

Object-Centered Shifts of Receptive Field Positions in Monkey Primary Visual Cortex

Amy M. Ni,¹ Scott O. Murray,^{2,*} and Gregory D. Horwitz¹

¹National Primate Research Center and Department of Physiology and Biophysics, University of Washington, Seattle, WA 98195, USA

²Department of Psychology, University of Washington, Seattle, WA 98195, USA

Summary

Stimuli that project the same retinal visual angle can appear to occupy very different proportions of the visual field if they are perceived to be at different distances [1–8]. Previous research shows that perceived angular size alters the spatial distribution of activity in early retinotopic visual cortex [7, 9–11]. For example, a sphere superimposed on the far end of a corridor scene appears to occupy a larger visual angle and activates a larger region of primary visual cortex (V1) compared with the same sphere superimposed on the near end of the corridor [7]. These previous results, however, were obtained from human subjects using psychophysics and fMRI, a fact that fundamentally limits our understanding of the underlying neuronal mechanisms. Here, we present an animal model that allows for a finer examination of size perception at the level of single neurons. We first show that macaque monkeys perceive a size-distance illusion similarly to humans. Then, using extracellular recordings, we test the specific hypothesis [12] that neurons in V1 shift the position of their receptive fields (RFs) in response to complex monocular depth cues. Consistent with this hypothesis, we found that when ring-shaped stimuli appeared at the back of the corridor, RFs of V1 neurons shifted toward the center of the rings. When the same stimuli appeared at the front of the corridor, RFs shifted outward. Thus, our results show for the first time that V1 RFs can shift, potentially serving as the neural basis for the perception of angular size.

Results

Psychophysics

We first established that the behavior of macaque monkeys is consistent with a well-known size-distance illusion. In psychophysical sessions, two monkeys were trained to report which of two briefly presented rings on a uniform gray background was larger, by making an eye movement to the remembered location of the larger ring. Once the monkeys could accurately perform the task, a background with an image of a corridor (Figure 1A) was introduced in blocks of trials alternating with blocks with a uniform gray background. In the blocks with the corridor image, the monkeys were rewarded for making an eye movement to either ring. We found that when identically sized rings were presented on the gray background, the monkeys chose the “near” and “far” rings equally often. (Here and throughout, we use the terms “near” and “far” to refer to the bottom-left and top-right of the display, respectively; on the

corridor background, stimuli at these two locations appear near to or far from the observer.) Thus, the point of subjective equality (PSE) on the gray background occurred when the rings had the same size on the retina, as we expected. However, when the rings were presented on the corridor background, the PSE shifted, indicating that the near ring had to be larger than the far ring for the rings to be chosen equally often and, presumably, to appear the same size (Figure 1B) (shift for monkey 1 = 0.27°; shift for monkey 2 = 0.29°; 6% and 4% of the mean ring diameter, respectively). This behavior was similar to that of two human observers (Figure 1C). Overall, the humans had steeper psychometric functions—indicative of greater sensitivity to size differences—but, similarly to the monkeys, the PSE was shifted on the corridor background (PSE for human 1 = 0.18°; PSE for Human 2 = 0.12°; 3% and 2% of mean ring diameter, respectively).

Electrophysiology

Experiment 1

Previous fMRI experiments have demonstrated a change in the spatial distribution of activity in primary visual cortex (V1) in response to stimuli that have apparent differences in angular size [7, 9–11], which implies a change in receptive fields (RFs); a neuron that does not respond to a stimulus in one context but does in another has undergone an RF change. For example, the size of a stimulus representation across the cortex could be increased by shifting the RFs of individual neurons toward the center of the stimulus. Conversely, to activate a smaller region of cortex, RF positions could shift outward (Figure 2A; [12]). However, the center position of a neuron’s RF is believed to be fixed and determined by the pattern of feedforward connections from the retina to the cortex [13–18]. Shifting RFs is something that, to our knowledge, has not previously been documented in V1 neurons.

To probe the neural basis of the angular size illusion measured psychophysically, we conducted two electrophysiological experiments. Identically to the psychophysical experiments, stimuli were thin rings [9], allowing us to compare the retinotopic positions of the RF centers of neurons in V1 precisely (Figure 2B). Unlike the psychophysical experiments, the monkey fixated at the near or far end of the corridor in pseudorandomly interleaved trials. In alternating blocks of trials, rings were presented on a uniform gray background and the corridor background. In experiment 1, rings were concentric with the fixation point. The hypothesized shifts in RF position make predictions about how V1 neurons will respond to rings of different sizes at near and far apparent distances on the corridor background. If, as hypothesized, RFs shift inward at far apparent distances, then a given V1 neuron would be maximally driven by a smaller ring at far apparent distances than at near apparent distances. Thus, we expect size-tuning functions to peak at smaller ring sizes at far than at near apparent distances (Figure 2C).

For each unit, responses to rings of seven different sizes were recorded. We found that the size-tuning curves—average spike rate as a function of ring size—were well fit by a Gaussian function, and we used the peak of the Gaussian fit to estimate the ring size that drove the maximal response. Example units

*Correspondence: somurray@uw.edu

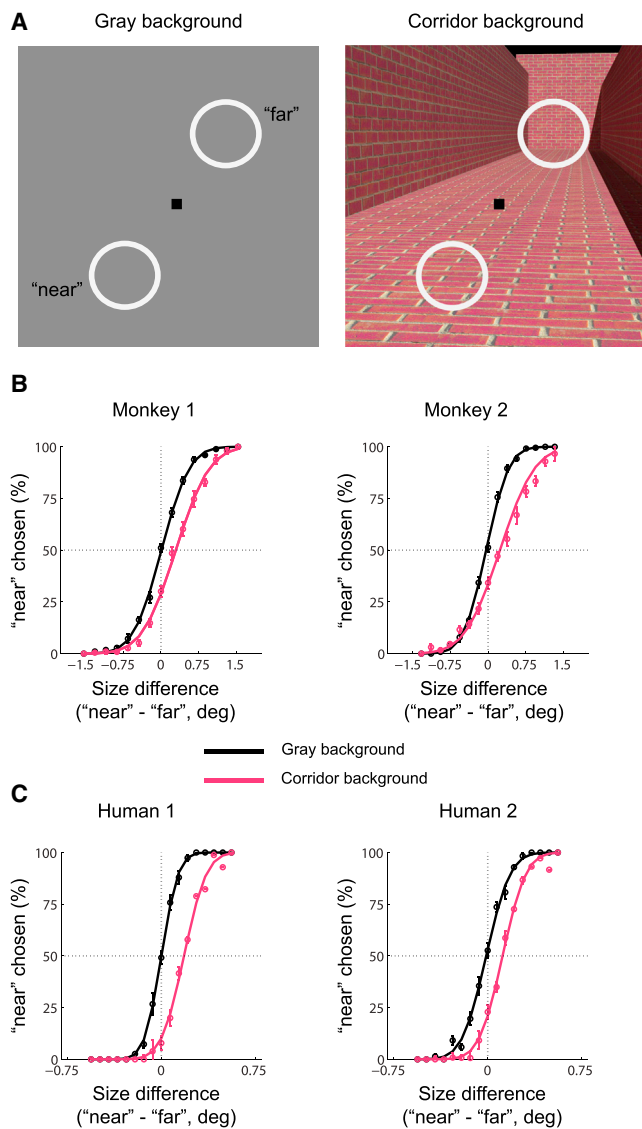


Figure 1. Psychophysical Measurements of Visual Size Perception

(A) Display used in psychophysical sessions. In this example, the two rings are identical, and they appear identically sized on the gray background. On the corridor background, however, the ring in the “far” location appears larger than the ring in the “near” location. The black square is the fixation point.

(B and C) Psychophysical data for monkey (B) and human (C) subjects. Rings were shown against a gray background (black) and a corridor image (red) in separate blocks of trials. A rightward shift of the psychometric function on the corridor background indicates a tendency for subjects to choose the ring at the far location as larger on the corridor background. The flattening of the monkeys’ psychometric functions on the corridor background may be due to the reward contingencies in this condition or to distraction from the novelty or complexity of the corridor image (see [Supplemental Experimental Procedures](#)). Error bars are ± 1 SEM.

from each monkey show representative shifts in optimal ring size ([Figure 3A](#)). For each unit, the optimal ring was smaller at far than at near apparent distances on the corridor background, an effect consistent with our hypothesis that RF positions shift inward at far apparent distances and outward at near apparent distances (see [Figure 2C](#); note that the same pattern of results was obtained without using function fits). There was little or no difference in optimal ring size on the

gray background for these two example units. To characterize changes in size tuning across the population, we plotted the optimal ring size for each unit at the near versus far locations on the gray and corridor backgrounds ([Figure 3B](#)). On the gray background, the size of the optimal ring did not differ systematically between the near and far locations. In contrast, when the rings were displayed on the corridor background, the optimal ring was significantly larger at the near than at the far location. In both monkeys, a 2 (background) \times 2 (location) repeated-measures ANOVA demonstrated a main effect of location [monkey 1, $F(1,42) = 20.4$, $p < 0.00001$; monkey 2, $F(1,14) = 15.6$, $p < 0.001$] and a significant interaction [monkey 1, $F(1,42) = 21.9$, $p < 0.00001$; monkey 2, $F(1,14) = 31.6$, $p < 0.00001$] ([Figure 3C](#)). Planned comparison paired two-tailed *t* tests demonstrated that the effect was driven by the larger optimal ring at the near versus far location on the corridor background (monkey 1, $p < 0.00001$; monkey 2, $p < 0.00001$). No significant effects were found on response magnitude or RF width (see [Figures S1A](#) and [S1B](#) available online). The average size-tuning curve shift was 0.17° for monkey 1, which is 63% of the shift in the psychometric PSE for this animal. It was 0.07° for monkey 2, which is 25% of the shift in the psychometric PSE for this animal. A time course analysis indicated that the shifts occurred at extremely short latency ([Figures S1C](#) and [S1D](#)).

In principle, these effects could be mediated by chance conjunctions of low-level visual features between the ring and corridor background. To control for this possibility, we conducted two variants of experiment 1: either the rings were concentric with the fixation point, or their centers were displaced vertically so that each ring appeared to touch the corridor floor at the same location (see [Supplemental Experimental Procedures](#)). In the latter condition, the vertical position of the fixation point, and thus the RFs, changed from trial to trial, causing the portion of the corridor background inside the RF to vary across trials. RF shifts on the corridor background did not differ significantly between these two experiment variants. A 2 (fixation condition) \times 2 (near versus far location) ANOVA with fixation condition as a between factor and location as a within factor revealed no main effect of fixation condition [$F(1,40) = 1.3$, $p = 0.26$] and a main effect of corridor location, $F(1,40) = 32.2$, $p < 0.00001$. The main effect of corridor location was significant in both fixation conditions individually [fixation concentric, $F(1,28) = 8.12$, $p = 0.008$; fixation displaced, $F(1,12) = 16.7$, $p = 0.002$]. Thus, it does not appear that the RF shifts are caused by the fine details of the corridor background image inside the RF.

The shifts in RF position we observed are consistent with the hypothesis that changes in the spatial distribution of V1 activity are correlated with changes in perceived size induced by apparent distance. However, RF location in the visual field is primarily determined by the position of the eyes: as the eyes move, so do RFs. Thus, systematic differences in fixation at the near and far locations could conceivably generate the RF shifts we observed. To examine this possibility, we calculated the average eye position across trials in each session at the near and far locations on the gray background and on the corridor background. Indeed, eye position was not distributed identically about the fixation point when the fixation point was at the near location versus when it was at the far location ([Figures S1E](#) and [S1F](#)). However, for differences in eye position to account for the RF shifts on the corridor background, the eye position differences need to be in a specific direction: to account for an inward shift at the far position, the eye has to

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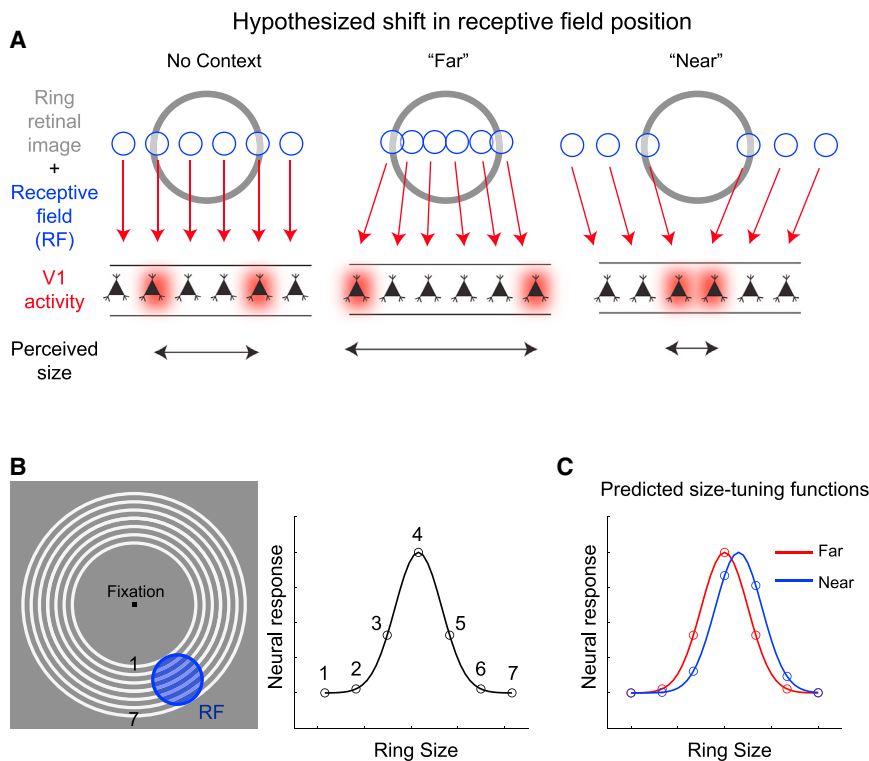


Figure 2. A Model of Size Representation in V1

(A) A ring stimulus presented with no context (left) activates V1 neurons (tufted triangles) through whose receptive fields (RFs, blue circles) it passes. The spatial distribution of the activated neurons is related to RF positions. Stimuli that appear to be far from the observer are perceived as large, consistent with an inward shift of RFs and a large cortical representation (middle). Conversely, stimuli that appear to be near are perceived to be small, consistent with an outward RF shift and a small cortical representation (right). (B) The amount and the curvature of the ring inside the RF (blue disk) depend on the ring size. (C) Under the model, the ring that activates a V1 neuron maximally will be smaller when the ring appears to be far from the observer (red) than when it appears to be near (blue).

move away from the RF. Conversely, to account for the outward shift at the near position, the eye has to move toward the RF. The distribution of eye positions was predominantly opposite to that required to explain the RF shift (Figures S1E–S1H). Eye position thus appears to be inconsistent with the RF shifts in experiment 1. Stronger evidence that RF shifts are not due to systematic shifts in eye position derives from experiment 2, described in the next section.

Experiment 1 demonstrates that RFs shift systematically and in accordance with the relationship hypothesized between the size of the visual representation in V1 and the perception of object size. However, this interpretation depends on the relative position of the stimulus and the fixation point. Critically, the illusory size difference exists independent of the position of the eyes (easily confirmed by viewing Figure 1A in the periphery). Thus, for the RF shifts to underlie the illusion, the shifts must be object centered and not fixation centered. In experiment 1, fixation-centered and object-centered RF shifts are impossible to distinguish because fixation was at the center of the ring on every trial.

Experiment 2

In experiment 2, we moved the fixation point outside of the rings, enabling us to distinguish fixation-centered from object-centered shifts (Figure 4A). If the shifts are fixation centered, we expect size-tuning curves at the near location to peak at a smaller ring size and size-tuning curves at the far location to peak at a larger ring size. If, on the other hand, the shifts are object centered, we expect RFs to shift in the opposite direction: size-tuning curves at the near location should peak at a larger ring size, and size-tuning curves at the far location should peak at a smaller ring size.

Consistent with object-centered shifts, the optimal ring was larger at the near than the far location for both monkeys in experiment 2 (Figures 4B, 4C and S2). This result implies that the direction of RF shifts (relative to the fovea) reverses

when the stimulus is moved from the center of gaze to the periphery. On the gray background, the optimal ring size did not differ significantly between the near and far locations. On the corridor background, the optimal ring was larger at the near than the far location, consistent with object-centered shifts. A 2 (background) × 2 (location) repeated-measures ANOVA

demonstrated a main effect of location for monkey 1, $F(1,18) = 14.78$, $p = 0.001$] and a significant interaction for both monkeys [monkey 1, $F(1,18) = 8.49$, $p = 0.009$; monkey 2, $F(1,9) = 10.12$, $p = 0.01$] (Figure 4C). Planned comparison paired two-tailed *t* tests demonstrated that the effect was driven by the larger optimal ring at the near versus far location on the corridor background (monkey 1, $p = 0.003$; monkey 2, $p < 0.00001$).

Discussion

Experiment 1 shows that RFs of V1 neurons shift in the visual field in response to stimuli presented at perceptually near and far locations in a manner consistent with the perception of a size-distance illusion. We propose that the relatively complex depth information in the corridor image is extracted in later stages of the visual system and that this depth information is then used, via feedback, to shift the position of RFs in V1. The fact that the effect occurs during the earliest part of the visual response (see Figures S1C and S1D) is consistent with fast-conducting feedback signals [20, 21]. We note that the average size of the shifts—approximately 0.1° —is small compared to the $\sim 1.0^\circ$ diameter that is typical of V1 RFs at the eccentricities we investigated, and it is smaller than the psychophysical effect. However, the fixation geometry was different in the psychophysical and electrophysiological experiments, which may have contributed to differences in the magnitude of the neural and psychophysical effects.

Our results significantly extend recent findings in humans showing a functional [7, 9, 10] and anatomical [22] relationship between V1 and the perception of angular size. Experiment 2 shows that the RF shifts are object centered—a necessary property if the shifts mediate perception. A secondary implication of the results of experiment 2 is that they rule out a set of low-level, stimulus-based explanations of the results. There

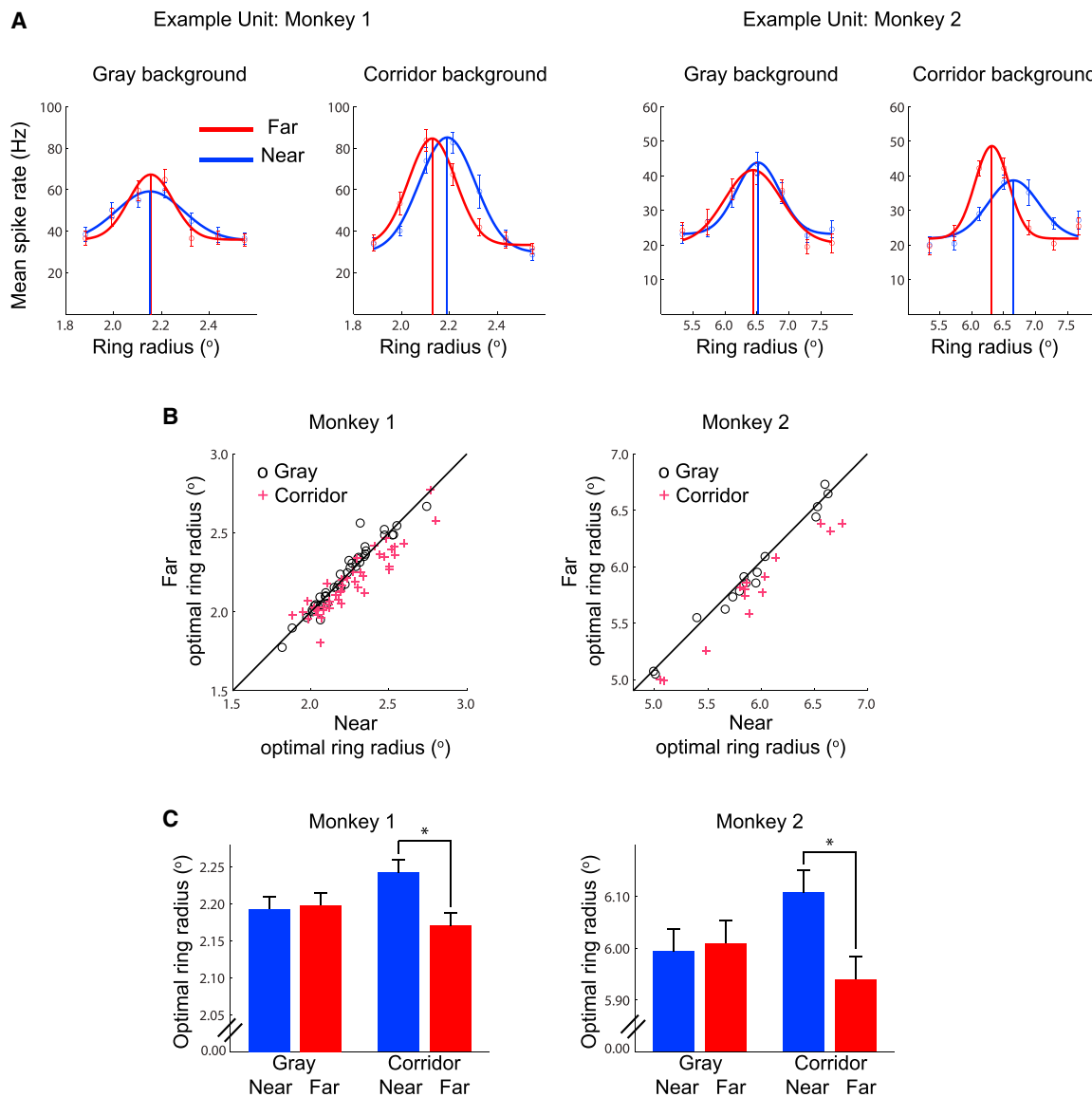


Figure 3. Electrophysiological Measurements of Receptive Field Shifts

(A) Data from example units. On the gray background, size-tuning curves peaked at the same ring radius whether the fixation point was at the far (red) or near (blue) location. On the corridor background, size-tuning curves were offset, consistent with the model prediction (Figure 2C).

(B) Optimal ring radii at the near (abscissa) and far (ordinate) fixation locations, measured on the gray (○) and corridor (+) backgrounds.

(C) Bar plots of mean optimal ring radii across conditions (error bars are 95% confidence intervals based on [19]). * $p < 0.05$.

See also Figure S1.

are obvious differences in the corridor image between the near and far locations. For example, luminance contrast differs between the near and far locations in the corridor image, and RFs are known to change size as a function of luminance contrast [23–26]. Thus, considering experiment 1 in isolation, it is possible that a combination of simple stimulus properties (e.g., luminance contrast, spatial frequency, etc.) that differs between the near and far locations in the corridor image changes the spatial characteristics of the RF in a direction that happens to be consistent with our hypothesis. But all of these stimulus-related differences between the near and far locations remain in experiment 2 and, like the fixation-centered prediction, would have been expected to shift the RFs in a consistent direction relative to the fovea. Instead, the RF shifts we have observed appear to be relative to the center of the

object and related to the interpretation of depth in the corridor image.

Previous studies have shown that RFs in extrastriate cortex can shift in the direction of the focus of attention [27–29]. It seems unlikely that the same attention-based mechanism underlies our result. It would require, for example, that in experiment 1 spatial attention was directed more toward the center of the ring at the far location than at the near location. Moreover, these relative differences in the focus of attention would need to reverse to explain the results of experiment 2. It is also unlikely that gain changes that are frequently observed with attention are relevant to our results. First, in the electrophysiology measurements, the rings were behaviorally irrelevant, so there is no a priori reason to suspect that the magnitude of attention should differ between the near and far rings.

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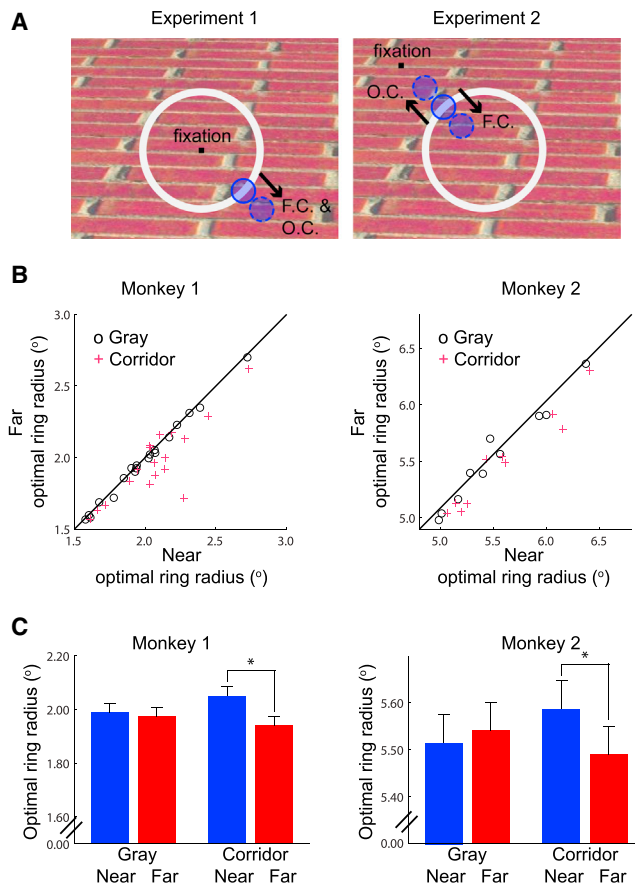


Figure 4. Dissociation of Fixation-Centered from Object-Centered RF Shifts (A) In experiment 1, the ring centers were always at the fixation point, so RF shifts were equally consistent with being relative to the fixation point or the ring center (left). In experiment 2, fixation-centered shifts predict smaller optimal rings at the near location; object-centered shifts predict larger optimal rings at the near location, as was observed (B) and (C). F.C., fixation centered; O.C., object centered. (B and C) Conventions are as in Figures 3B and 3C, respectively. See also Figure S2.

Second, it is unclear how a gain change could manifest in an RF shift. Third, there were no obvious magnitude differences in the response to the near and far ring indicative of a gain change.

Repeating the neurophysiological measurements while the monkey performs a task that controls the allocation of visual attention would provide a rigorous test of the attentional hypothesis. Monkeys could be trained to attend to the fixation point, but under these conditions, the RF shifts are predicted to be very small [9]. Alternatively, monkeys could be trained to report the color, shape, or some other irrelevant dimension of the ring. In this case, however, the monkey could perform the task by attending to one arc of the ring in the near position and a different arc at the far position, complicating the interpretation of RF shifts between fixation conditions.

Although it is possible that the mechanisms underlying our results and those observed with attention share similar feedback circuits, our results are inconsistent with any simple attention-based explanation. Instead, our results are more consistent with recent findings showing a relationship between the topographic response in monkey V1 measured with voltage-sensitive dye imaging and shape perception

[30]. Overall, our results reveal a simple code for visual object size whereby complex distance cues produce shifts in V1 RF position.

Supplemental Information

Supplemental Information includes three figures and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.06.003>.

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