5 = 5.93$ ,  $P = 0.004$ ), and not when they performed an equally difficult color-comparison task on the same stimuli ( $t_5 = 2.8$ ,  $P = 0.070$ ). This task dependence was supported by a significant two-way interaction of task  $\times$  same/different category ( $F_{1,5} = 58.38$ ,  $P = 0.001$ ; Fig. 6). Furthermore, task modulated object information more strongly in the foveal ROI than in LOC (significant interaction of task  $\times$  ROI  $\times$  same/different category,  $F_{1,5} = 8.12$ ,  $P = 0.036$ ; Fig. 6), where there was no



**Figure 5** ROIs in one example subject and the corresponding mean correlations. (a) Inflated cortical surface with this subject's functionally defined ROIs in color: outer ring (object location; outer ring > middle ring) in blue, middle ring (middle ring > outer ring + foveal ring) in green and foveal retinotopic cortex (foveal ring > middle ring) in red on the cortical surface (inflation was performed using Freesurfer<sup>34</sup>). (b) Mean correlations ( $\pm 1$  s.e.) within and between categories (always between locations) for three ROIs in Experiment 3. Five subjects participated in this experiment, which was identical to Experiment 1, except that a checkerboard eccentricity mapping and meridian mapping were conducted.



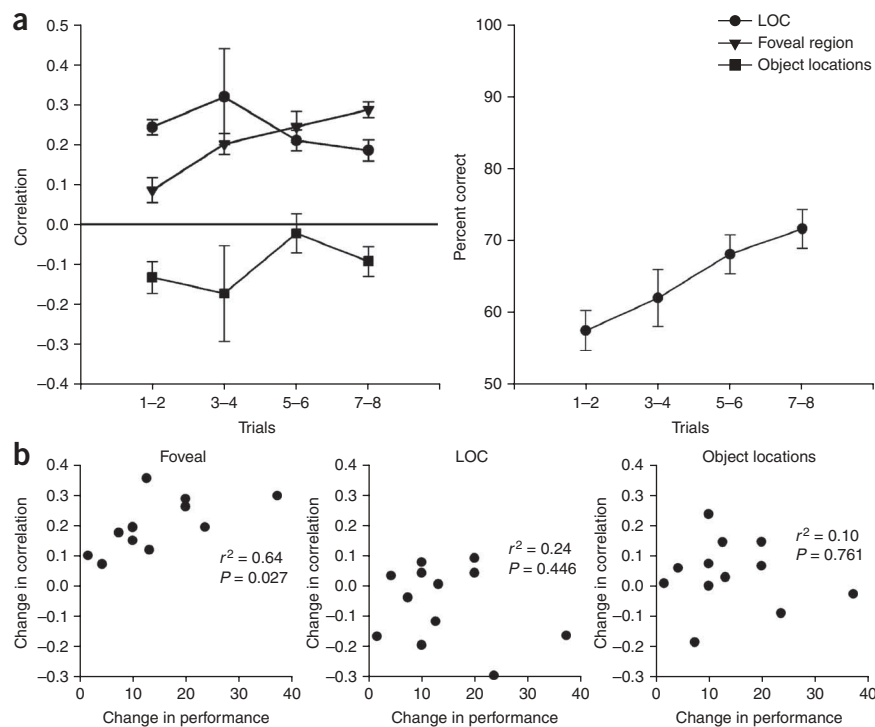
**Figure 6** Correlations within and between categories (always between locations) for LOC and the foveal retinotopic cortex in Experiment 4, showing that task modulated object information more strongly in the foveal ROI than in LOC. **(a)** Results from the object-discrimination task showing object information in both LOC and foveal retinotopic cortex. **(b)** Results from the color task demonstrating object category information in LOC but not in foveal retinotopic cortex.

significant difference between the strength of object information in the color and shape tasks.

To further test the link between the object information in foveal retinotopic cortex and behavioral performance, we binned the data from Experiments 1 and 6 into four consecutive 4-s time bins in each block of a particular stimulus category. Notably, both behavioral accuracy (**Fig. 7a**) and object information in foveal retinotopic cortex (**Fig. 7a**) built up gradually over the course of each block. This increase in pattern information over the course of each block was specific to the foveal ROI (significant interaction of ROI  $\times$  time bin,  $F_{1,11} = 3.32$ ,  $P = 0.032$ ; **Fig. 7a**). Finally, the magnitude of behavioral improvement over the block was correlated across subjects with the magnitude of the increase in category information for foveal retinotopic cortex ( $r^2 = 0.64$ ,  $P = 0.027$ ), but not for LOC ( $r^2 = 0.24$ ,  $P = 0.446$ ) or for the object location ROI ( $r^2 = 0.10$ ,  $P = 0.761$ ) (**Fig. 7**). Thus, position-invariant object information accrues in foveal retinotopic cortex over successive trials of the same stimulus type in lockstep with improved behavioral performance.

In sum, the object information that we found in foveal cortex is behaviorally relevant both in the sense that it is found only when the task requires object form information and that stronger information in foveal cortex is correlated with higher task performance.

**Figure 7** Time course and behavioral relevance of position-invariant information in foveal retinotopic ROI in Experiments 1 and 4. **(a)** Top, time course of appearance of object category information (between locations) across each block for foveal ROI, LOC and Object Location ROI; each time bin represents two trials and 4 s. Bottom, corresponding behavioral data collected from the same subjects during scanning. Performance increased across trials in a block, mirroring the increase in category information in the foveal ROI. **(b)** Scatter plots showing the correlation across subjects between the amount of increase in performance from the beginning to the end of blocks and the increase in the amount of object information in each ROI. Note that category information correlated with behavioral performance only for foveal retinotopic cortex<sup>15</sup>.



## DISCUSSION

We have replicated in six independent experiments the finding of significant position-invariant information in foveal retinotopic cortex about peripherally presented objects (for Experiment 6, see **Supplementary Fig. 5** online). Our data cannot be explained by differential eye movements across object categories or activation from the fixation cross itself. These results cannot be explained by spillover activation from peripheral to foveal retinotopic cortex, as the latter is position invariant, whereas the former is not (**Fig. 3**), or from LOC, as the object information in foveal retinotopic cortex is task dependent, whereas object information in LOC is not (see below and **Figs. 6** and **7**). Although fMRI cannot directly distinguish feedback from feedforward responses, it is difficult to account for our results without invoking feedback, as the object information was only present in foveal retinotopic cortex when the subject performed an object-discrimination task (as shown in Experiment 4). Passive propagation of information across retinotopic cortex in the absence of feedback from higher areas would not explain why the information would be propagated to the fovea and not to other locations in retinotopic cortex, or how the object information can be position invariant in foveal retinotopic cortex when it is not position invariant in the object location ROI. Furthermore, the lateral spread of monosynaptic horizontal connections is less than 3 degrees of visual angle<sup>24</sup>, much less than the eccentricity of our peripheral stimuli from the fovea. Instead, our data strongly suggest that position-invariant object information from higher cortical areas (possibly including LOC) is fed back to foveal retinotopic cortex.

In contrast with the predictions of virtually all prior theories of feedback in perceptual processing, the feedback representation described here occurs in a completely different cortical location from the corresponding feedforward representation. Although one recent study reported information in retinotopic cortex that was adjacent to the region directly activated by the stimulus<sup>25</sup> and another reported the presence of feature-based attention signals across the entire visual field<sup>20</sup>, our findings show a case in which the feedback representation

occurs far from the stimulus location, in foveal retinotopic cortex, and not in other regions of retinotopic cortex (see **Figs. 3** and **5**). Finally, unlike all prior reports, the object information that we describe in retinotopic cortex is invariant to stimulus location.

Notably, the object information in foveal cortex that we report here is related to behavior. The foveal information was present only when subjects performed an object-discrimination task and not when they performed a color task on the same stimuli, and the strength of the object information in foveal retinotopic cortex was correlated with subjects' accuracy discriminating the peripherally presented objects.

How exactly might feedback of object information to retinotopic cortex improve task performance? Automatic predictions of imminent saccades to peripheral stimuli might lead to predictive signals in foveal retinotopic cortex (where peripherally attended stimuli frequently land next)<sup>26</sup>. However, this hypothesis cannot easily account for our findings that information in foveal cortex was weak or nonexistent at the beginning of each block and built up over successive trials with the same object category (in which subjects never successfully foveate the object). Instead, the gradual improvement in behavioral performance over the course of each block suggests that subjects developed a more precise mental representation of the particular object category (and/or its diagnostic features) as the block proceeded. Furthermore, this improvement in performance was correlated with the appearance of category information in foveal retinotopic cortex. Thus, one possibility is that foveal retinotopic cortex may serve as a kind of scratch pad to store or compute task-relevant visual information<sup>27</sup>. This proposal is consistent with the previous theories<sup>28,29</sup>, according to which "the best description of V1 is not the first stage in a feedforward pipeline (or the last in a fully top-down conception of brain function), but rather the unique high-resolution buffer in the visual system for geometric calculations"<sup>28–30</sup>. Note that our results do not constrain the neuro-anatomical pathways through which the feedback modulates the information contained in foveal retinotopic cortex. For example, feedback might directly modulate the activity of foveal neurons or it might modulate the influence of horizontal connections<sup>29</sup>.

Another open question is whether the fMRI patterns in foveal retinotopic cortex reflect a subthreshold synaptic signal rather than the spiking output of neurons. The fMRI BOLD signal is strongly related to synaptic activity, as measured by local field potentials<sup>31,32</sup>, and some cognitive signals have been shown to be stronger in local field potentials than in spiking output<sup>33</sup>. Thus, it is possible that the fMRI patterns that we observed in our experiments are not associated with differences in spiking output. To test this prediction, invasive extracellular recordings are needed, which will require the implementation of our procedure in monkeys.

Whatever the ultimate understanding of its precise function, our data demonstrate for the first time, to the best of our knowledge, the existence of position-invariant information in foveal retinotopic cortex and strongly suggest that this information arises by feedback from higher cortical areas. These findings open the door to a broad new landscape of investigation. Exactly what kind of object information is fed back to foveal retinotopic cortex and over what range of information-processing tasks does feedback occur? Why is position-invariant information fed back to the foveal region of retinotopic cortex in particular? By what mechanism does feedback improve task performance? The answers to these questions are bound to have fundamental implications for our understanding of visual information processing.

## METHODS

**Subjects.** Eight subjects were recruited for Experiment 1. One had to be excluded as a result of excessive head movement (>8 mm across experiment)

and another participant was removed because of a technical issue with the eye-tracking system. Six subjects were recruited for the color experiment (Experiment 2) and all were used during analysis. Eight subjects were recruited for the eccentricity-mapping experiment (Experiment 3). One was excluded because they withdrew from the experiment and two subjects were excluded as a result of nonsignificant localizer results. Eight subjects were recruited for Experiment 4. One was excluded because of chance-level behavioral performance and two were excluded as a result of excessive eye movements. Four subjects were recruited for the no central fixation experiment (Experiment 5). One had to be excluded because of excessive head movement (>8 mm across experiment). Seven subjects were recruited for Experiment 6. One had to be excluded because of excessive head movement (>8 mm across experiment).

**Experiment 1.** Subjects viewed three categories of novel objects (spikies, smoothies and cubies). Two objects of the same category were presented in diagonally opposite quadrants of the visual field (upper left/lower right or upper right/lower left) and participants indicated whether the objects were same or different (that is, within category discrimination) via a two-button response box. Objects (mean width, 1.8° of visual angle) were presented 7° from fixation to center of objects for 100 ms, followed by a blank inter-stimulus interval for 1,900 ms. Each block contained eight trials (that is, 16 s per block) with four blocks of each object category in each run. The order of object category was counterbalanced across runs and subjects. The accuracy of the participants' responses (across all three object categories) was 68% ( $\pm 9$  s.e.) over the scan. Fixation was monitored using an I-Scan eye-tracking system (ISCAN).

We identified the critical ROIs in four independent localizer runs. Each run consisted of four 16-s blocks of faces, scenes, common objects and scrambled objects (totaling 16 blocks per category). These stimuli were 8° of visual angle and presented at the fovea to ensure that there was no overlap with the objects in the experimental run. We defined the LOC (objects > scrambled), the foveal representation in retinotopic cortex (objects and scrambled > rest taking active voxels only on the occipital poles) and the retinotopic representation of the experimental stimuli (smoothies, spikies and cubies > rest, using half experimental runs restricted to voxels close to the calcarine sulcus). To confirm that there was no overlap between the ROIs, we conducted a conjunction analysis using Functional Analysis Stream ROI toolbox (fROI, <http://froi.sourceforge.net/>).

To ensure that our foveal ROI did not accidentally contain a few voxels that included the cortical region representing the peripheral stimuli, we checked that there was no overlap between the foveal ROI and an ROI containing all active voxels in retinotopic cortex during presentation of the objects (**Fig. 2**). The foveal ROI included all early retinotopic visual areas, as there is no way of separating these regions at the occipital pole in humans with fMRI<sup>34</sup>.

To ensure that the effects could not be explained by differences in the number of voxels in each ROI, we adjusted the threshold (minimum threshold was  $10^{-6}$ ) to approximately equate the number of active voxels (foveal ROI,  $839 \pm 61$ ; object location ROI,  $776 \pm 94$ ; LOC ROI,  $849 \pm 93$ ; mean  $\pm$  s.e.m.;  $F_{1,5} = 0.954$ ,  $P = 0.374$ ).

**Experiment 2.** The no fixation cross experiment was carried out similar to Experiment 1, except that there was no central fixation. Instead, four crosses were placed permanently in the location of the objects and subjects were asked to fixate at the intersection of these fixations.

**Experiment 3.** The eccentricity-mapping experiment was carried out similar to Experiment 1, except that it included an independent localizer task. The localizer included three disc or ring-shaped stimuli composed of a flashing checkerboard texture: a foveal disc with a radius of 2 degrees, a middle eccentricity annulus with a radius extending from 2 to 4 degrees and an outer annulus with a radius extending from 4 to 6.7 degrees (excluding the four stimulus locations). Standard meridian mapping was also conducted to ascertain the V1/V2 borders using with flashing horizontal and vertical checkerboards.

**Experiment 4.** To examine stimuli both above or both below fixation, and not on a diagonal-straddling fixation, we carried out an experiment that was similar to Experiment 1, except that the two stimuli were presented either in the two upper positions or the two lower positions, rather than along diagonals.

Eye position was monitored. The foveal ROI and the between-location ROI (midway between the two stimuli) were localized by independent localizer scans in which square-shaped stimuli with a flashing checkerboard pattern (3.3 degrees) were presented in the corresponding location.

**Experiment 5.** The color and shape Experiment was carried out similar to Experiment 1, except that the objects were colored red, blue, or green. In half of the runs, subjects were asked to perform the original object-discrimination task, and they were asked to perform a difficult color-discrimination task (same/different color judgment) in the other half. Six runs of each task were performed in addition to the four independent localizer runs.

**Experiment 6.** We carried out this experiment similar to Experiment 1, except that no eye tracker was used; This experiment was conducted before the others and is included here simply to show an additional replication of the basic effect (see **Supplementary Fig. 3**).

**fMRI scanning.** Scanning was done on a 3T Siemens Trio scanner at the Athinoula A. Martinos Imaging Centre at the McGovern Institute for Brain Research at the Massachusetts Institute of Technology. fMRI data analysis was conducted using FreeSurfer Functional Analysis Stream (FS-FAST; <http://surfer.nmr.mgh.harvard.edu/>) and ROI analysis was conducted using FS-Fast ROI toolbox (fROI; <http://froi.sourceforge.net/>). fMRI runs were acquired using the standard 12-channel head matrix coil and a gradient-echo echo-planar sequence (repetition time = 2 s, echo time = 40 ms,  $1.4 \times 1.4 \times 2.0$  mm + 20% spacing). The processing steps for both the localizer and experimental runs included motion correction and spatial smoothing with a 3-mm kernel and linear trend removal. Note that only the localizer task was smoothed (correlation analysis was performed on unsmoothed data).

**Data analysis.** Spatial response patterns were extracted separately for each subject and for each ROI. Thus, we obtained a different spatial pattern for each combination of stimulus configuration (upper left and lower right versus lower left and upper right) and stimulus type (smoothie, spikie and cubie) for each subject and ROI. The color experiment contained three runs in each half and all other experiments contained four runs in each half for each combination of ROI and stimulus category. Each run contained six blocks for each condition (eight trials in each block) and seven fixation blocks. A gamma function with  $\Delta = 2.25$  and  $\tau = 1.25$  was used to estimate the hemodynamic response for each voxel for the different category and location conditions. The mean response in each voxel across all conditions was then subtracted from the response to each individual condition in each half of the data before calculating the correlations. In each ROI, we then computed the correlation between the spatial patterns of fMRI responses resulting from the same stimulus category versus different stimulus categories. For example, we compared the pattern of responses in the LOC for spikies with other spikies versus spikies with smoothies. If the region carries information about the category (spikie, smoothie or cubie), there will be a higher correlation between the same-category spatial patterns than between the different-category spatial patterns<sup>11,15</sup>.

Note: Supplementary information is available on the Nature Neuroscience website.

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#### AUTHOR CONTRIBUTIONS

M.A.W. conducted Experiments 1–3, 5 and 6, designed Experiment 4 and wrote the manuscript. C.I.B. and H.P.O.d.B. were involved in the design and implementation of all of the studies and writing the manuscript, and H.P.O.d.B. also created the stimuli. W.M.S. conducted Experiment 4. S.D. wrote specialized eye tracking analysis programs, programmed the experiments and helped with data collection. C.T. optimized the neuroimaging sequences and N.K. supervised the entire project, including writing the manuscript.

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