Systems/Circuits

Remapping of Border Ownership in the Visual Cortex

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We see objects as having continuity although the retinal image changes frequently. How such continuity is achieved is hard to understand, because neurons in the visual cortex have small receptive fields that are fixed on the retina, which means that a different set of neurons is activated every time the eyes move. Neurons in areas V1 and V2 of the visual cortex signal the local features that are currently in their receptive fields and do not show "remapping" when the image moves. However, subsets of neurons in these areas also carry information about global aspects, such as figure–ground organization. Here we performed experiments to find out whether figure–ground organization is remapped. We recorded single neurons in macaque V1 and V2 in which figure–ground organization is represented by assignment of contours to regions (border ownership). We found previously that border-ownership signals persist when a figure edge is switched to an ambiguous edge by removing the context. We now used this paradigm to see whether border ownership transfers when the ambiguous edge is moved across the retina. In the new position, the edge activated a different set of neurons at a different location in cortex. We found that border ownership was transferred to the newly activated neurons. The transfer occurred whether the edge was moved by a saccade or by moving the visual display. Thus, although the contours are coded in retinal coordinates, their assignment to objects is maintained across movements of the retinal image.

Introduction

Areas V1 and V2 of the visual cortex contain several hundred million neurons that encode a huge amount of optical detail. Each neuron "sees" an image through a small window, its receptive field (RF), and analyzes that patch of the image, but our eyes change gaze continually, sampling selected parts of the scene with the fovea, the high-resolution center of the retina. When we inspect, for example, a sculpture for 10 s, our gaze sequentially visits 30–40 points, and, because the RFs are fixed on the retina, each neuron is presented with a new patch of the image at every new fixation. At one time, it will see features of the sculpture, then features of background objects, and sometimes a mixture. Thus, each neuron will give a series of responses encoding totally incoherent information. Nonetheless, we are able to integrate these responses into a coherent percept of the sculpture. Recent discoveries have deepened our understanding of the brain mechanisms that integrate eye movement signals and visual signals and led to new ideas about how the brain achieves perceptual stability despite the frequent image movements caused by saccades (Duhamel et al., 1992; Sommer and Wurtz, 2002; Goldberg et al., 2006; Wurtz, 2008; Cavanagh et al., 2010; Hall and Colby, 2011; Melcher, 2011; Wurtz et al., 2011), but how the brain derives coherent object representations from the stream of unrelated feature signals is not well understood.

One observation that suggests object-related coding in the visual cortex is that of border-ownership selectivity (Zhou et al., 2000; Qiu and von der Heydt, 2005). Placing an edge of a figure (e.g., a square) in the RF of a neuron, Zhou et al. found that approximately half of the neurons in V2 are selective for the location of the figure relative to the RF. Each such neuron has a fixed side preference, responding with a higher firing rate to an edge if the figure is on the preferred side compared with the identical edge produced by a figure on the opposite side. Zhou et al. proposed that this side-of-figure selectivity reflects mechanisms that use the global configuration of edges to infer border ownership (for a discussion of border ownership in perception, see Nakayama et al., 1989, 1995). Indeed, a large proportion of these neurons are also sensitive to stereoscopic depth (Qiu and von der Heydt, 2005) in a way that is consistent with a role in detecting occluding contours and the direction of occlusion. The underlying processes are not fully understood, but recent experiments indicate that border-ownership selectivity reflects the emergence of early object representations: the responses of border-ownership-selective neurons parallel the changes in perceived border assignment when the perceptual object interpretation of the visual stimulus changes (Qiu and von der Heydt, 2007; O'Herron and von der Heydt, 2011) and are influenced by object-based attention (Qiu et al., 2007).

These observations suggest that border-ownership-selective neurons might code the assignment of contours to objects. However, coding this assignment in neurons that have fixed retinotopic RFs does not seem to make sense. After each response, the next saccade will carry the border to RFs of a different set of neurons and the assignment information will be lost. To resolve this conundrum, we studied border-ownership-selective neurons under conditions in which the image moves across the retina, either because of a saccade or as the result of an object movement.

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Materials and Methods

We studied neurons in two male adult rhesus monkeys (*Macaca mulatta*). The details of our general methods have been described previously (O'Herron and von der Heydt, 2009, 2011).

Preparation. The animals were prepared by implanting, under general anesthesia, three small posts for head fixation and two recording chambers (one over each hemisphere). Fixation training was achieved by controlling fluid intake and using small amounts of juice or water to reward steady fixation. All animal procedures conformed to National Institutes of Health and United States Department of Agriculture guidelines as verified by the Animal Care and Use Committee of the Johns Hopkins University.

Stimuli and experimental design. Stimuli were generated with Open Inventor on a Pentium 4 Linux workstation with NVIDIA GeForce 6800 graphics card using the anti-aliasing feature of the software and were presented on a 21-inch EIZO FlexScan T965 color monitor with 1600 × 1200 resolution at 72 Hz refresh rate. Stereoscopic pairs were presented side by side and superimposed optically at 40 cm viewing distance. The field of view subtended 15 ° × 19° visual angle. A white (93 cd/m^2) cross inside a 20 arc minutes diameter disc of 9 cd/m^2 served as fixation point.

The color tuning of neurons was determined with stationary flashing bars, and minimum response fields were mapped with bars and drifting gratings (Zhou et al., 2000). Orientation and disparity tunings were determined with moving bars. Square figures were used for measuring border-ownership selectivity and the transfer of border-ownership signals. The squares were typically 4° on a side. Occasionally, larger figures were used so that the figure was at least twice the linear size of the RF. The figure was presented in a circular field whose diameter was three times the size of the square, i.e., typically 12°. One edge of the square (the test edge) was oriented at the preferred orientation of the neuron. This edge was centered in the circular field. All stimuli were viewed stereoscopically. The circular border was given a disparity relative to the fixation point so that it appeared ~58 mm in front. Thus, figures and fixation point were seen like through a circular window. Half a second after stimulus onset, the square was replaced by an edge that coincided with the test edge and was a diameter of the circular field. The stimuli were positioned so that the test edge was at a distance equal to half the square size from the RF. The edge was then brought into the RF, either by a saccade (experiment 1) or by displacing the stimulus (i.e., edge and circular window; experiment 2). The saccade was elicited by moving the fixation point appropriately. This occurred 250 ms after the change to ambiguous edge (750 ms after stimulus onset), and the object movement occurred after 300 ms (800 ms after stimulus onset).

The direction of gaze was monitored for one eye with an infrared video-based system (Iscan ETL-200) at 60 Hz with a spatial resolution of 5120 (horizontal) and 2560 (vertical). The eye was imaged through an infrared reflecting mirror virtually placing the camera on the axis of fixation. The optical magnification in our system resulted in a resolution of the corneal position signal of 0.08° visual angle in the horizontal and 0.16° in the vertical. Noise and drifts of the signal of course reduced the accuracy. To determine the saccade times (see below), the eye position signal was corrected for the delay in the recording system. This was measured by recording movements of an artificial pupil simultaneously with the video-based system and a photometer.

Behavioral trials began with the presentation of the fixation mark on a blank screen. A test sequence was initiated when gaze was in a predetermined fixation window (1° radius), and the first stimulus appeared 300 ms after fixation was detected. The monkey was rewarded for keeping its gaze in the fixation window for a fixed duration of 2.3 or 3.3 s, depending on the experiment. After successful termination of a trial, the display was blanked for an interval of 0.5–1.2 s. When fixation was broken, the trial was terminated and the following intertrial interval was increased by 1 s. Analysis of the eye movement recordings showed that there were no systematic deviations of fixation depending on the border-ownership condition (O'Herron and von der Heydt, 2009).

For both the object movement and the saccade experiments, the stimulus variation was controlled by three parameters: (1) the contrast polarity of the test edge, (2) the side of the edge on which the initial square was presented, and (3) the direction of the initial offset of the edge relative to the RF. Factorial designs were used, and all conditions of a test were presented in a pseudorandom order in which each condition was presented once before moving on to the next repetition. The edge was always offset perpendicular to the preferred orientation of the cell, and the size of the offset was always half of the width of the square (usually a 2° offset with a 4° figure). This allowed the RF to be placed in the center of the figure on half the trials and on the background on the other half.

Recording procedures. Single-neuron activity was recorded extracellularly with epoxy-insulated tungsten microelectrodes inserted through the dura mater. A spike detection system (Alpha Omega MSD 3.22) was used. Spike times, stimulus events, and behavioral events were digitized and recorded by computer.

Cells in area V2 were recorded in either the lunate sulcus after passing through V1 and the white matter or the lip of the post-lunate gyrus. The eccentricities of the RFs ranged from 0.6 to 7° (median of 1.9°). After isolating a cell, we first characterized its selectivity for color, bar size, and orientation and mapped its RF. Next, border-ownership selectivity was determined by a standard test using the edge of a square, both contrast polarities, and square sizes of 3° and 8° (Zhou et al., 2000; Qiu and von der Heydt, 2005). If a cell was color selective, the preferred color and a 28 cd/m^2 gray were used for the two figure colors, otherwise white (93 cd/m^2) and gray (28 cd/m^2). The display surrounding the circular field was set to the color intermediate between figure and ground colors, which was also the color of the blank screen between trials.

Data analyses. A three-way ANOVA was performed on the square-root-transformed spike counts of the single responses in the standard test, the factors being side of figure, contrast polarity, and figure size. The square root transform helps to stabilize the variance, because the variance of spike counts typically increases in proportion to the mean (Vogels et al., 1989). Only border-ownership-selective cells, as determined by significance of the factor side of figure ($p < 0.05$), were included in the analysis. Three cells in which the border-ownership preference reversed between the two contrast conditions were also excluded.

For the time course plots (see Figs. 2, 3, 5–7), the peristimulus time histograms (2 ms bin width) were computed for each neuron and smoothed with a Gaussian kernel (Fig. 2*A*, $\sigma = 50$ ms; Fig. 2*B*, $\sigma = 100$ ms; Figs. 3, 5, $\sigma = 30$ ms; Fig. 6, $\sigma = 60$ ms; Fig. 7, $\sigma = 10$ ms). For each neuron, the preferred side was determined based on the result of the standard test. The histograms for preferred and nonpreferred sides were averaged. Note that the preferred side assignment does not bias the results, because it is based on the independent data from the standard test.

The border-ownership signal in the remapping test was computed by averaging over a time window of 1050–2000 ms after stimulus onset in the saccade experiment and 900–2200 ms after stimulus onset in the object movement experiment. The significance of the this signal was determined by a permutation test. We generated 1000 random populations with the same number of neurons for each experiment by randomly assigning side-of-figure among trials that had the same local contrast polarity and offset direction for each neuron (null hypothesis). We then calculated the mean spike counts in the same intervals as above for each population.

To estimate the saccade times, we calculated the eye position Y perpendicular to the test edge and fit it with the following function:

$$Y = a + b\frac{t^{\delta}}{t^{\delta} + t_o^{\delta}},$$

where t is time and a, b, t_o, and δ are parameters. Specifically, b is the amplitude, and t_o is the saccade time at half-amplitude. Trials with poor fits (adjusted $r^2 < 0.95$) were discarded (<2%). The mean adjusted r^2 for the accepted data was 0.984.

To compare the onset of the border-ownership signal in the two experiments, we fit functions by two-phase regression (a least-squares fit of a concatenation of two functions, in which the transition point is determined by the fit). For the saccade experiment, the responses were aligned to the saccade time t_o and averaged. The average response histograms were fit with a two-phase function: a constant estimating the baseline activity, and a sum of two exponentials with independent amplitudes and

time constants (O'Herron and von der Heydt, 2011). The transition point was taken as the latency of the response. The border-ownership signal was fit with an initial phase of zero and a second phase of a single exponential. The transition point was taken as the latency of the border-ownership signal.

In the small group of cells that responded during the first phase of the remapping test (when illumination in the RF was uniform), we ran a correlation test to see whether the activity in the first phase may have driven the border-ownership signal after the edge moved into the RF. The baseline activity was computed as the average response in the window from 200 to 0 ms before stimulus onset. Any cells that had a response in the window from 200 to 400 ms after stimulus onset that was >0.5 Hz greater than the baseline response were included in the correlation analysis. We tested whether the border-ownership signal in phase 1 (100–500 ms after stimulus onset) was correlated with the border-ownership signal in phase 3 (1050–2000 ms in the saccade experiment; 900–2200 ms in the object movement experiment).

Results

The following analysis is based on a sample of 140 neurons recorded in four hemispheres of two monkeys, which we refer to as JA (54 neurons) and JO (86 neurons). All but one of these were assigned to area V2, the other to V1. Note, however, that some of our recordings were close to the V1/V2 border, in which the assignment can be in error. We mainly studied cells that were border-ownership selective, as determined by the standard test using a significance criterion of $p < 0.05$ (see Materials and Methods), which was the case in 52% of cells in JA and in 44% in JO. Cells that did not meet this criterion are excluded here and also three cells in which the side preference reversed between the two contrast conditions. After the border-ownership test, we usually assessed persistence first, by presenting the edge of a square in the RF and then substituting it with an ambiguous edge, as described previously (O'Herron and von der Heydt, 2009). The remapping tests were performed next and usually only if inspection of raster plots of the responses indicated some degree of persistence. Offline analysis indicated that 32% of cells in JA and 14% of cells in JO showed significant persistence in this test ($p < 0.05$, ANOVA). However, many cells that did not reach this criterion were nevertheless tested for remapping, and these are included in the analysis.

To see whether border-ownership information is transferred across cortex, we have to distinguish any information that is transferred to the neuron at the electrode from the information that is provided by the current stimulus. We can do this by using an ambiguous edge as a probe (Fig. 1). We first present the edge of a figure outside the RF (phase 1), then substitute the figure edge with an ambiguous edge (phase 2), and then induce a saccade that moves the RF onto the ambiguous edge (phase 3). This way, the stimulus that evokes a response (the ambiguous edge) provides no information about border ownership. The edge is related to a figure only through the display history. We found previously that border-ownership signals persist when the edge of a square is substituted with an ambiguous edge (O'Herron and von der Heydt, 2009). After the substitution, the neurons continue to fire at different rates depending on the initial border ownership, despite the visual stimuli being identical. This persistence enables us here to test whether border-ownership signals generated before an image movement transfer to the neurons that are activated after the movement. We first studied the effect of saccades, which we induced by moving the fixation point. In a second set of experiments, we kept the fixation point still and moved the stimulus instead.

The responses of an example neuron are illustrated in Figure 2. We first determined the border-ownership selectivity of the neuron by recording the responses to two opposite edges of a square (Fig. 2*A*, green oval indicates RF). The firing rate was higher when the edge was owned by a figure on the left. Red and

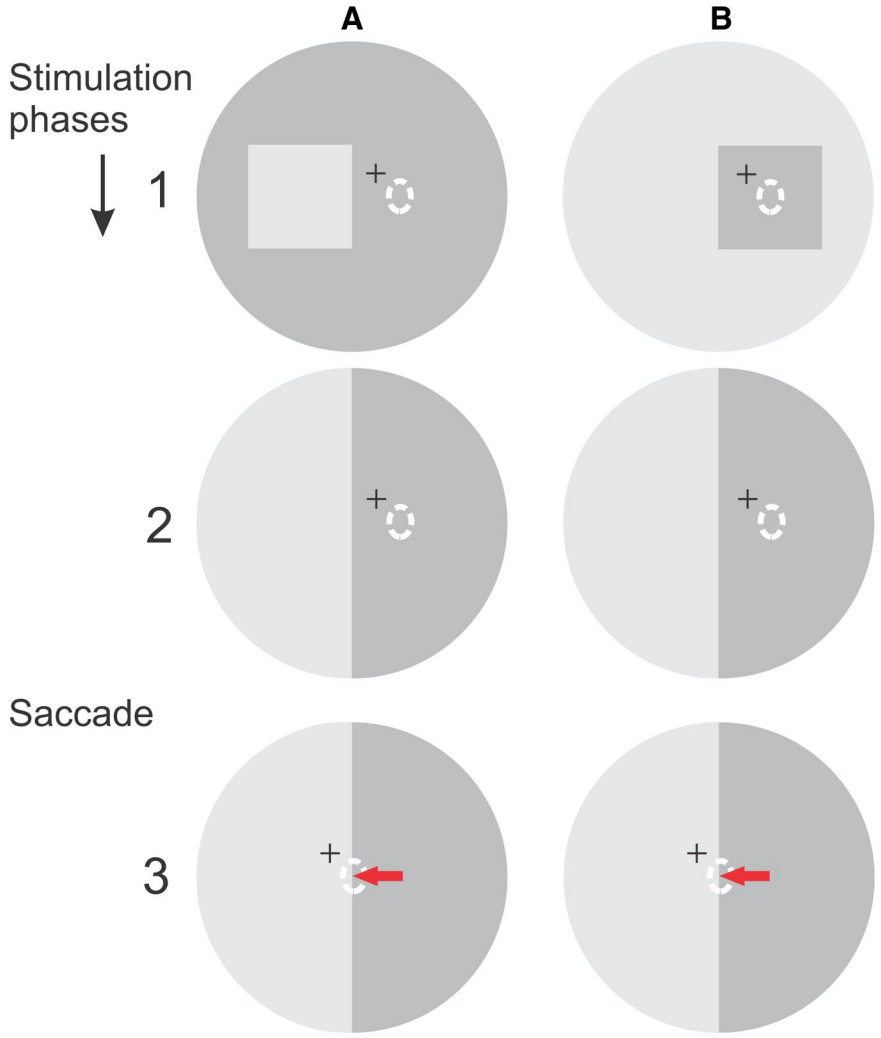

Figure 1. Paradigm for studying remapping of border-ownership signals across saccades. Monkeys fixated a cross on a computer display while single-neuron activity was recorded in the visual cortex. Cross, Fixation point; dashed oval, RF. A fixation trial consisted of three display phases, labeled ***1–3***. A square was presented (***1***) and one edge of it was replaced by an ambiguous edge (***2***), which was then brought into the RF by a saccade (***3***, red arrow). ***A***, ***B***, The two border-ownership conditions, which differ only in phase 1. In ***A***, the ambiguous edge is inherited from the right-hand edge of the square; in ***B***, it is inherited from the left-hand edge of the square. The illustration is for vertical orientation of the test edge. In the experiments, the orientations of square and test edge were matched to the preferred orientation of the neuron under study, and the saccade was perpendicular to it. In addition to the illustrated displays, each cell was also tested with the corresponding displays in which the colors of square and ground were reversed and with sequences with opposite direction of saccade.

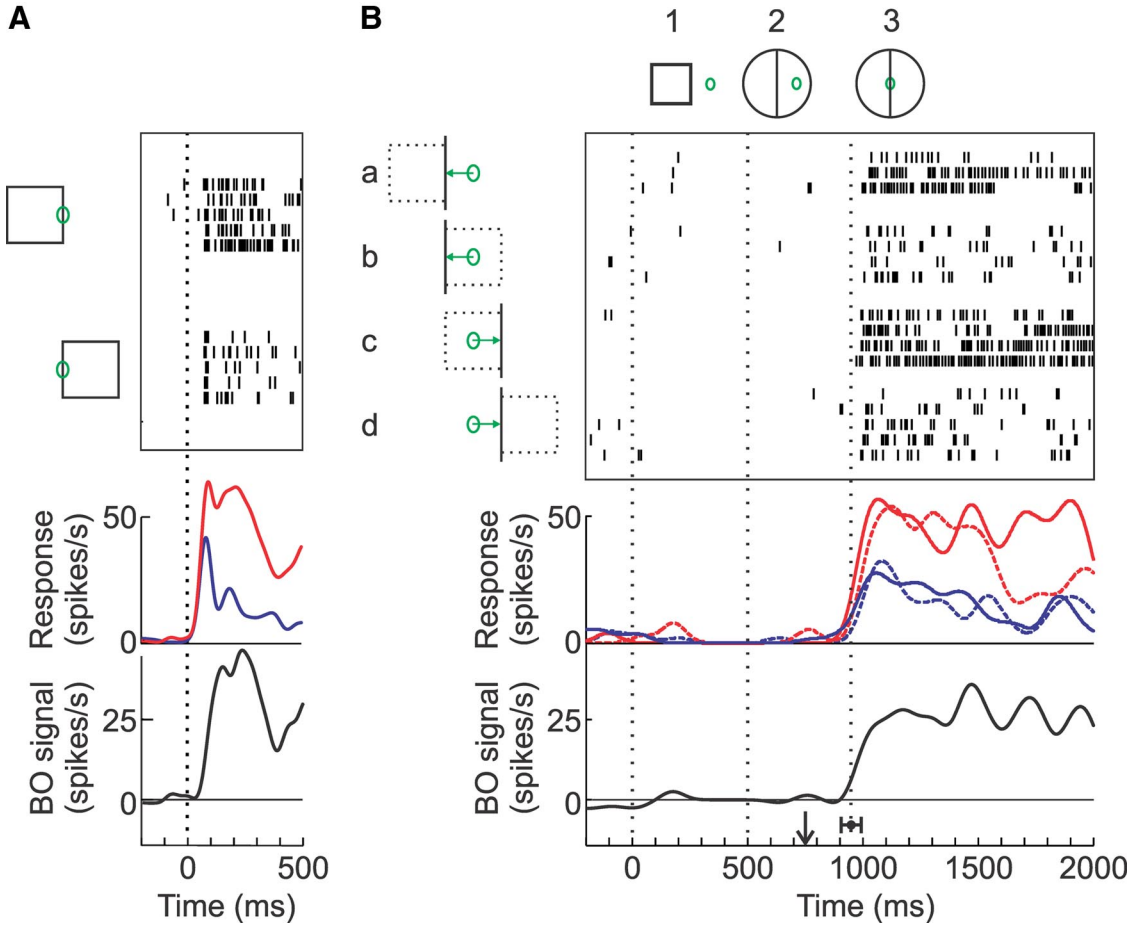

Figure 2. Transfer of border ownership across saccades: responses of an example V2 neuron. Green oval, RF. ***A***, Initial assessment of border-ownership (BO) selectivity. Top, Raster plots of responses to preferred and nonpreferred border ownership as illustrated on left. Red and blue curves show corresponding mean firing rates, and the black curve shows the difference between the two, the "border-ownership signal." ***B***, Saccade test. Raster plots show the activity during the three phases of stimulation illustrated at the top: ***1***, figure edge outside RF; ***2***, ambiguous edge at the same position; and ***3***, ambiguous edge in RF after saccade. Vertical dotted lines indicate time onset of the three respective display phases (***1–3***). Arrow on time axis indicates the time when fixation point was moved, and the dot with horizontal error brackets represents the median time of saccade and its interquartile range. Rows ***a*** and ***b*** of the raster plots show the responses to displays in which the edge inherits "left" and "right" border ownership, respectively, as depicted on the left, where dotted outlines indicate the position of the square relative to the edge (compare with Fig. 1). Rows ***c*** and ***d*** of the responses are for the same kind of displays but with reversed direction of saccade (arrows). Curves below show corresponding mean firing rates. Red and blue indicate the inherited left and right border ownership, respectively, and solid and dashed lines represent the two saccade directions. The black curve is the border-ownership signal (average of both saccade directions). The neuron responds only after the saccade moves its RF onto the edge in phase 3, but the responses reflect the border ownership defined by the figure in phase 1. The influence of remembered border ownership was similar for the two directions of saccade. Raster plots illustrate only the responses for the preferred contrast polarity, whereas the curves show the average over both.

blue curves depict the time course of responses in the two situations, and the curve at the bottom shows the difference. We call this the border-ownership signal. Although the signal is measured here by presenting the two border-ownership conditions to the same neuron, it is equivalent to the difference between the responses that would be obtained from two neurons with opposite side preference responding simultaneously to one edge of the square.

Saccades

In the saccade experiment, we test whether border ownership, defined by the square, is inherited by the ambiguous edge and transferred across the saccade (Fig. 2*B*). We applied the display sequences of Figure 1 and similar sequences with opposite movement direction. The stimulus diagrams at the top show the three display phases: figure, ambiguous edge, and ambiguous edge with new fixation. The four display conditions are depicted to the left of the response traces (*a–d*). Dotted outlines indicate the location of the square relative to the edge in phase 1. After the square was removed and only the test edge remained, a saccade was elicited that moved the RF onto the edge (arrows). The neuron does not respond during the first two phases, because all edges are outside the RF. It responds during the third phase when the saccade brings the RF onto the edge. Now, the strength of the responses varies between the four conditions despite the actual stimuli being identical: in trials in which the edge was derived from the right-hand edge of the square (*a* and *c*), the firing rate is higher than in trials in which the edge was derived from the left-hand edge of the square (*b* and *d*). A comparison of the four groups of responses shows that the response difference is not related to the direction of the saccade (both saccade directions produce strong responses in conditions *a* and *c* but weak responses in conditions *b* and *d*) or the location of the figure relative to the RF (conditions *b* and *c*, which have the same location, produce different responses). It relates to the initial border ownership. Thus, border ownership, defined by the square, is inherited by the ambiguous edge and transferred across the cortex at the time of the saccade.

The differential firing rate persists for at least 1 s, as can be seen in the time course plots below, in which colors represent border-ownership history (red for preferred and blue for nonpreferred),

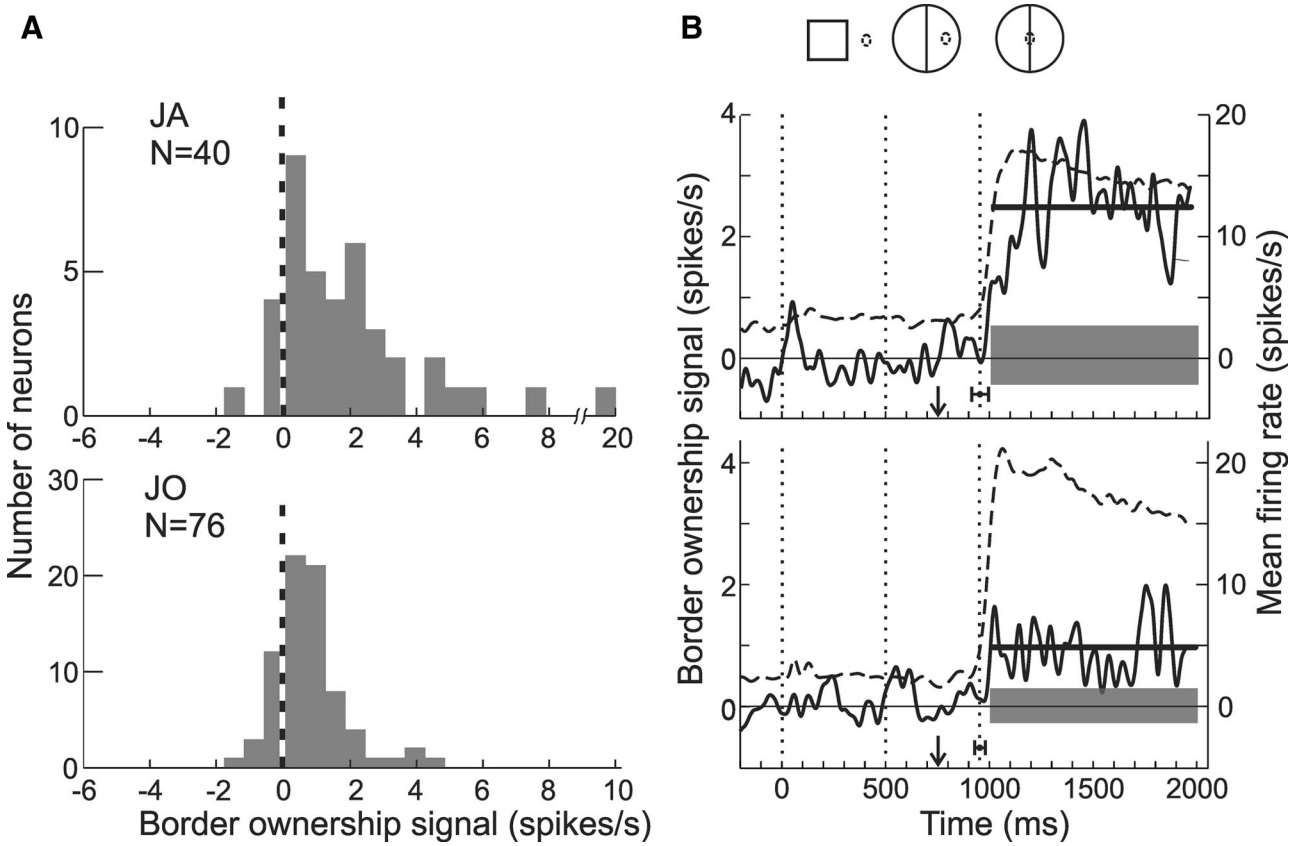

Figure 3. Transfer of border ownership across saccades: population response. Top and bottom plots represent the data from two animals. ***A***, Distributions of the border-ownership signal (firing rate difference) during presentation of the ambiguous edge after the saccade. Positive values indicate higher firing rate after preferred-side presentation of the figure. ***B***, Time course of population signal. Vertical dotted lines indicate time onset of the three display phases. Dashed curves, Mean firing rates; solid curves, border-ownership signal. Horizontal heavy lines indicate mean level of transferred signal, and shaded bands represent 95% CIs under the null hypothesis (no transfer), as determined by permutation test. Arrows on time axis indicate the time when fixation point was moved, and dots with horizontal error brackets represent median and interquartile range of saccade time.

and solid and dashed lines correspond to the two directions of saccades. The black line shows the border-ownership-related difference, averaged over saccade directions and contrast polarities (raster plots are shown only for one polarity).

The neuron of Figure 2 was unusual in the strength of the transferred signal, but the vast majority of the neurons tested did show a higher mean firing rate during the final ambiguous edge phase when the initial figure presentation was on the preferred side than on the nonpreferred side, indicating border-ownership transfer (88%, $n = 40$, in animal JA, $p < 10^{-5}$; 82%, $n = 76$, in animal JO, $p < 10^{-7}$, Wilcoxon's rank-sum test). Figure 3*A* shows the distribution of the response difference of the individual neurons in the two animals. Note that the sign of the response difference (the preferred side of border ownership) was determined for each neuron by the standard test independently of the main experiment, as shown in Figure 2*A*. Thus, the distributions of Figure 3*A* are unbiased.

The time course of the population firing rates (Fig. 3*B*, dashed curves) shows that the mean activity was at the resting level during the first two phases, when the edges were outside the RF, and then rose steeply after the saccade. The border-ownership signal (Fig. 3*B*, solid curves) fluctuated around zero during the initial phases but turned positive shortly after the onset of responses. This shows that border ownership, which is defined by the initial presentation of the square and inherited by the ambiguous edge, is transferred across the saccade.

Object movements

To see the effect of image displacements caused by an object movement, we ran a second experiment in which we moved the edge instead of the fixation point (Fig. 4). The displays in the first two phases were identical to those of the saccade experiment (1–2). Then, the edge and the circular aperture were moved, landing the edge in the RF (3). The results (Fig. 5) were similar to those of the saccade experiment, except that the onset of responses and the rise of the border-ownership signal were more abrupt (one reason for this is that, here, the responses are aligned to the edge movement, whereas in Figure 3 they were aligned to the movement of the fixation point and the response onset varied with saccade latency). The amplitudes of the transferred signals were not significantly different between saccade and object movement conditions.

A control

Although the vast majority of neurons were not activated when the square was presented, a small fraction of neurons did show changes in firing rate despite the absence of contrast features in the RFs. Some response is to be expected, because a small proportion of oriented V2 neurons responds to color change of a uniform field (surface-responsive cells; Friedman et al., 2003), and the color in the RF did change in our experiments when the figure was presented. However, the color change occurred in figure and ground regions and was balanced across border-ownership condi-

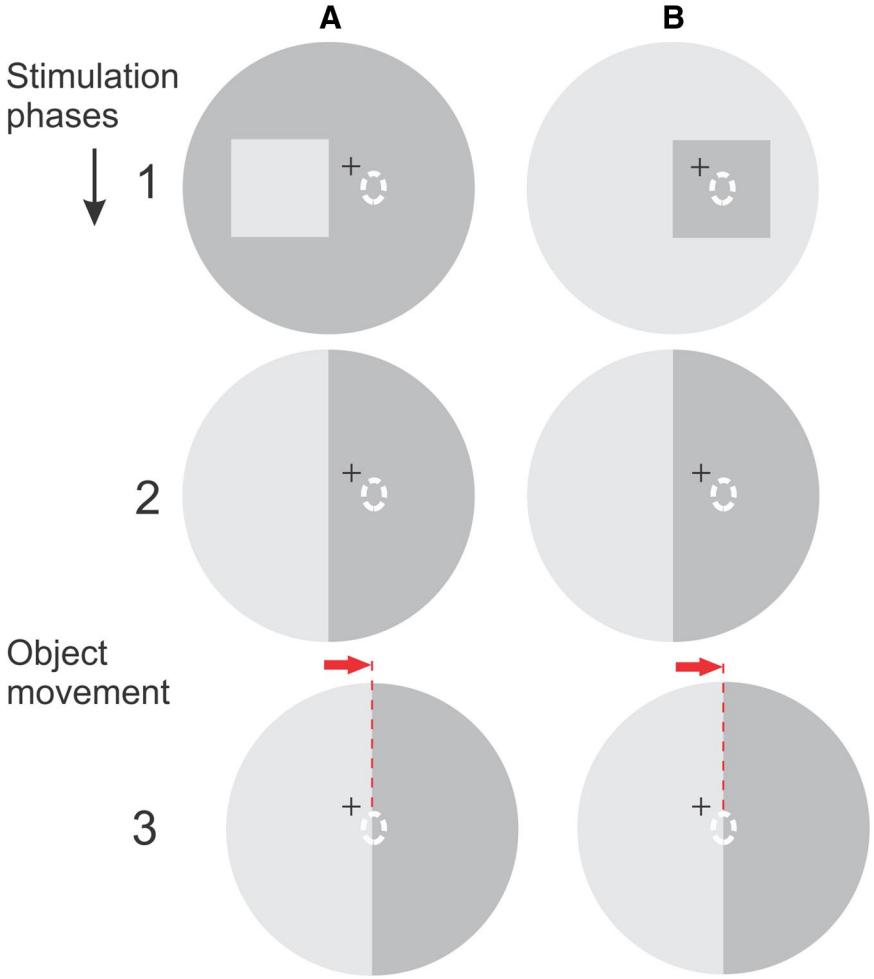

Figure 4. Paradigm for studying remapping of border-ownership signals across object movements. Conventions as in Figure 1. A fixation trial consisted of three display phases, labeled ***1–3***. One edge of a square (***1***) was replaced by an ambiguous edge (***2***), which was then moved into the RF (***3***; red arrow indicates movement vector). ***A***, ***B***, The two border-ownership conditions, which differ only in phase 1. Each cell was also tested with the corresponding displays in which the colors of square and ground were reversed and with sequences with opposite direction of movement.

tions (see Materials and Methods). To ensure that the initial response in this subset of neurons was not driving the border-ownership selectivity in the final phase, we compared the border-ownership signals in the initial and final phases. They were not correlated (Pearson's $r = 0.09$, $n = 26$, $p = 0.67$ in saccade experiments; $r = -0.14$, $n = 26$, $p = 0.49$ in object movement experiments). Thus, the remembered signal is not the result of a previous differential activation of the neurons but indicates transfer of information.

Signal decay

In most neurons, the transferred border-ownership signals were small compared with the border-ownership signals observed when figure edges were presented in the RFs. There are two possible explanations for the attenuation: (1) a decay of border-ownership signals in the neurons that are directly activated during the first ambiguous edge phase and (2) a loss during the transfer. To see how much loss occurs during the transfer, we also recorded the responses of the same neurons during static presentations in which figure edge and ambiguous edge were present in the RF from the beginning. We then compared the transferred border-ownership signals with the decaying border-ownership signals in the static condition. The dotted lines in Figure 6 show the decay of the signals in the static condition, and solid lines show the transferred border-ownership signals in the movement conditions. The comparison shows that, at the time when the transferred signal appears, it is approximately as strong as the decaying signal in the static display condition. This indicates that the attenuation is attributable to the decay of signals in the ambiguous situation. There seems to be no significant loss in the transfer.

Signal latency

The transfer of border-ownership signals in our experiments is reminiscent of the "remapping of receptive fields" that was first found in the lateral intraparietal cortex (Duhamel et al., 1992). Remapping is an apparent shift of the RF that occurs before a saccade: for a short period, a neuron can be activated by a stimulus outside its RF if the impending saccade will land that stimulus in the RF. Remapping is frequently found in areas that control attention and saccades but rarely in V1 and V2 (see Hall and Colby, 2011, for a recent review). An important aspect of remapping is that it can anticipate the saccade. The system can use the internal motor command signal to predict the movement of the retinal image. We wondered whether, in the case of border ownership, the latency of the emerging signal would also be shortened in the saccade condition, in which the displacement is anticipated, compared with the object movement condition, in which the displacement is controlled from outside.

To compare the latencies in the two conditions, we recalculated the mean border-ownership signal in the saccade condition after aligning the individual responses to the saccade times (i.e., the midpoints of the sigmoid functions fit to the eye position data). We then fit functions to the border-ownership signals consisting of a straight line and an exponential function (see Materials and Methods). Only cells that were tested with both conditions were included in this comparison. Reliable fits were obtained only for the data of monkey JA. For JO, the border-ownership signals were too small. The fits for JA (Fig. 7) show that the transferred border-ownership signals emerged approximately equally fast in both conditions: 105 ms after a saccade and 84 ms after an object movement, with confidence intervals (CIs) of 74–136 and 72–97, respectively, indicating that the difference is not statistically significant. The response latency was significantly longer in the saccade condition (48.6 ms, CI of 47.1–50.0 compared with 38.7 ms, CI of 37.2–40.2). The reason for this is probably the finite duration of the saccade (40 ms on average): the 10 ms difference might be the time it took on average from the midpoint of the saccade until the edge reached the RF. The border-ownership signal of the saccade condition might also include this delay. In summary, our data do not indicate an anticipation effect in the saccade condition. Of course, we might not see such an effect because the

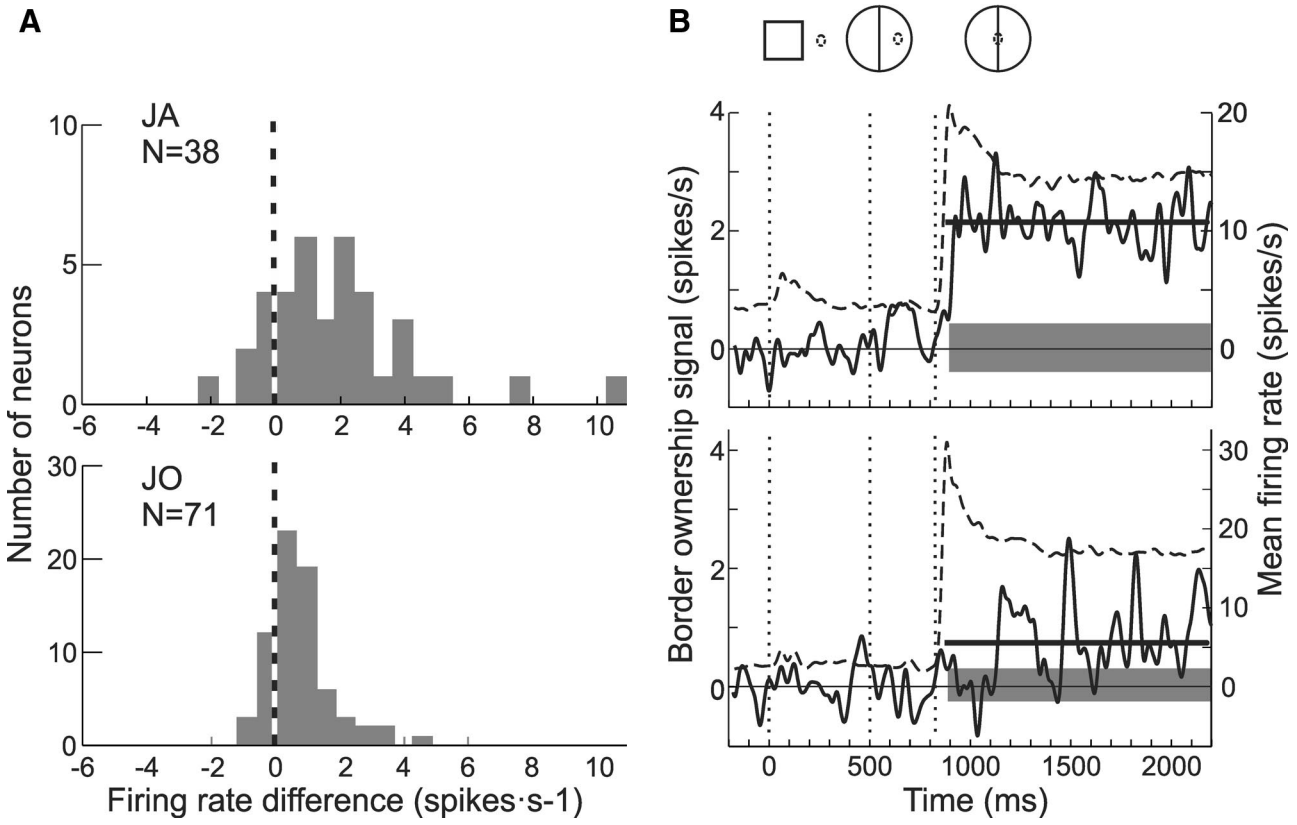

Figure 5. Transfer of border ownership across object movements. Top and bottom plots represent the data from two animals. ***A***, Distributions of the border-ownership signal (firing rate difference) during presentation of the ambiguous edge after the movement. Positive values indicate higher firing rate after preferred-side presentation of the figure. ***B***, Time course of population signal. Dotted vertical lines indicate the display phases. Dashed lines, Mean firing rates; solid lines, border-ownership signal. Horizontal heavy lines indicate mean signal level during transfer phase, and shaded bands represent 95% CIs under the null hypothesis (no transfer), as determined by the permutation test.

border-ownership signal can only emerge after activity is evoked by the edge.

A model

The transfer of border-ownership assignment shows that the system preserves figure–ground structure across image movements. It is not obvious how a difference between local edge responses can be transferred across cortex in an area in which RF positions are mapped retinotopically. The transfer occurred over considerable distances and even across hemispheres. For an RF at the median eccentricity of our sample (1.0°, −1.4°), a 2° movement toward the RF corresponds to a minimum distance of ~6–12 mm in V2 cortex, depending on the direction of movement (calculation based on the retinopic mapping function; Polimeni et al., 2006; Sugihara et al., 2011).

We propose here a simple conceptual model to illustrate how the remapping might be achieved (Fig. 8). The model builds on the previously proposed grouping cell model (Craft et al., 2007; Mihalas et al., 2011), which has two layers. The border-ownership cell layer B consists of edge-selective cells that are driven by classic simple or complex cells but in addition receive modulatory input from grouping cells in a second layer G. The G cells have large, annular integration fields that sum edge signals from B cells with RFs in co-circular arrangement, and, by feedback, set the gain of the same B cells. Each B cell receives feedback from G cells on one side of its RF, and it has a partner cell that receives similar feedback from G cells on the other side, while the two partner cells inhibit each other (cells and RFs labeled red and green, respectively; Fig. 8). The feedback makes the B cells border-ownership selective: when a figure is present, as in Figure 8*A*, its contours stimulate a large number of B cells, leading to strong activation of a G cell, which in turn enhances the responses of the same B cells. At the right-hand edge of the figure, for example, the left-pointing B cell (red) will be boosted, whereas the right-pointing B cell (green) will be suppressed. This specific enhancement and suppression by co-circular contour segments has been demonstrated in V2 neurons (Zhang and von der Heydt, 2010), but the G cells are as yet hypothetical. We illustrate here only the connections between B cells and G cells, but it is assumed that the main projection of the B cells goes to higher-level processing areas that are not shown here. This is an important point. B cells are feature selective and signal contour details, whereas G cells are not particularly selective. The loop between B cells and G cells only serves to bind a number of contour segments together, creating a perceptual unit and enabling top-down attentive selection (Mihalas et al., 2011).

The remapping of border ownership can be explained by two additions to this model: (1) a shifter circuit (SH) and (2) a set of object pointer (OP) cells. The SH flexibly connects the OP cells to the grouping cells. OP cells have persistence: once activated by a G cell, OP cells maintain their firing rate in the absence of G-cell input for some time. A model of an SH has been proposed (Anderson and Van Essen, 1987). The SH envisioned here might be similar in principle, except that it only needs to keep track of the locations of a few salient objects represented by peaks of activity in the G-cell layer as opposed to rerouting the entire visual information, i.e., potentially millions of signals. We assume that the circuit conducts excitatory signals in both direc-

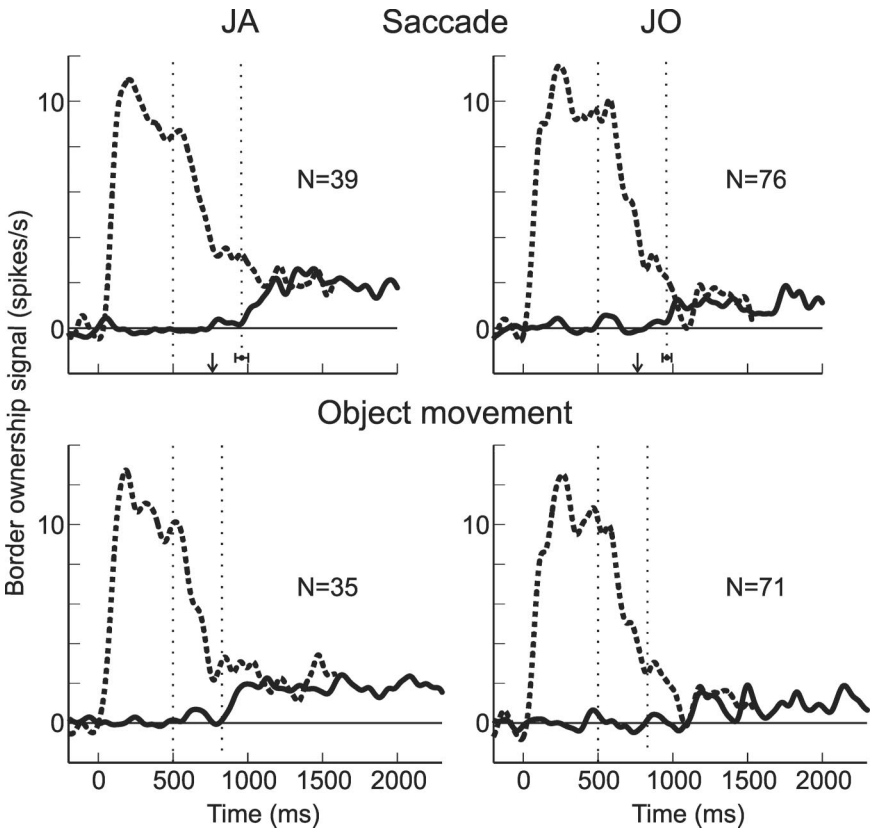

Figure 6. Decay and transfer of border-ownership signals. Left and right, Data from two monkeys. Comparison of the magnitude of the remapped border-ownership signal (solid line) with the magnitude of the local signal, i.e., the border-ownership signal that is obtained when a figure edge is presented and replaced by an ambiguous edge in the RF (dashed line). First vertical dotted line indicates beginning of ambiguous edge display. Second vertical dotted line indicates time when ambiguous edge appeared in RF in the remapping experiments (arrow on abscissa, time of movement of fixation point; bracket, median and interquartile range of saccade time). When the remapped signal appears, its magnitude is similar to that of the local signal. This indicates that the amplitude of the remapped signal reflects the decay of border-ownership signals during ambiguous edge presentation at the first location, whereas the transfer does not cause additional attenuation.

tions, from G cells to OP cells and back. The shift vector may be provided by signals from eye movement control centers or derived visually, from the retinal image displacement (see Discussion).

The appearance of an object creates a focus of activity in the G-cell layer. Under normal conditions, when the image of an object moves on the retina, the G-cell activity moves to a new place, but SH maintains the connection to the same OP cell (Fig. 8*A*,*B*). This enables the system to keep track of the identity of objects (Pylyshyn, 2001) and to relate the image features of an object at one moment to corresponding image features at the next moment. In our experiments, there is an intermediate phase: the figure is first converted to an ambiguous edge before the movement is applied. This is illustrated by the sequence *A*–*C*–*D* in Figure 8. After the display changes to an ambiguous edge, the initially activated G cell loses most of its driving input from B cells, but it still receives recurrent activation from the previously activated OP cell (Fig. 8*C*). The subsequent movement of the visual stimulus generates a corresponding shift in SH, which routes the activity of the OP cell to a new G cell. The recurrent activation now induces a border-ownership left bias in the newly stimulated B cells (Fig. 8*D*).

Discussion

The principal finding of this study is that border-ownership signals are remapped when the retinal image moves. The assignment of a visual edge is transferred across cortex to the neurons corresponding to the new location of the edge. The transfer occurs whether the movement is caused by a saccade or a displacement of the stimulus. The vast majority of neurons that showed persistence in signaling border ownership also showed this transfer.

As in previous experiments (O'Herron and von der Heydt, 2009), we studied the differential responses during periods of identical stimulation, comparing two conditions that only differ in the stimulus history. Thus, the observed signal reflects a memory trace. This method ensures that the emerging border-ownership signal is not computed from the actual stimulus. It can only be derived from the initial display phase. This means that it was transferred to the recorded neurons from neurons that responded differentially to the border-ownership conditions, because the recorded neurons were not activated differentially: either they were silent during the initial phase or their activity was not correlated with border ownership and thus not informative.

The transferred signal was smaller than the initial border-ownership signal. However, the remaining strength was equal to the strength of the decaying signal without transfer, i.e., when the figure edge and the subsequent ambiguous edge were in the RF from the beginning. A decay of border-ownership signals at the ambiguous edge was also found in previous experiments (O'Herron and von der Heydt, 2009). Our results show that this decay fully accounts for the reduced strength of the transferred signal. The transfer itself did not seem to attenuate the signal further.

The paradigm of our experiments requires that the ambiguous edge be presented for some time before the movement to produce apparent motion in the object movement condition (without this intermediate phase, the movement vector would not be defined). Thus, by the time the edge appeared in the RF, inevitably much of the border-ownership signal had decayed. However, this is an artificial situation. When image movements are caused by a saccade under natural conditions, which takes only a few tens of milliseconds, the signal would still be strong (see the decay functions in Fig. 6). For rapid object movements or brief occlusions, the transferred signal would also be strong. At any rate, it is remarkable that a remapped trace of border ownership can still be found under these conditions and as late as 1 s after the disappearance of the object.

We propose that the remapping of border-ownership signals serves to maintain the assignment of local features to an external object despite the frequent displacements of its image on the retina. Keeping such assignment is essential for integrating the details of an object into a coherent percept. The persistence of border-ownership signals across image movements is consistent with psychophysical studies in humans. Ambiguous figure–ground displays produce phases of stable perception that can last several seconds despite intervening eye movements (Leopold et al., 2002).

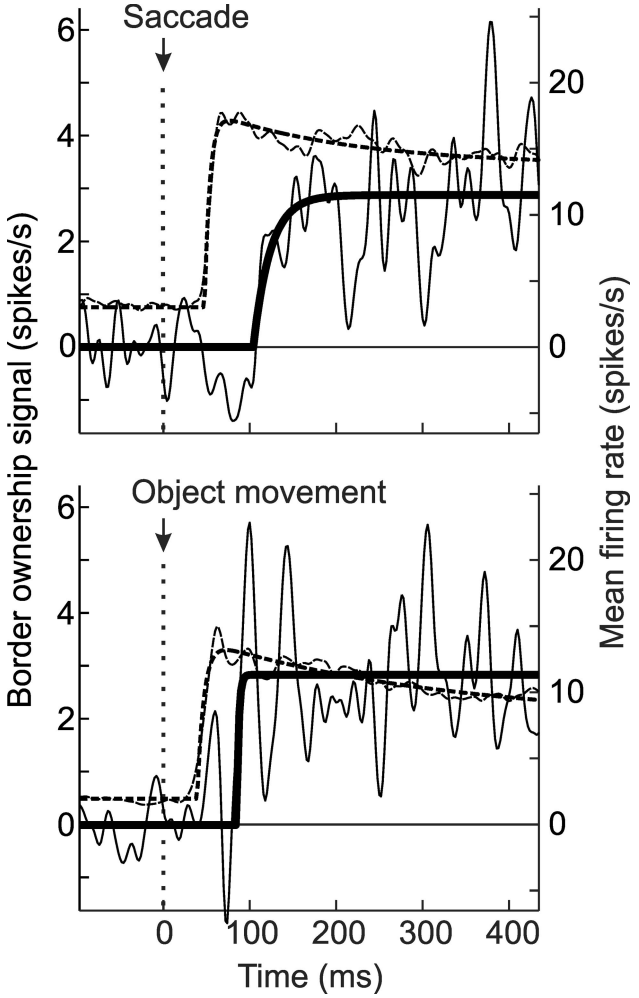

Figure 7. Comparison of signal latencies between saccade and object movement conditions. The time course of border-ownership signals (solid line, left scale) and mean responses (dashed line, right scale) is shown for the neurons that were tested in both conditions (monkey JA, $n = 26$). The responses in the saccade experiment were aligned to the individual saccade times before computing the average. The border-ownership signals were fit with a concatenation of a zero line and an exponential by two-phase regression. The mean responses were fit with a concatenation of a constant and a sum of two exponentials.

Relation to previous studies of remapping

The emergence of border-ownership modulation in a neuron whose RF has not seen a figure border is analogous to classic remapping in which a stimulus activates a neuron whose RF has not seen the stimulus (Duhamel et al., 1992). Neurons showing classic remapping are frequent in areas that are involved in control of visual attention and planning of eye movements, such as the lateral intraparietal area, but rare in lower-level visual areas, such as V1 and V2 (Nakamura and Colby, 2002), whereas remapping of border ownership is common in V2, as Figure 3*A* shows. One difference is that, in remapping of border ownership, the neurons are directly activated by a stimulus in its RF, and only the modulation of activity comes from a previous border-ownership stimulus outside the RF. The neurons would be activated by the ambiguous edge with or without the initial presentation of a figure, whereas in the classic remapping paradigm, the neurons are not activated without the preceding stimulus.

Remapping of response modulation was also found for attentive enhancement. Khayat et al. (2004) had monkeys perform a curve tracing task in which they had to make two successive saccades along a single curve while ignoring another curve. Multiunit activity was recorded in V1. The cells representing the selected curve were enhanced all along the curve, and, after the first saccade, the enhancement appeared in the cells representing the curve in the new retinal location. Thus, the attentive enhancement was transferred across cortex. As in our experiments, response modulation appeared in neurons that had not been activated initially. A difference is that our monkeys performed a fixation task for which the stimuli were irrelevant, whereas in the study by Khayat et al. (2004), the response modulation relates to attentive selection of one stimulus over the other. In our experiments, the response modulation is not related to attention but to the one-sided assignment of the test edge, and this assignment is transferred. Any attentive enhancement would not have biased the responses between border-ownership conditions, because the figure was presented equally often on either side of the test edge, and the initial position of the test edge was on either side of the RF with equal frequency. At first glance, the two studies seem to differ about the role of attention in remapping, but they are in fact complementary, and both can be explained with the model sketched in Figure 8.

The mechanism

The observation that border-ownership signals can be remapped in the cortex has significant implications considering the underlying mechanism. If border ownership and its persistence were generated within the area (e.g., V2), the memory trace would have to be either in the state of activity or in another substrate, such as the excitability or strength of synapses, of neurons in that area. We ruled out previously the state of activity as a possibility by showing that the activity in V2 can be interrupted by presenting a blank field without affecting the decay of the memory trace (O'Herron and von der Heydt, 2009). The present results argue against the alternative, modification of excitability or synaptic strength, because it is unlikely that these modifications could be instantaneously transferred across several millimeters of cortex. Thus, the memory must reside outside V2.

The most likely scenario is that the memory trace is carried by neurons in another area that modulate the activity of the V2 neurons. Such a scheme is illustrated in Figure 8. It combines the previously proposed grouping circuits for figure–ground organization with a circuit for remapping. The remapping circuit consists of a number of object pointer neurons that are flexibly connected to grouping cells. An object pointer is established when a stimulus strongly activates a grouping cell, which then, through a shifter circuit, excites an object pointer cell. This type of cell produces elevated activity for some time after cessation of excitatory input. Evidence for this activity is the persistence of border-ownership signals (O'Herron and von der Heydt, 2009, 2011). The prolonged activity is sufficient to bridge the interval of a saccade or a movement or transient occlusion of an object. The shifter circuit might be similar to the one proposed for remapping of V1 RFs (Anderson and Van Essen, 1987; Olshausen et al., 1993), although much smaller in capacity. This is because the grouping circuit reduces the number of signals to be rerouted. Instead of remapping a large number of RFs (e.g., all the feature signals of an object), only the peak of activity in the grouping cell layer is remapped. This means a huge reduction. Only the object pointers need to be remapped, because object details, such as contours and colors, represented in the retinotopic maps of V1 and V2, can be accessed through the grouping circuits at any time (top-down attention, Mihalas et al., 2011).

We did not specify the signal that drives the shifter circuit in Figure 8. Somehow the system needs to compute the displace-

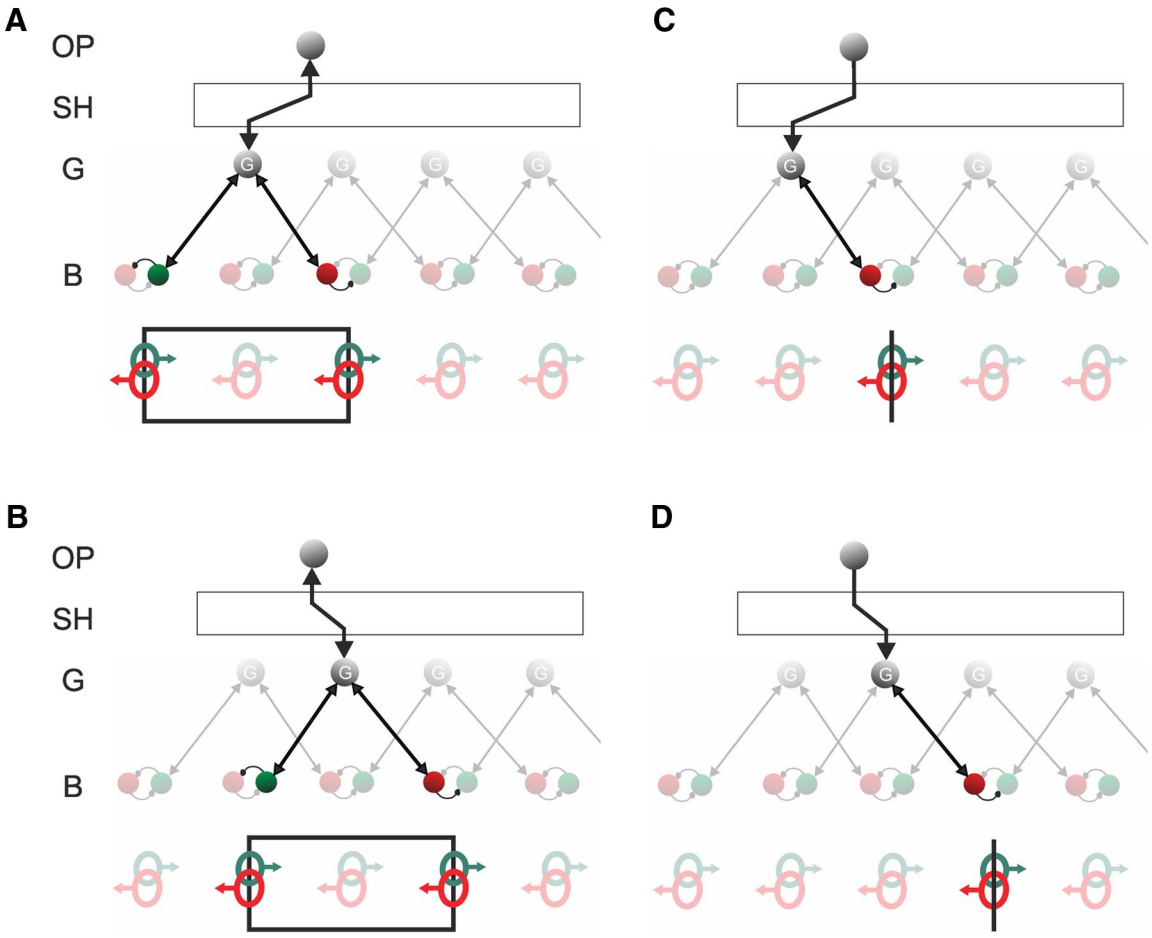

Figure 8. Sketch of a model that explains the transfer of border-ownership signals. Ovals with arrows represent RFs and side preference of border-ownership cells. Black lines represent stimuli: a square (***A***, ***B***) or an ambiguous edge (***C***, ***D***). G cells sum signals from a wide range of B cells (only those on 2 opposite sides of the square are illustrated) and, by feedback, enhance the responses of the same B cells. Focal activation in the G-cell layer creates a link to an OP cell, consisting of bidirectional activation through the shifter circuit. When the retinal image moves, SH moves the link from the active OP cell by a corresponding step to another G cell. Sequence ***A–B*** illustrates an image movement caused by a saccade or object movement under natural conditions. The focus of activity in the G-cell layer remains connected to the same OP cell. Sequence ***A–C–D*** illustrates the stimulus sequence in the present experiments: presentation of a figure (***A***)– conversion to ambiguous edge (***C***)–movement of the edge to a new location (***D***). As the SH moves the link, activity from the active OP cell is routed to the new G cell, which in turn creates a bias of activity in the B cells responding to the new position of the edge. Thus, the enhancement of the red partner in a pair, originally produced by the figure, is transferred to the cells in the new location.

ment vector for the shift (Wurtz et al., 2011). In classic remapping, the observation that some neurons anticipate the saccade shows that the displacement vector is supplied by the eye movement command centers (predictive remapping; Duhamel et al., 1992; Sommer and Wurtz, 2002). For object movements, the signal must be derived visually, from the retinal image displacement. The absence of predictive remapping and the similarity of the results for eye movement and stimulus movement in the present study (Fig. 7) suggest that, in our experiments, the signal had a visual origin.

Role of attention

Do the present results depend on attention being deployed to the figure? Previous studies showed that border-ownership modulation and its persistence do not require attention: when the task involves attending selectively to one object of several, border-ownership signals emerge at the target object as well as the distractor objects (Qiu et al., 2007). Moreover, in experiments like the present one, in which animals just fixate a point and the other stimuli are not behaviorally relevant, the persistence of border-ownership signals at one figure is not reduced by the onset of a second figure (O'Herron and von der Heydt, 2009), although in this situation attention tends to be drawn to the new figure (Yantis and Jonides, 1996).

Based on these findings, we speculate that the remapping of border ownership demonstrated here also does not require top-down attention. However, this needs to be demonstrated by additional experiments. For example, if saccadic remapping of border ownership were measured similarly as in the present study, but with several objects displayed simultaneously, one of which is attended, would transfer occur for each object, or only for the attended object? Studies of the lateral intraparietal area have shown that remapping occurs selectively for sudden onset stimuli (that are not necessarily saccade targets) and for stable stimuli that are attended because they are task relevant (Gottlieb et al., 2005). This suggests that the onset of stimuli invariably creates object pointers (which may then be visited by attention or not) and that object pointers decay if they are not attended.

It seems plausible that the system can maintain multiple object representations, because it must be able to attend to one object and at the same time track the identity of others. For example, a soccer player must focus attention on the ball and simultaneously track the movements of other players. This example also shows that, when the eyes follow one object, the image of

other objects will often move on the retina independently. This means that border assignment needs to be maintained not only across saccades but also across object movements. That is indeed what we found (Figs. 5, 6). Thus, object movements can produce transfer of border assignment, and the generation of a saccade is not necessary for inducing the transfer.

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