

Centre-surround interactions in response to natural scene stimulation in the primary visual cortex

Kun Guo, Robert G. Robertson, Sasan Mahmoodi and Malcolm P. Young

Institute for Neuroscience and Psychology, Brain and Behaviour Group, School of Biology, Henry Wellcome Building for Neuroecology, University of Newcastle, Newcastle upon Tyne NE2 4HH, UK

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Abstract

Centre-surround interaction in the primary visual cortex (area V1) has been studied extensively using artificial, abstract stimulus patterns, such as bars, gratings and simple texture patterns. In this experiment, we extend the study of centre-surround interaction by using natural scene images. We systematically varied the contrast of natural image surrounds presented outside the classical receptive field (CRF), and recorded neuronal response to a natural image patch presented within the CRF in area V1 of awake, fixating macaques. For the majority of neurons (67 out of 111), the natural image surrounds profoundly modulated, mainly by suppressing, neuronal responses to CRF images. These modulatory effects started at the earliest stage of neuronal responses, and often depended on the contrast and higher-order structures of the surrounds. For 47 out of 67 neurons, randomising the phases of the Fourier spectrum of the natural image surround diminished the centre-surround interaction. Our results suggest that the centre-surround interaction in area V1 can be extended to natural vision, and is sensitive to the higher-order structures of natural scene images, such as image contours.

Introduction

It has been proposed that our visual system evolved so as to be optimized for processing the statistics of natural scenes (Barlow, 1961; Kersten, 1987; Simoncelli, 2003). The properties and statistical structures of natural scene images, containing elements with various orientations, local contrasts and spatial frequencies, are different from the simplified artificial stimuli that are commonly used in vision research, such as bars, gratings and simple texture patterns (Field, 1987; Tolhurst *et al.*, 1992; Ruderman & Bialek, 1994). Conveniently, the statistical properties of natural images can be analysed according to different orders or levels of their statistics (Simoncelli & Olshausen, 2001). First-order statistics of an image refer to the measurement of individual pixel values without regard to any other pixels. In general, first-order statistics capture very little information about meaningful visual structures in a scene. Second-order statistics refer to the measurement of correlations between pairs of pixels, such as the amount of similarity of luminance between two points in an image. The amplitudes of the Fourier spectrum of an image are often used to determine the second-order statistics (Field, 1987; Tolhurst *et al.*, 1992). However images of natural scenes contain conspicuous local features, such as complex contours, surfaces, corners and junctions, which are not captured by the second-order statistics. Therefore, the phases of the Fourier spectrum are employed to correspond to the higher-order statistics of natural images (Field, 1994; Thomson, 1999).

Primary visual cortex (area V1) is the first stage of the cortical processing of visual information. Quantitative analyses show that

axons from the lateral geniculate nucleus, the principal relay between the eye and the visual cortex, account for no more than 5% of the total excitatory synapses on the average geniculate-recipient layer pyramidal neuron in V1 (e.g. Peters & Payne, 1993). Consequently, over 95% of the excitatory synapses, even in geniculate-recipient layers in area V1, are from other cortical neurons and other nuclei. This very extensive network of lateral and feedback connections should enable V1 neurons to have access to a wide variety of spatially and temporally dispersed evidence on which to base their computations. Using simplified artificial stimuli, electrophysiological studies have shown that responses of V1 neurons to visual stimuli presented within their classical receptive fields (CRFs) are modulated, and mainly suppressed, by the surrounding stimuli placed outside the CRFs (reviewed in Gilbert, 1998; Fitzpatrick, 2000; Albright & Stoner, 2002). Divisive gain control, assuming that a neuron can adjust its contrast gain or sensitivity to visual input, has been proposed as a possible function served by this centre-surround interaction (Heeger, 1992; Wilson & Humanski, 1993; Levitt & Lund, 1997). On the other hand, other studies suggest that this centre-surround interaction enables V1 neurons to integrate visual information available from regions beyond their CRFs, and is critical for contour integration (Gilbert, 1998; Fitzpatrick, 2000); corner and local curvature detection (Wilson & Richards, 1992; Sillito *et al.*, 1995); perceptual pop-out and grouping (Knierim & Van Essen, 1992; Kastner *et al.*, 1997; Mizobe *et al.*, 2001); surface perception (Rossi *et al.*, 1996; MacEvoy *et al.*, 1998); and figure-ground segregation (Lamme, 1995; Zipser *et al.*, 1996).

However, our understanding of this well-documented centre-surround interaction in area V1 is primarily based on neuronal responses to simplified artificial stimulus patterns. We have little direct knowledge of the function and impact of centre-surround interactions under natural/relevant conditions. A few recent neurobiological studies across different species (cat, ferret and monkey) have shown that the activity patterns of V1 neurons elicited by naturalistic stimuli

Correspondence: Dr Kun Guo, at *present address below.
E-mail: kguo@lincoln.ac.uk

*Present address: Department of Psychology, University of Lincoln, Lincoln, LN6 7TS, UK.

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are qualitatively and quantitatively different from those elicited by simplified stimuli (Baddeley *et al.*, 1997; Kayser *et al.*, 2003). Using natural image sequences (i.e. movies), Vinje & Gallant (2000, 2002) showed that surround stimuli presented outside the CRF can both enhance and suppress neuronal responses recorded in area V1 of awake monkeys. However, these experiments did not control for the possible change of mean luminance in the surround stimuli, which could also modulate neuronal responses to CRF stimulation (Rossi *et al.*, 1996; MacEvoy *et al.*, 1998). It is also not clear whether the centre-surround interaction in natural vision is sensitive to contrast normalization (divisive contrast gain control, in which a neuron can adjust its contrast gain or sensitivity to visual input to accommodate limited dynamic range) or to higher-order structures of the natural images.

In the current experiment, we use a briefly presented natural image patch for CRF stimulation, and systematically manipulate the contrast and the higher-order statistics of the surrounding natural image, while keeping this surround at a constant mean luminance. The neuronal responses recorded in area V1 of awake, fixating monkeys reveal that the centre-surround interaction in response to natural scene stimulation is contrast-dependent, and is sensitive to the higher-order structures of the surround.

Materials and methods

Animal preparation

Two adult rhesus monkeys (*Macaca mulatta*, 4.5–6.5 kg), with implanted scleral eye coil, head restraint and recording chambers over area V1, were trained to fixate a small fixation point (FP) for several seconds in a dimming fixation detection task (Guo & Benson, 1998; Guo *et al.*, 2004). All procedures complied with the 'Principles of laboratory animal care' (NIH publication no. 86–23, revised 1985) and UK Home Office regulations.

During the experiment, the monkeys sat in a primate chair with head restrained. Their eye movements were monitored by an 18-inch cubic scleral search coil assembly with 3 min arc sensitivity (500 Hz sampling frequency, CNC Engineering, USA). Trials were started with a 0.2° red FP (15 cd/m²) presented in the centre of a screen. After a 500 ms delay, a visual stimulus (bars, gratings and natural scene images) that varied in size and position was also presented. The FP dimmed (30% contrast) after a random period of 1–6 s. The monkeys were required to maintain stable fixation without reacting to other visual stimulation throughout the trial in exchange for a water reward. Operationally, stable fixation meant that the monkey's eye position remained within a fixation window (not visible on the stimulus display) that was centred on the FP. The typical size of the fixation window was 1° × 1°. Occasionally, a larger fixation window (2° × 2°) was used to facilitate the recording. If the monkey disengaged fixation, the trial was aborted automatically. The intertrial interval was 1500 ms. When trained, the monkeys could perform 1000–2000 correct trials (≥ 95% correct performance) in a recording session lasting no more than 3 h. Only neuron data obtained during correct trials was included in further analysis.

Visual stimulation and data collection

Visual stimuli were generated by VSG 2/3 graphics system (Cambridge Research Systems, UK) and displayed on a gamma-corrected high frequency noninterlaced colour monitor (Sony GDM-F500; mean luminance 15 cd/m²; frame rate 100 Hz) with the resolution of 1024 × 768 pixels. At a viewing distance of 57 cm, the monitor subtended a visual angle of 36 × 28°.

Fourteen black/white natural scene images (including trees, landscapes, animals and buildings; see Fig. 1 for an example), sampled with a Nikon (D1) digital camera and previewed by the monkeys during the training period, were used in the experiment. These images were chosen as they contained clear and continuous image contours with various orientations and spatial frequencies. All images (full-screen size, 1024 × 768 pixels, 256 grey-levels) were gamma-corrected. Their first-order statistics, although having some bias, are not strongly

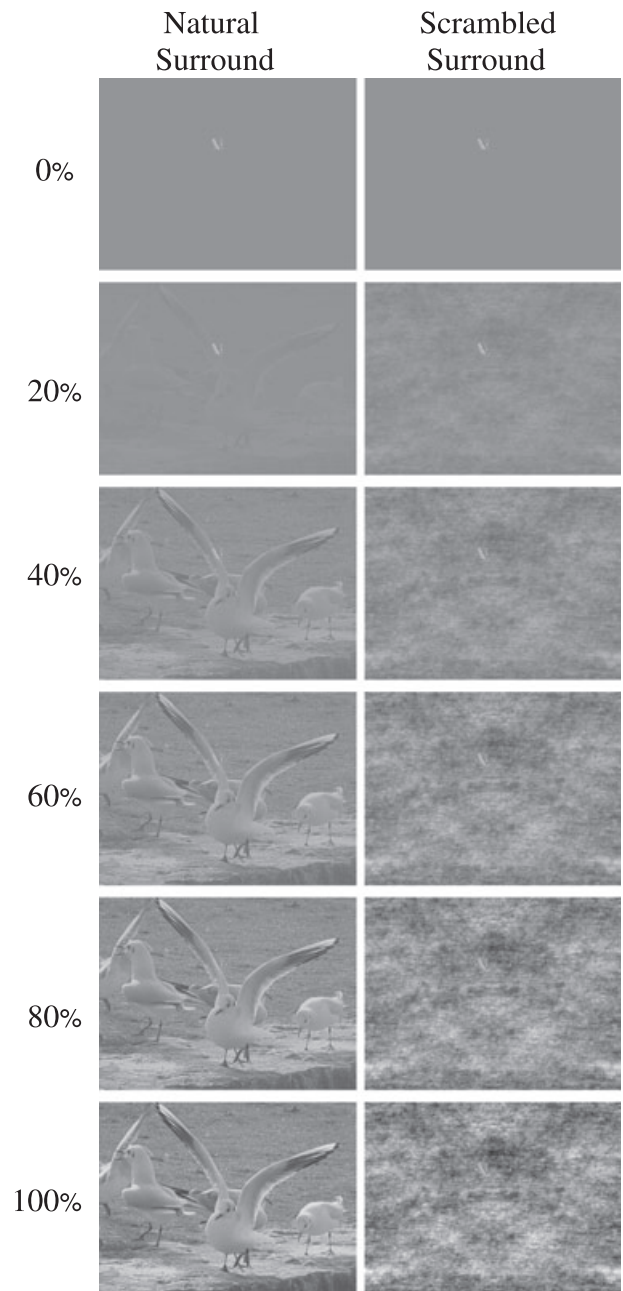


FIG. 1. Example of a natural scene image and its scrambled version used in the recording. The monkey was trained to make and hold fixation of a coloured spot so that a region of the image that contained a contour of the neuron's preferred orientation was positioned within the CRF (plus fixation window) of the recorded neuron. The surrounding image outside the CRF was either the rest of the natural image (left column) or the scrambled version of the original natural image (right column), in which the phase spectrum of the image outside the CRF was randomised in the Fourier domain to remove higher-order structures. The contrast of the surrounding image was systematically varied, from full contrast (100%) of the original image to 0% contrast with a 20% step.

skewed, and cover most of the range of possible pixel values. For each original natural scene image, we created a scrambled version with the same first- and second-order statistics (image properties determined by the amplitudes of the Fourier spectrum) but different higher-order correlations (image properties determined by the phases of the Fourier spectrum). This was performed by computing the Fourier transform over the natural scene images and randomising the phase spectrum ($0-2\pi$) in the frequency domain. The Fourier amplitude spectrum of the images was not affected by this procedure. Without higher-order statistical structures that correspond to sparse distributions of local features, these scrambled images lack any visual objects and have a cloud-like appearance (see Fig. 1 for an example), although images have the same mean luminance as the corresponding natural scene. Over all the images used, the root-mean-square (RMS) contrast of the whole image was not significantly different between the original natural scene images and the corresponding scrambled images (paired *t*-test, $P > 0.05$), the average ratio of RMS contrast between them was 0.98 ± 0.09 (mean \pm SEM).

The activities of single and multiunits in area V1 were recorded using glass-coated tungsten microelectrodes, and were amplified and sampled through CED1401 plus digital interface (Cambridge Electronic Design, UK). Spikes were stored with a 0.1-ms interval resolution. Single neuron activity was determined on the basis of the size and shape of the spike waveform, and was confirmed by a spike-sorting programme (Spike2, Cambridge Electronic Design, UK) with a template-matching procedure. The approximate laminar position of recorded neurons was determined by the depth of the microelectrode and the characteristic features of layer 4 (such as nonorientation selective, high spontaneous activity and brisk 'on' and 'off' responses). No attempt was made to select neurons from a particular layer of cortex, although the majority of the recordings were made from layers 2 and 3.

Having isolated a neuron, its CRF was carefully mapped using a sweeping bar and sinusoidal grating (with the neuron's preferred orientation/direction) patch moving across the screen with variable length, width and velocity (Guo *et al.*, 2004). To avoid underestimating the size of the CRF, the CRF was covered with a uniform grey background and an annular window was centred on the CRF. A drifting sinusoidal grating with moderately high contrast (30–50%) and the neuron's preferred direction was presented within the window. The outer diameter of the annulus was fixed at 10° , while the inner diameter was adjusted until there was no response in excess of spontaneous activity. The final size of the inner diameter of the annulus was treated as the size of the CRF of the recorded neuron. A sinusoidal grating with the size of the neuron's CRF plus fixation window ($1^\circ \times 1^\circ$) was then placed at the centre of the CRF. The grating's orientation/direction, spatial and temporal frequency were systematically varied to determine a neuron's preferred tuning characteristics. No attempt was made to classify the neurons as 'simple' or 'complex'. Previous recordings in area V1 showed that simple and complex cell types exhibit equal incidences and strength of centre-surround interaction (Levitt & Lund, 1997; Walker *et al.*, 2000; Cavanaugh *et al.*, 2002a).

A small natural image patch with its original contrast (100%) and the size of CRF plus fixation window was then selected from a set of full-screen natural scene images and placed at the centre of the CRF for 500 ms. Different images were chosen for each neuron according to their tuning properties to ensure that the natural contour inside the patch was closely matched to the neuron's preferred orientation and spatial frequency. To achieve this, we plotted a transparent static grating with the size of CRF plus fixation window and with the neuron's preferred orientation and spatial frequency (and contrast polarity for 'simple' cells) overlying the nature images, and manually

changed its location until the grating was closely matched to part of the natural image contours (overlap with each other). If necessary, the FP was re-positioned within 5° of the centre of the screen so that the appropriate natural image patch could be placed at the centre of the CRF. Previous studies have shown that for both simple and complex cells in area V1, the orientation and spatial frequency tuning characteristics under natural image stimulation are compatible with those under stimulation with simplified stimuli, such as drifting sinusoidal gratings used in our experiment (Ringach *et al.*, 2002; Smyth *et al.*, 2003). The surround outside the CRF natural image patch was either the remainder of the natural image, or the scrambled version of the original natural image. The size of the surrounding image outside the CRF was at full-screen size and its contrast was systematically varied, from full contrast (100%) of the original image to 0% contrast with 20% step (see an example in Fig. 1). This was achieved by covering an additional masking layer over the original surrounding images and systematically varying its transparency.

Each stimulus condition was presented 10–20 (normally 15) times in a random sequence. The interstimulus interval was 1000 ms. Limited by possible sampling duration of single neuron recording in behaving monkey experiment, typically one natural image was chosen for each neuron in quantitative study.

As the experimental design comprised two levels of image category (natural image surround vs. scrambled image surround) and six levels of surrounding contrast (0–100% with 20% interval), two-way analysis of variance (ANOVA) was carried out after averaging and normalizing the neuron's discharge for the duration of stimulus presentation (500 ms). Appropriate *posthoc* testing of differences between levels of surrounding contrast (Tukey's least significant procedure) was carried out following detection of significant overall variable ratios.

Results

The responses of V1 orientation selective neurons, spanning a range of CRF sizes from 0.6° to 2.2° and visual field eccentricities from 1° to 8° , were recorded from four hemispheres of two awake, fixating monkeys. As observed by other researchers (Baddeley *et al.*, 1997; Gallant *et al.*, 1998), the majority of V1 neurons responded to the natural image patch briefly presented within their CRFs, but the firing rate of the response was much lower when compared with the optimal abstract artificial stimuli (i.e. bars and sinusoidal gratings). In total, 134 V1 neurons were tested with the stimulation of the CRF natural image patch. Twenty-three of them showed reliable responses to the grating stimuli but not to the chosen natural image patches. Their responses (spikes) either were too weak to be discriminated from the neuronal noise or had relatively large trial-to-trial variance. The remaining 111 neurons had reliable discharges to the CRF natural image patch. For the majority (67) of these neurons, their responses to the central CRF stimulation were significantly modulated by the natural image surround at various contrasts.

Figure 2 shows two example neurons. The natural images used in the recording (one image per neuron) were shown in the right-hand column. The RMS contrasts of the CRF natural image patch and full-contrast (100%) natural image surround were 0.55 and 0.54 for the image used for neuron A-20; and 0.43 and 0.43 for the image used for neuron A-9. The responses of the neurons (minus spontaneous firing rates) were plotted as a function of the contrast of the surround. The briefly presented CRF stimulation, part of the natural image contours matching a neuron's preferred orientation, elicited reliable discharges. When a natural image surround was copresented with the CRF natural image patch, however, the responses to the same CRF stimulation

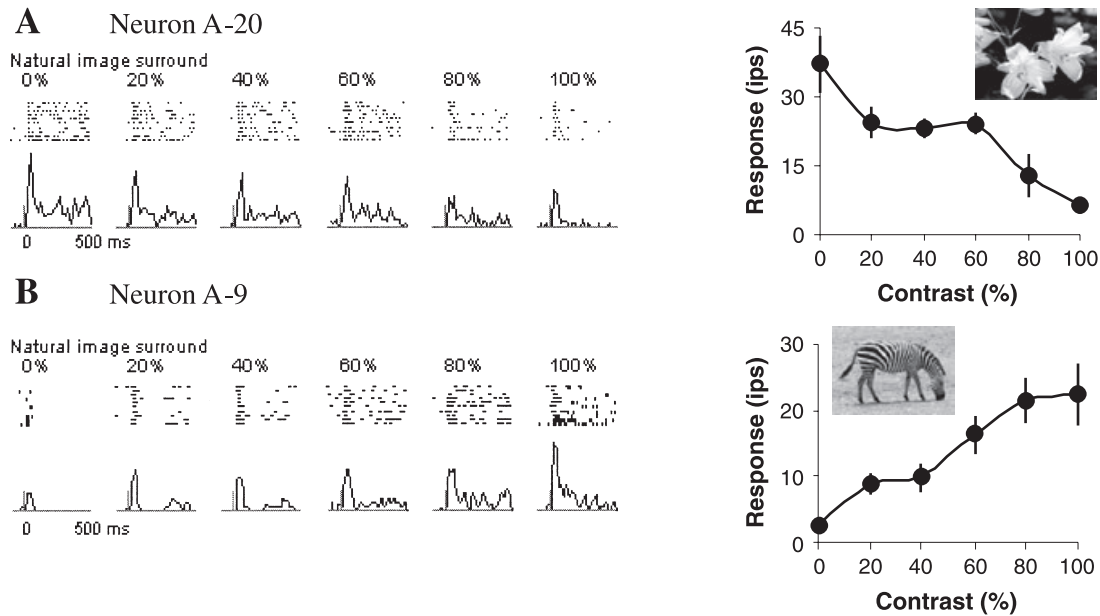


FIG. 2. Examples of two V1 neurons whose responses to the CRF natural image patch stimulation were profoundly modulated by the natural image surround at various contrasts. One natural image was used for each neuron (shown in the right-hand column). In the left-hand column, the response to each stimulus condition (same CRF natural image patch with different surround contrasts) is shown both as rasters (top of each panel), in which each dot represents a single spike and successive lines represent different trials, and as average spike density functions (bottom of each panel). The stimulus duration was 500 ms beginning at time 0, indicated by a short vertical line at the bottom of each panel. In the right-hand column, the averaged responses of the neurons (minus spontaneous firing rates) are plotted as a function of the contrast of the surround. Error bars indicate SEM.

decreased (Fig. 2A) or increased (Fig. 2B) with the increasing contrast of the surround. Compared with the CRF stimulation alone (0% surround contrast), the firing rate of neuron A-20 was reduced by 83% with the full contrast (100%) of the natural image surround (ANOVA, $F_{5,59} = 7.25$, $P < 0.001$; Fig. 2A), while the firing rate of neuron A-9 was increased by 761% (ANOVA, $F_{5,59} = 6.74$, $P < 0.001$; Fig. 2B).

Approximately 60% (67 out of 111) of our samples exhibited centre-surround interaction with these natural image stimuli (ANOVA, $P < 0.05$). When the contrast of the natural image surround was increased from 0% to 100%, 62 V1 neurons (56%) showed suppressed responses to the CRF natural image patch stimulation, while five neurons (4%) showed facilitated responses. In general, those neurons showing facilitated surround modulation had lower discharges to the CRF stimulus compared to the neurons showing suppressed surround modulation (see Fig. 2 for an example). The mean firing rates (spikes per s) were 6.45 ± 1.88 and 27.3 ± 1.99 , respectively (t -test, $P < 0.01$).

A modulation index was used to quantify the type and degree of centre-surround interaction. This index was the ratio of the average response elicited by the natural image surround with 20–100% contrast to that elicited by the CRF stimulation alone (0% surround contrast). An index < 1.0 indicates responses suppressed by the surround, while an index > 1.0 indicates responses facilitated by the surround.

Figure 3 illustrates the distribution of the modulation index for neurons that were studied with different surround contrasts. The darker solid bins represent neurons whose responses to the CRF stimulation were significantly modulated by the natural image surround (*posthoc* test, $P < 0.05$), and the black arrows above the histograms indicate the median value of the modulation index of these neurons at each contrast level. When the contrast of the surround was increased from 0 to 100%, the distribution of the modulation index was gradually shifted away from 1.0 (Z -test, $P < 0.05$), and to the left (< 1.0), indicating stronger modulation (mainly suppression) for more neurons (Fig. 4A). The average

modulation index was monotonically decreased to 0.36 ± 0.08 for 62 neurons showing suppressed modulation (Fig. 4B), and increased to 5.3 ± 1.29 for five neurons showing facilitated modulation (Fig. 4C). Due to weak and/or variable responses to the CRF natural image stimulation, some neurons showed nonsignificant surround modulation (*posthoc* test, $P > 0.05$; indicated by open bins in Fig. 3) although their modulation indexes were near 0 (indicating suppression) or 2 (indicating facilitation). When stimulated by the CRF natural image patch alone, those neurons showing significant surround modulation had mean firing rate of 26.02 ± 2.13 spikes/s with mean SEM of 4.07 ± 0.3 , while those neurons showing nonsignificant surround modulation but having very low (< 0.5) or high (> 1.5) modulation index had a significantly lower mean firing rate of 9.69 ± 2.69 spikes/s (t -test, $P < 0.01$) with relatively higher mean SEM of 4.98 ± 1.1 .

In this study, the CRF natural image patch was always kept at the full contrast of its original image (defined as 100% contrast) while the contrast of the natural image surround was systematically varied between 0% and 100% of the original image contrast. Therefore, our data addresses only surrounds with the same or lower contrast than the centre. However, due to local differences in image structure, the CRF image might actually correspond to a different contrast setting than 100% of the surround image. To quantitatively compare the contrast of the centre and surround images, we calculated RMS contrast of the CRF natural image patch and natural image surrounds. Over all images used in this experiment, there was no significant difference between the contrast of the centre and surround images (paired t -test, $P > 0.5$). The mean RMS contrast of the CRF natural image patch and natural image surrounds were 0.49 ± 0.02 and 0.50 ± 0.02 , respectively. Furthermore, there was no clear relationship between the contrast of the CRF image and the types of centre-surround interaction (ANOVA, $P > 0.1$). The mean RMS contrast of the CRF natural image patches were 0.50 ± 0.03 , 0.52 ± 0.04 and 0.49 ± 0.03 for those neurons showing suppressed, facilitated and nonmodulated

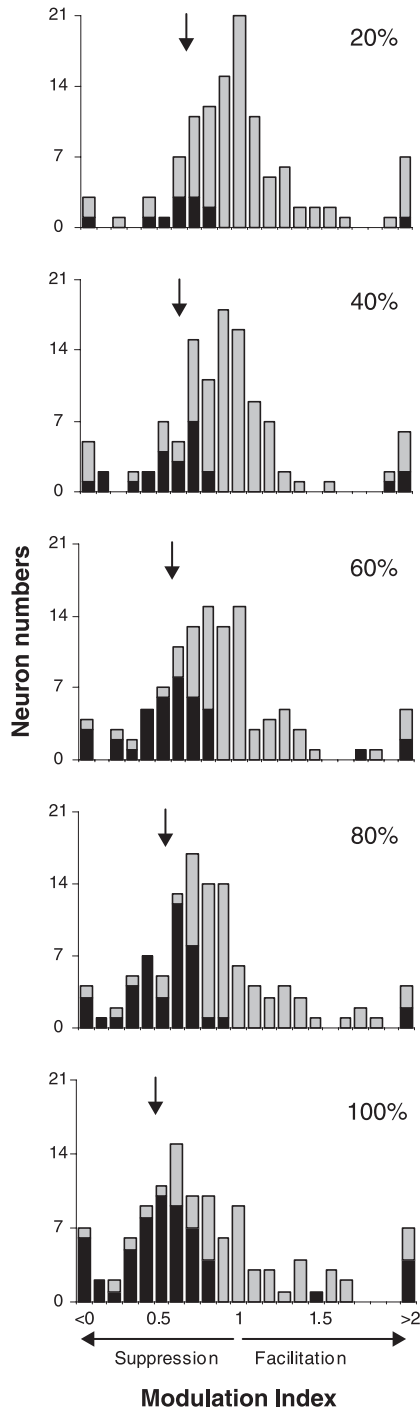


FIG. 3. Distribution of the modulation index for centre-surround interaction tested with natural image stimulation. Histograms indicate the distribution of the modulation index (bin-width, 0.1) in different surround contrasts (20–100%). The darker bins represent neurons whose responses to the CRF stimulation were significantly modulated by the natural image surround, and the black arrow above each histogram indicates the median value of the modulation index of these neurons.

centre-surround interactions, and the mean RMS contrast of the natural image surrounds were 0.50 ± 0.02 , 0.54 ± 0.05 and 0.49 ± 0.03 .

While varying stimulus properties, such as orientation contrast (iso-orientated or cross-orientated), of simple texture patterns concurrently presented inside and outside the CRFs, previous recordings in area V1

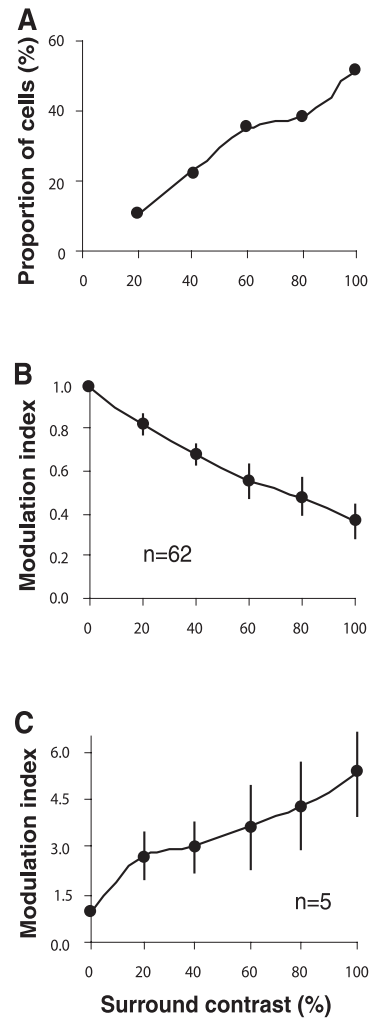


FIG. 4. (A) Proportion of V1 neurons showing significant centre-surround interaction at each surround contrast level. (B and C) Average modulation index for neurons showing suppressed (B) and facilitated (C) centre-surround interaction with the increasing contrast of the natural image surround. Error bars indicate SEM.

of anaesthetized and awake monkeys suggest two types of centre-surround interaction: neurons exhibit centre-surround interaction that is sensitive to the orientation of texture surrounds, and neurons show general suppressive centre-surround interaction but are not sensitive to the orientation of texture surrounds (Knierim & Van Essen, 1992; Nothdurft *et al.*, 1999). In our study, neuronal responses to the CRF natural image stimulation are suppressed or facilitated as the contrast of the natural image surround is increased. However, is this contrast-dependent centre-surround interaction also sensitive to the higher-order statistics of the natural images, such as the image contours? When considering comparisons between images to which we removed the higher-order structures of the natural image surround (scrambled image), and those we did not, three types of modulation were observed: decreased firing rate with the increasing contrast of the natural image surround but not the scrambled image surround; decreased firing rate with the increasing contrast of both natural and scrambled image surrounds; and increased firing rate with the increasing contrast of both natural and scrambled image surrounds.

Figure 5 shows three example neurons. The natural images used in the recording (one image per neuron) were shown in the right-hand column. The responses of these neurons (minus spontaneous firing

rates) are plotted as a function of the contrast of the surround. For neuron I-38 (Fig. 5A), the briefly presented CRF natural image patch without surround (0% surround contrast) elicited reliable discharges. When the CRF was surrounded by the scrambled image, the responses to the CRF stimulation were constant regardless of the contrast of the surround (*posthoc* test, $P > 0.05$). When the CRF was surrounded by the original natural image, however, the responses to the same CRF stimulation gradually decreased with the increasing contrast of the surround (surround contrast $F_{5,132} = 5.42$, $P < 0.0001$; surround category $F_{1,132} = 34.53$, $P < 0.0001$). Comparing with the CRF stimulation alone, the firing rate was reduced by 53% with the full contrast (100%) of the original natural image surround (*posthoc* test, $P < 0.05$). Hence, the centre-surround interaction of this neuron was sensitive to the higher-order structures of the natural image surround.

Some neurons, however, were only sensitive to the contrast change of the surround presented outside their CRFs. When the contrast of the surround was increased, the response of neuron I-57 to the CRF natural image stimulation was gradually decreased (up to 49.2%; Fig. 5B). No significant difference was observed between the natural and scrambled image surrounds (surround contrast $F_{5,119} = 5.87$, $P < 0.0001$; surround category $F_{1,119} = 1.22$, $P = 0.27$). Neuron A-9 (Fig. 5C), on the other hand, showed enhanced responses with the increasing contrast of the surround regardless of the categories of the surround images (surround contrast $F_{5,119} = 13.47$, $P < 0.0001$; surround category $F_{1,119} = 0.4$, $P = 0.53$). Its response was increased by nearly 800% when the contrast of the surround was changed from 0% to 100%.

Population analysis revealed that the centre-surround interaction for the majority of V1 neurons is sensitive to the higher-order structures of natural images. The neuronal response to the CRF stimulation alone was treated as 100%. Out of 67 neurons showing centre-surround interaction to natural images, 47 showed suppressed responses to the CRF stimulation by the copresented natural image surround, when compared to the scrambled surround (surround contrast $P < 0.05$; surround category $P < 0.05$; Fig. 6A). On average, the response to the CRF natural image patch was decreased from 100% to $41.13\% \pm 5.42$ when the contrast of the natural image surround was increased from 0% to 100% (*posthoc* test, $P < 0.05$). The variation of the contrast of the scrambled image surround did not have any evident effect on the neuronal response to the CRF stimulation (*posthoc* test, $P > 0.05$). Fifteen other neurons showed statistically indistinguishable suppressed responses with the increasing contrast of the natural and scrambled image surrounds (Fig. 6B). The mean response to the CRF natural image patch was decreased from 100% to $40.36\% \pm 14.02$ and $45.78\% \pm 9.34$ when the contrast of the natural and scrambled image surround was increased from 0% to 100% (surround contrast $P < 0.05$; surround category $P > 0.05$). Only five neurons showed indistinguishable facilitated responses to the natural and scrambled image surrounds (Fig. 6C). The mean response to the CRF natural image patch was increased from 100% to $530.38\% \pm 129$ and $531.3\% \pm 113.42$ when the contrast of the natural and scrambled image surrounds was increased from 0% to 100% (surround contrast $P < 0.05$; surround category $P > 0.05$). For the majority of neurons (47 out of 67), then, the suppressed centre-surround interaction for natural images was dependent on the higher-order structures of natural images. For the remaining 44 neurons that did not show significant surround modulation to the natural image surrounds, the scrambled image surrounds with various contrasts also did not have significant modulatory effect on these neurons (Fig. 6D). Their responses to the CRF natural image patch copresented with the natural and scrambled image surrounds of different contrast were indistinguishable (surround contrast $P > 0.05$; surround category $P > 0.05$).

In the suppressive centre-surround interaction, normally the suppression increases as the CRF stimulus extends to the CRF periphery, until further expansion into the surround no longer produces additional suppression. With retinal eccentricities similar to those in the present study (1° – 8°), previous recordings using simplified stimuli showed that the minimum stimulus size that can cause maximum suppression in area V1 of awake and anaesthetized monkeys was at least 2–5.6 times the size of the CRF (Zipser *et al.*, 1996; Angelucci *et al.*, 2002; Cavanaugh *et al.*, 2002a; Levitt & Lund, 2002). To evaluate the spatial extent of centre-surround interaction in response to natural images, we systematically varied the size of the CRF natural image patch from one to eight times the original size, which was the size of the mapped CRF plus fixation window (typically $1^\circ \times 1^\circ$). The background was kept as the scrambled image with full contrast, and we tested only neurons showing suppressed modulation for the natural image surround. Figure 7A and B show an example of neuron I-33. The increasing contrast of the natural image surround significantly suppressed this neuron's response to the CRF presentation (surround contrast $P < 0.01$; surround category $P < 0.01$; Fig. 7A), while the increasing contrast of the scrambled image surround did not have a modulatory effect relative to that of the unscrambled natural image surround (*posthoc* test, $P > 0.05$). Increasing the size of the CRF natural image patch also significantly affected this neuron's activity (ANOVA, $P < 0.01$; Fig. 7B). The response of this neuron is plotted as a function of CRF stimulus diameter. As the size of the CRF stimulation was gradually increased, there was a corresponding decrease in the neuronal firing rate until the CRF natural image patch was four times its original size (*posthoc* test, $P < 0.05$). Further expansion of the stimulus size did not produce additional suppression (*posthoc* test, $P > 0.05$). In total, we obtained CRF stimulus expansion tuning curves for 23 neurons (Fig. 7C). The neuronal response to the smallest CRF stimulus size was treated as 100%. Stimulation by the large natural image patches caused a measurable reduction in response (up to $43.2\% \pm 8.58$). The average minimum stimulus size that caused maximum suppression was around six times the original mapped CRF size plus fixation window. As the fixation window we used (typically $1^\circ \times 1^\circ$) roughly equals the size of the mapped CRF, the V1 neurons thus appeared capable of integrating image information as far as 6° beyond their CRFs. This spatial extent of surround modulation assessed with the natural images is consistent with measures obtained using the simplified stimuli like gratings (Zipser *et al.*, 1996; Angelucci *et al.*, 2002; Cavanaugh *et al.*, 2002a; Levitt & Lund, 2002).

Centre-surround interaction takes a wide range of times to manifest itself (Zipser *et al.*, 1996; Nothdurft *et al.*, 1999). Once the neurons start to respond to the centre stimulation, the surround modulation can either occur immediately or only after some delay. To investigate whether there was a temporal evolution of the V1 response properties while integrating the natural image information presented outside the CRFs, we compared time courses of neuronal responses to the CRF natural image patch copresented with the natural image surrounds of different contrast. From neuron examples shown in Fig. 5 (spike density curves shown in the left column), it appears that the modulation from the surround started at an early stage of these neuronal responses. Population analysis was performed for those neurons only showing suppressed responses for the natural image surround, as the suppressive modulation is the main effect of the surround and we have a reasonable sample size for this group of neurons ($n = 47$). The neuronal discharges were plotted as peristimulus time histograms (PSTHs) with 10 ms bins (time 0 indicates the time of the stimulus onset), each curve represented average neuronal response to the CRF stimulation in the presence of a single surround

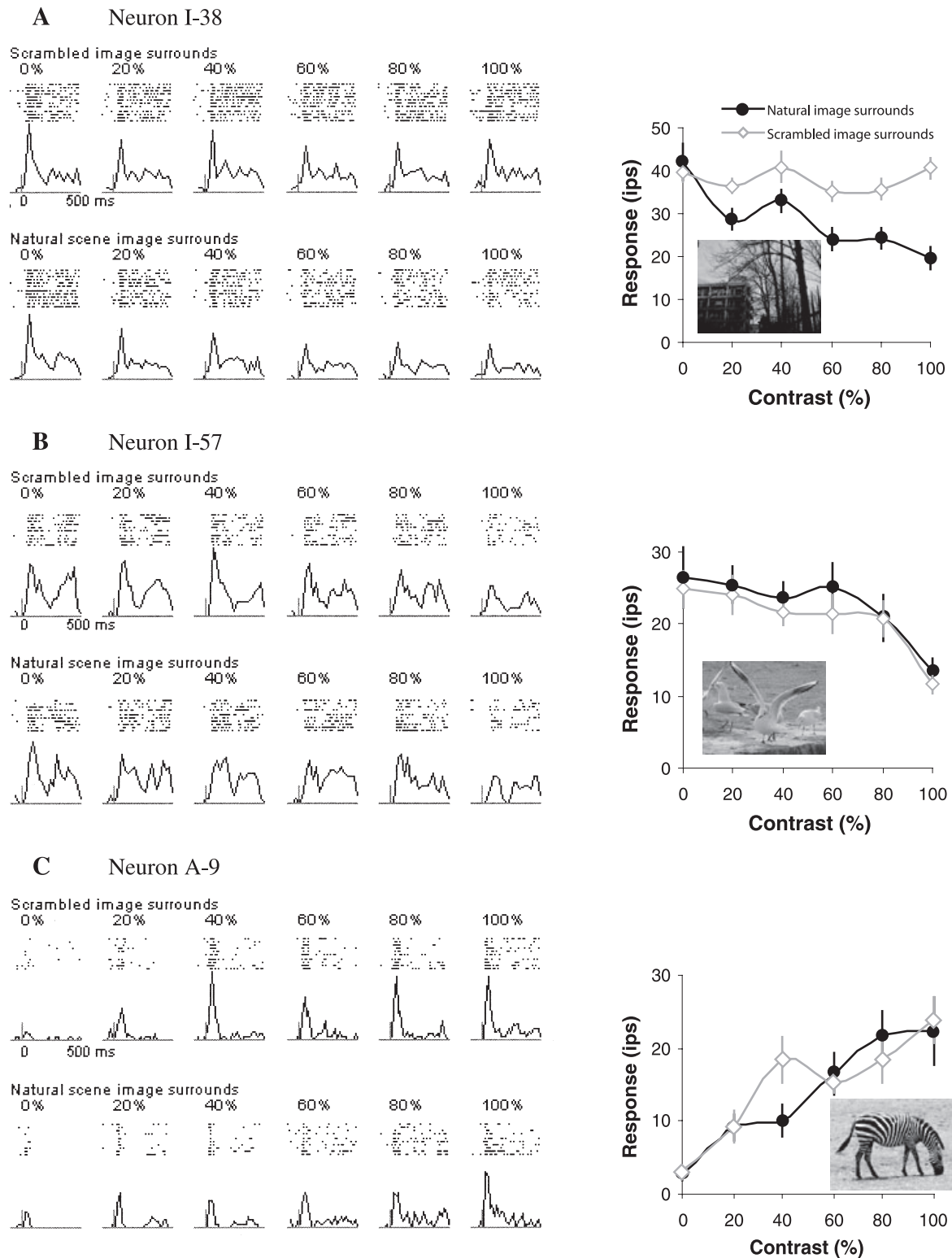


FIG. 5. Examples of three V1 neurons whose responses to the CRF natural image stimulation were profoundly modulated by the contrast and statistics of the natural image surround. One natural image was used for each neuron (shown in the right-hand column). In the left-hand column, the response to each stimulus condition is shown both as rasters (top of each panel) and as average spike density functions (bottom of each panel). In the right-hand column, the averaged responses of these neurons (minus spontaneous firing rates) are plotted as a function of the contrast of the surround. Response to the natural image surround is represented by black solid circles, and the response to the scramble image surround is represented by grey open diamonds. Error bars indicate SEM.

contrast (Fig. 8A). The response latencies were calculated using cumulative sum analysis (Maunsell & Gibson, 1992; Raiguel *et al.*, 1999). The latency was taken to be the time corresponding to the first

bin after stimulus onset where the bin exceeded the spontaneous discharge rate by two standard deviations and which was followed by at least two successively increasing bins. No obvious response latency

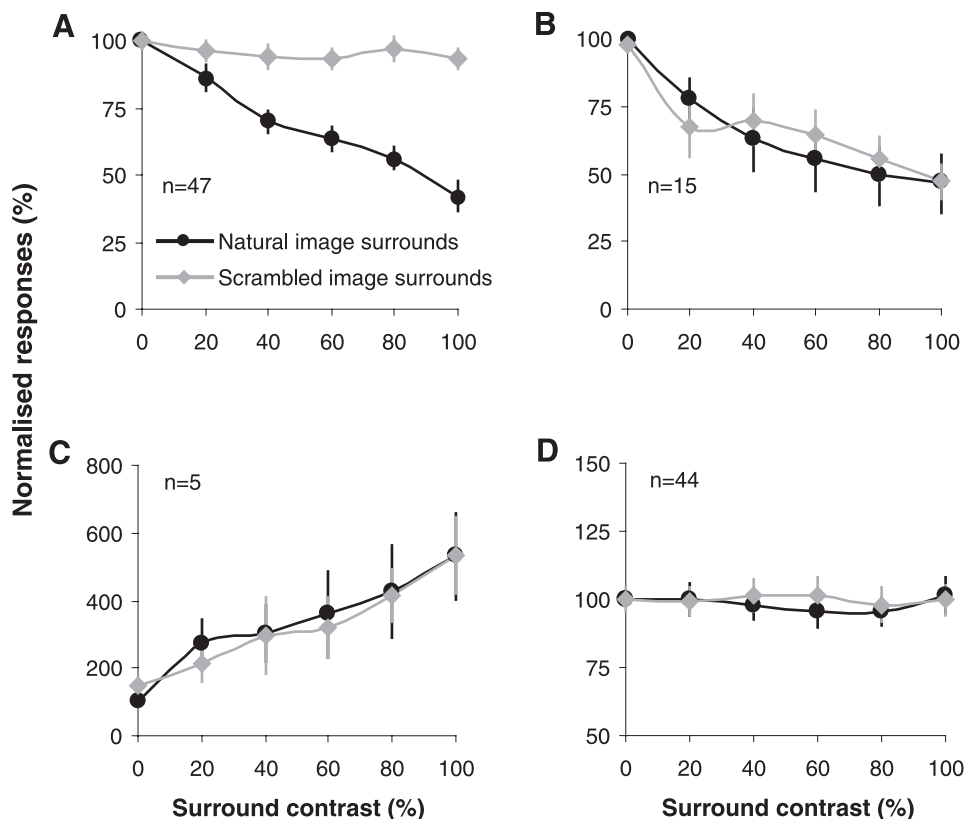


FIG. 6. Average effect of the statistics (natural or scrambled images) and contrast (0–100%) of the surround on neuronal responses to CRF stimulation. (A) Forty-seven neurons showed suppressed modulation with increasing contrast of the natural image surround but not the scrambled image surround. (B) Fifteen neurons showed suppressed modulation with increasing contrast of both natural and scrambled image surrounds. (C) Five neurons showed facilitated modulation with increasing contrast of both natural and scrambled image surrounds. (D) Forty-four neurons showed nonsignificant modulation for both natural and scrambled image surrounds. Neuronal response to the CRF stimulation alone was treated as 100%. Error bars indicate standard error of mean.

change was observed among the neuronal responses to different surround contrasts (ANOVA, $P = 0.92$; Fig. 8B). The mean latency was $46.62 \text{ ms} \pm 1.21$. Compared with the response to the CRF stimulation alone (0% surround contrast), the onset of the suppressed modulation introduced by increasing the surround contrast appeared to diverge from one another approximately halfway up the rising phase of the initial response transient ($< 50 \text{ ms}$ after stimulus onset; Fig. 8A). It appears that the surround suppression began from the earliest stage of the neuronal responses, and lasted for the whole duration of the stimulus presentation.

To see more clearly the time course of the surround suppression, we normalized the population responses shown in Fig. 8A, for each bin between 40 and 500 ms, to the CRF stimulation alone condition (0% surround contrast). Forty milliseconds was taken as the response latency of the population responses (see Fig. 8B). For any given time window, the neuronal responses activated by CRF natural image patch alone were always taken as 100%. By doing this, we can compare the relative firing rate within any given time window (i.e. 40–50 ms, 50–60 ms, and so on) between CRF stimulation alone condition (black horizontal line in Fig. 8C) and CRF stimulation in the presence of different surround contrasts (colour curves in Fig. 8C). As shown in Fig. 8C, the surround suppression, especially introduced by high contrast natural image surrounds, started in the initial phase of neuronal responses and increased rapidly to maximal values (occurred at approximately 170–180 ms after stimulus onset). This immediate centre–surround interaction suggests that the surround modulation acts as quickly as the responses arising through the stimulation of the CRF.

When the phase spectrum of the surrounding natural images was randomized, a border was created between the centre (CRF) and surround regions, which itself could affect V1 neuronal responses (i.e. Rossi *et al.*, 2001). In our experiment, in the stimulus condition of lower surround contrast (i.e. 20% and 40% surround contrast), the border was clearly visible for both natural and scrambled image surrounds (see Fig. 1 for examples). The population responses, however, started to show suppressed modulation only for the natural image surrounds (Fig. 6A). It seems that the border between the centre and surround regions itself can not fully account for the suppression introduced by the 100% natural image surround (no detectable CRF border). To examine this question further, we introduced a gap between the centre and surround natural images with full contrast (see bottom insets in Fig. 9). The gap was filled with the scrambled images and its size was either 0.5° or 1° . If a V1 neuron is only sensitive to the CRF border, its response to these stimuli should be indistinguishable from the response to the CRF natural image patch with scrambled image surround as the visual information extracted from the CRF was identical. If, on the other hand, the neuron is also sensitive to the surround information, its response should be modulated according to the different surround images (i.e. scrambled image surround, natural image surround with or without gap). Figure 9 shows a neuron example. The increasing contrast of the natural image surround significantly suppressed this neuron's response to the CRF natural image patch presentation (ANOVA, $P < 0.05$; Fig. 9A). When a 0.5° or 1° gap was inserted between the CRF and surround regions, the neuronal response was slightly increased compared with the stimulus

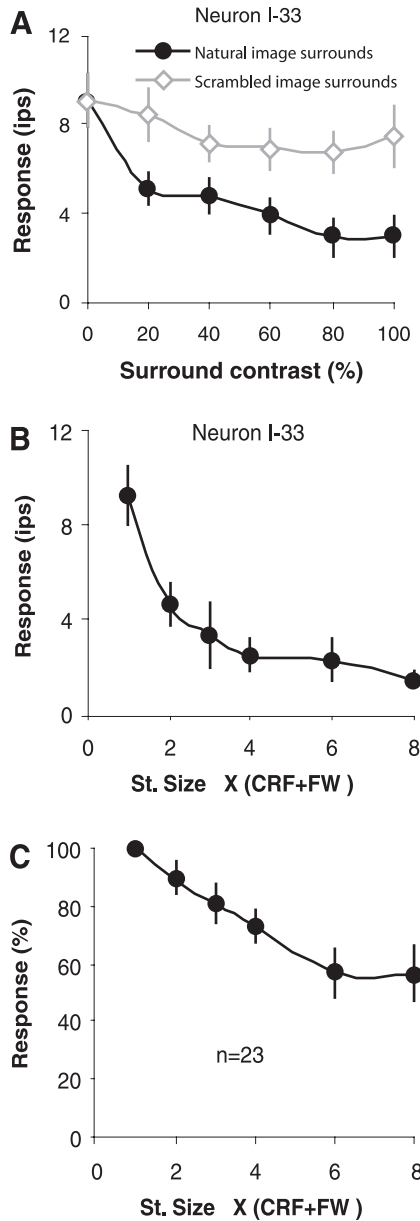


FIG. 7. (A) Example of a neuron showing suppressed modulation with increasing contrast of the natural image surround but not the scrambled image surround. (B) Response of this neuron as a function of the size of the CRF natural image patch. (C) Average neuronal responses as a function of the CRF stimulation size. The response to the smallest CRF image size (CRF + Fixation Window) was treated as 100%. Error bars indicate SEM.

condition of intact surround (no gap between the centre and surround regions), but was significantly suppressed compared with the stimulus condition of CRF presentation alone (ANOVA, $P < 0.05$; Fig. 9B). Therefore, the difference between neuronal responses to the natural and scrambled image surrounds (i.e. Figure 6A) can not be fully attributed to the border between the CRF and scrambled image surround.

If the surround region of a neuron has lower contrast sensitivity and the scrambled image surround presented outside its CRF also has relatively lower contrast compared to the original natural image surround, then it is possible that the suppressed modulation introduced by the natural image surround is due to its higher contrast distribution

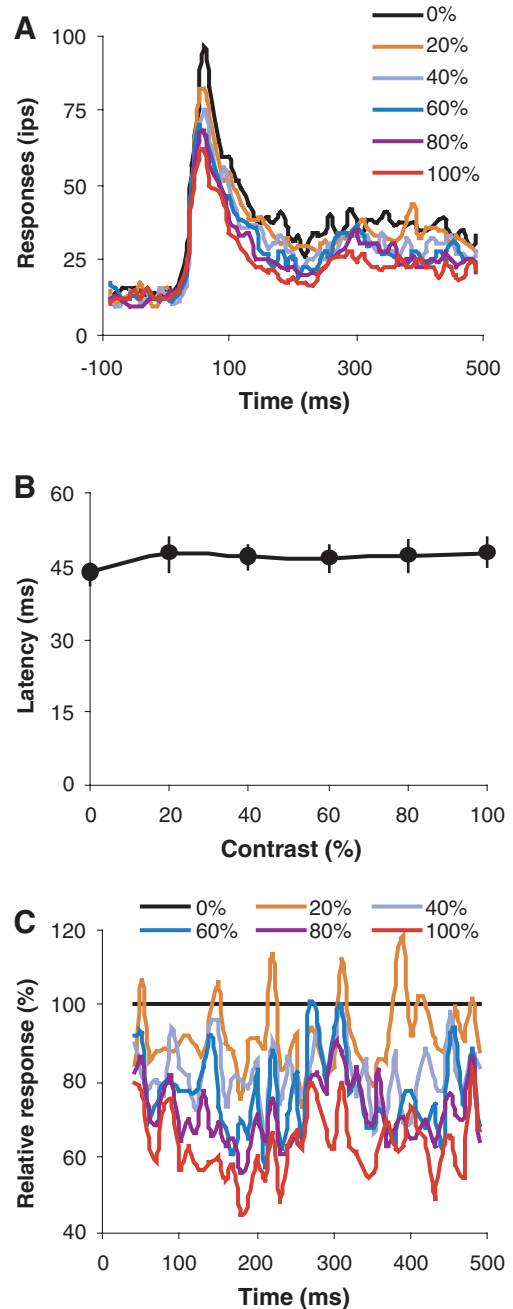


FIG. 8. (A) For 47 neurons only showing suppressed modulation to the natural image surround, their responses to the CRF natural image patch copresented with different contrast of natural image surround were plotted as peristimulus time histograms (PSTHs) with 10 ms bins, time 0 indicates the time of the stimulus onset. Each curve represents average neuronal response to the CRF stimulation in the presence of a single surround contrast. (B) Average response latency as a function of the contrast of the natural image surround for these 47 neurons. Error bars indicate SEM. (C) Time course of surround suppression for these 47 neurons. Population PSTHs under various surround contrast conditions shown in Fig. 8A were normalized, for each bin (bin width, 10 ms) between 40 and 500 ms, to the CRF stimulation alone condition (0% surround contrast). Forty milliseconds was taken as the response latency of the population responses (see Fig. 8B). For any given time window, the neuronal responses activated by CRF natural image patch alone were always taken as 100%. Time 0 indicates stimulus onset.

rather than its higher-order structures, and the nonmodulated response in the presence of the scrambled image surround is simply due to the effectively lower contrast distribution of the surround. Although the

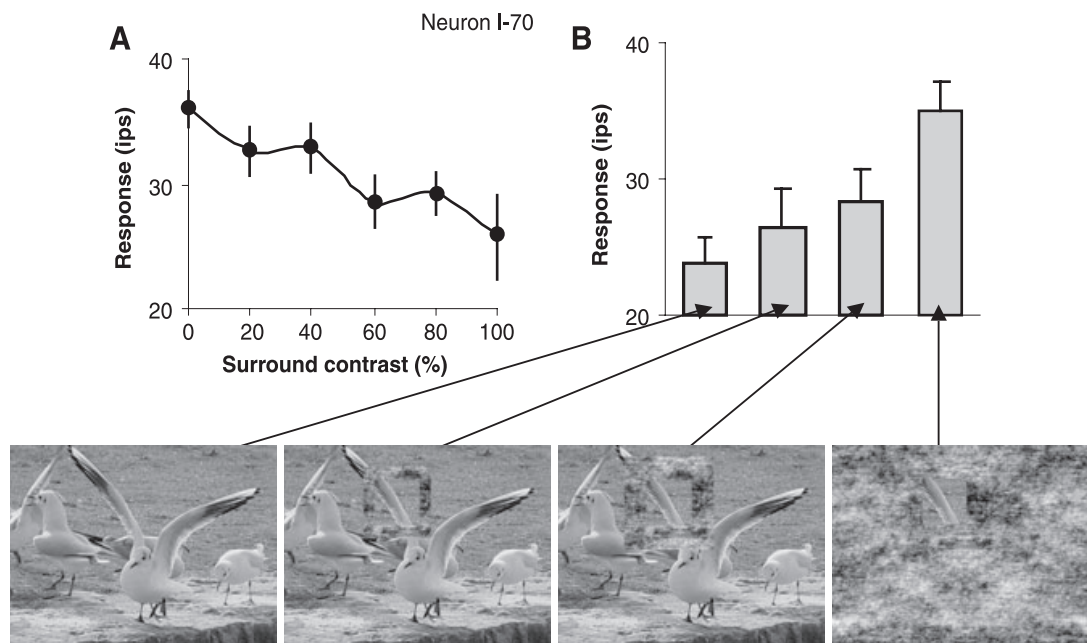


FIG. 9. (A) Example of a neuron showing suppressed modulation with increasing contrast of the natural image surround. (B) The averaged responses of this neuron to the same CRF natural image patch with different surround conditions. The natural image used for this neuron and different test conditions were shown at the bottom. From left to right; intact natural image surround (no gap), 0.5° and 1° gap between the centre and surround regions, and scrambled image surround. The CRF natural image patch is enlarged for the demonstration. Error bars indicate SEM.

RMS contrast of the entire natural image is compatible with its scrambled version (see the Materials and methods), due to local differences in image structure and redistribution of the pixel intensities after phase randomization, it is not clear whether there is contrast difference in the adjacent regions outside the CRF natural image patch between the natural and scrambled image surrounds. To examine this, we compared RMS contrast of the natural and scrambled image surrounds outside the CRF natural image patch in different spatial scales. Figure 10 shows an example. This example image was one of the most frequently used images in the recording. The RMS contrast of the CRF natural image patch was 0.22. When presented with this image, some neurons, such as examples shown in Figs. 5A and 7A, exhibited suppressed responses with the natural image surround and nonmodulated responses with the scrambled image surround. Calcula-

tion of RMS contrast of different size of the surrounds (1°–9°) showed that there was no significant difference of contrast distribution between the natural and scrambled image surrounds up to 9° outside of the CRF natural image patch (t -test, $P = 0.19$; Fig. 10). Therefore, the difference in the surround modulation in the presence of the natural and scrambled image surrounds was mainly due to the image structure difference, such as image contours, between the surrounds rather than the local contrast difference.

Discussion

Centre-surround interaction has been well documented in the primary visual cortex through controlled experiments using artificial abstract

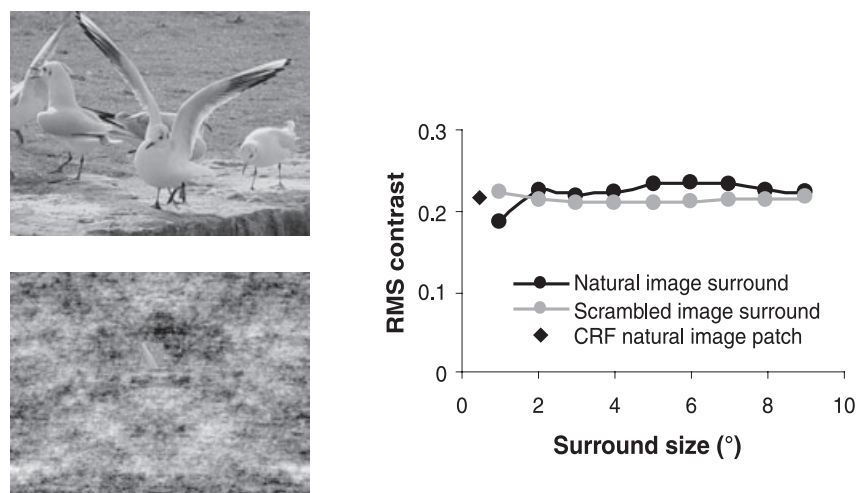


FIG. 10. Comparison of RMS contrast in different surround sizes between the natural and scrambled image surrounds. The CRF natural image patch shown in the example image is enlarged for the demonstration.

stimulus patterns (reviewed in Gilbert, 1998; Fitzpatrick, 2000; Albright & Stoner, 2002). In this study, we demonstrated that the V1 centre-surround interactions are also evident with natural images. The natural image surround, presented in visually unresponsive areas outside the CRFs, strongly modulated neuronal responses to the natural image patch copresented within the CRFs. These modulatory effects were primarily, but not exclusively suppressive; were contrast-dependent; started at the earliest stage of neuronal responses; and were often sensitive to the higher-order structures of the surrounding natural images (i.e. image contours). These results suggest that during natural vision, the neuronal computations in the primary visual cortex are unlikely to be restricted to the extraction of local features, but to be subject to influence from sparsely distributed aspects of natural image structures.

Comparison with the artificial abstract stimuli

In addition to feed forward connections, neurons in area V1 receive a good deal of input from lateral and feedback connections (Young, 2000). Presumably, by virtue of each neuron's embedding in this network, the responses to stimuli presented within the CRFs are markedly modulated by stimuli presented in the surrounding regions that are not normally capable of driving responses when presented alone (reviewed in Gilbert, 1998; Fitzpatrick, 2000; Albright & Stoner, 2002). This centre-surround interaction in V1 has been studied extensively using artificial, abstract stimulus patterns. The type (facilitation or suppression) and degree of modulation critically depends on the differences between stimuli inside and outside the CRF, such as binocular disparity and texture orientation, luminance and colour (Li & Li, 1994; Zipser *et al.*, 1996; Gilbert, 1998; MacEvoy & Paradiso, 2001; Jones *et al.*, 2002; Wachtler *et al.*, 2003).

Typically, when the stimuli inside and outside the CRF have the same or similar orientation, profound response suppression (relative to the CRF-alone condition) is often observed. Using stimulation with bars, gratings and texture patterns, single neuron recordings in area V1 of awake and anaesthetized macaque monkeys showed that around 65–85% of neurons were suppressed, by 38–69% of their maximum firing rate, by collinear stimuli extending beyond their CRFs (Knierim & Van Essen, 1992; Levitt & Lund, 1997; Nothdurft *et al.*, 1999; Rossi *et al.*, 2001; Cavanaugh *et al.*, 2002a). Our observation of natural image stimulation appears consistent with these previous findings. If the natural image contour falling on the CRF resembles those that surround it, on average, the responses of 56% of neurons were suppressed, by 64%, by the natural image surrounds.

Analysis of the time-course of centre-surround interaction showed that natural image surrounds began to suppress neuronal responses as soon as neurons began to respond to the CRF stimulation (Fig. 8). This observation is also consistent with previous findings using bar or grating stimuli covered and extended beyond the CRF (Nothdurft *et al.*, 1999; Müller *et al.*, 2003). However, studies of some forms of centre-surround interaction, such as texture pop-out and figure-ground segregation (centre pattern having contrasting structures as the surrounding pattern), show the influence of the surrounding patterns to be expressed later (15–50 ms) after the onset of the response to the central pattern (Knierim & Van Essen, 1992; Zipser *et al.*, 1996; Nothdurft *et al.*, 1999; Li *et al.*, 2000). This difference could perhaps be due to the complexity of the computations underlying these particular centre-surround interactions and the spatial extent of the surrounding stimulus; suppressive modulation that arises from stimulus presented in the immediate surround of CRF takes only a very

short time to develop (e.g. Lamme *et al.*, 2000). It could also reflect a different origin of the surround signals. Those surround signals expressed with long latencies could be conveyed through feedback connections from extrastriate cortex and might occur for more complex situation requiring higher level visual analysis and computation (top-down interaction) (i.e. Zipser *et al.*, 1996; Nothdurft *et al.*, 1999), while the surround signals expressed with short latencies might arise in connections from neurons within V1 (lateral interaction) (Müller *et al.*, 2003). In our study, the surround modulation acts on the same time scale as the CRF response itself, suggesting that these surround signals might come from lateral interactions. However, given the existence of fast speed feedback connections (Movshon & Newsome, 1996), and the animals were alert and were familiar with the visual stimuli (all images were previewed by them during training period), it is possible that some higher-level computations, such as figure-ground segregation and expectation, may also be involved in V1 centre-surround interactions in natural vision (top-down interactions).

One possible function served by centre-surround interaction is contrast normalization (divisive contrast gain control), in which a neuron can adjust its contrast gain or sensitivity to visual input to accommodate limited dynamic range (Heeger, 1992; Wilson & Humanski, 1993). In area V1 of anaesthetized monkeys, studies with grating stimulation show that identical stimulus configurations could be either facilitatory or suppressive, depending on the contrast of the central stimulus (Levitt & Lund, 1997). Furthermore, the suppressed modulation caused by the presence of a surround grating increases with surrounding contrast (Cavanaugh *et al.*, 2002a), suggesting that surround signals act divisively to regulate central sensitivity (Müller *et al.*, 2003), which could possibly be better modelled as a reduction in response gain rather than contrast gain (Cavanaugh *et al.*, 2002a; Webb *et al.*, 2003).

Some studies, on the other hand, have demonstrated that the type (facilitation or suppression) and degree of centre-surround interaction critically depends on properties of the stimuli presented inside and outside the CRF, such as texture orientation and binocular disparity. For example, the characteristic of orientation specific modulation is observed in V1 centre-surround interactions. That is, when the stimulus in the surround has a different orientation from the centre, the suppressive modulation is reduced (Knierim & Van Essen, 1992; Cavanaugh *et al.*, 2002b), or even reversed (Sillito *et al.*, 1995). It has been argued that such interaction constitutes the neurophysiological substrate of intermediate-level visual processes such as contour integration (Gilbert, 1998; Fitzpatrick, 2000), perceptual pop-out and grouping (Knierim & Van Essen, 1992; Kastner *et al.*, 1997; Mizobe *et al.*, 2001), surface perception (Rossi *et al.*, 1996; MacEvoy *et al.*, 1998) and figure-ground segregation (Lamme, 1995; Zipser *et al.*, 1996).

In our study, we observed that the V1 centre-surround interactions in response to natural images were contrast-dependent. The neuronal responses to the CRF natural image patch stimulation were systematically suppressed or facilitated by the increasing contrast of the image surrounds (Fig. 4), suggesting the role of contrast normalization. When manipulating the higher-order structures of the surrounding images, those neurons showing centre-surround interaction for natural images can be further divided into two groups (Fig. 6). A small group of neurons (20 out of 67) showed general suppression or facilitation to the surrounds. That is, they have indistinguishable modulated responses to the increasing contrast of the natural and scrambled image surrounds. The response modulation could be best explained by the level of contrast present in the surround and perhaps most readily interpreted as the integration of

luminance contrast from non-CRF regions. A relatively large group of neurons (47 out of 67), on the other hand, showed specific suppression to the increasing contrast of the natural image surrounds. Varying contrast of the scrambled image surrounds, which lack any visible image contours or visual objects, did not have significant modulatory effects on these neurons. This difference in surround modulation in the presence of different surround images could not be fully attributed to the mechanism of CRF border detection (Fig. 9) or surround contrast sensitivity (Fig. 10). It seems that the centre-surround interaction for this group of neurons is also sensitive to the higher-order structures of the natural image surrounds, such as continuous and colinear image contours, which commonly exist in the natural scenes (Geisler *et al.*, 2001; Sigman *et al.*, 2001; Simoncelli & Olshausen, 2001), and may contribute to image contour integration. This evidence suggests that when viewing natural images, the primary visual cortex may exploit both contrast and image structure signals in the visual diet, but may handle this information in separate channels or mechanisms.

For the majority of neurons recorded in this experiment, one natural image was presented to quantitatively study the centre-surround interactions. As the centre-surround contextual interactions can be stimulus specific, depending on the stimulus features inside and outside the CRF, detailed categorization of neurons in terms of contextual effects (suppression, facilitation, not feature-sensitive, nonmodulated, etc.) could be biased due to selections of the natural images. However, based on following reasons, we believe that the observed suppressive-dominant and feature-sensitive centre-surround interactions under natural image stimulation is a general character of V1 neurons rather than a consequence of arbitrary selections of image areas. (i) The CRF natural image contour approximated the neuron's preferred orientation and spatial frequency, and extended beyond the CRF. Therefore, for individual neurons the image areas inside and outside the CRF shared some important common features, such as RMS contrast, orientation and spatial frequency of the image contours. (ii) Previous studies have shown that the orientation and spatial frequency tuning characteristics of V1 neurons under natural image stimulation are compatible with those under stimulation with simplified stimuli, such as sinusoidal gratings (Ringach *et al.*, 2002; Smyth *et al.*, 2003). (iii) The percentage of neurons showing the contextual centre-surround interactions and the degree of modulation observed under natural image stimulation are also compatible with those under stimulation with simplified stimuli (see above discussion for details). (iv) For a limited number of neurons (14 neurons), we presented two or more different natural images. The responses of these neurons showed a similar trend of centre-surround interactions for different images. That is, the neurons either did not show modulated centre-surround interactions for all of the tested images or showed similar suppressive and feature-sensitive centre-surround interactions for all images.

Role of area V1 in natural vision

Natural images are statistically redundant (Field, 1987; Kersten, 1987; Tolhurst *et al.*, 1992; Ruderman & Bialek, 1994). This is shown by a correlational structure, such as intensity and colour similarity in neighbouring spatial locations that decline with increasing distance between regions (Field, 1987; Ruderman & Bialek, 1994; Simoncelli & Olshausen, 2001), and greater probability densities for the colinear and cocircular co-occurrence of line segments (Geisler *et al.*, 2001; Sigman *et al.*, 2001). In a neurobiological context, Barlow (1961) hypothesized that the role of early sensory neurons is to remove

statistical redundancy and maximize the information transmitted in the sensory input. This 'efficient coding' hypothesis has gained support mainly from computational neuroscience (reviewed in Barlow, 2001; Simoncelli & Olshausen, 2001).

Several electrophysiological studies across different species (cat, ferret and monkey) have shown that the activity patterns of V1 neurons elicited by natural stimuli are qualitatively and quantitatively different from those elicited by simplified stimuli, such as drifting gratings (Baddeley *et al.*, 1997; Kayser *et al.*, 2003). The neurons produce sparse, distributed responses to natural stimulation, consistent with predictions of efficient information coding in the early stages of visual information processing. For example, with localized CRF stimulation of static natural scene images or natural movies, V1 neuronal activities demonstrated high lifetime sparseness, population sparseness and high dispersal values. All of these are good indicators of efficient coding in terms of information processing (Vinje & Gallant, 2000; Weliky *et al.*, 2003).

Natural vision normally involves full-field visual stimulation. It is natural to conclude that confining visual stimuli only to the CRF will inevitably cause V1 neurons to operate outside their typical physiological range and transmit less information with lower efficiency (Vinje & Gallant, 2002). Recent studies show that in terms of centre-surround interaction, a surrounding natural image copresented with CRF stimulation can increase the selectivity and sparseness of V1 neurons' responses (Vinje & Gallant, 2000); reduce correlation among discharge rates of the population of neurons that respond to a particular stimulus (Vinje & Gallant, 2000; Müller *et al.*, 2003); and increase selectivity, information transmission rate, information per spike and efficiency (Vinje & Gallant, 2002). Interestingly, the enhancement of information transmission seems less obvious when using simplified surrounding stimuli, such as gratings or checkerboards (Reich *et al.*, 2000). It seems that the information transmission rates may be stimulus-type dependent, and V1 centre-surround interactions enable the transmission of relatively more information during vision of natural scenes.

In our study, we observed that V1 neuronal activities to CRF natural image contour stimulation are profoundly suppressed by the surrounding images. This result is consistent with the observation made by Vinje & Gallant (2000, 2002), indicating a reduction in redundancy. We also demonstrated that the higher-order structures of the natural images critically contribute to this centre-surround interaction. Thus, if the natural image contour falling on the CRF resembles those that surround it, V1 neuronal activity shows predominantly suppressive modulation, suggesting that centre-surround interactions could be important for signalling differences in higher-order structure between centre and surround, such as differences in orientation (Jones *et al.*, 2002). This behaviour seems well matched to the properties of natural scenes where the statistics of iso-orientated filters responding to adjacent natural image regions are highly correlated compared with those from cross-orientated filters or more separated regions (Geisler *et al.*, 2001; Sigman *et al.*, 2001; Simoncelli & Olshausen, 2001). Taken together, our results suggest that connectivity within area V1 is optimized for representing natural visual stimuli, and may be crucial for encoding higher-order structures of natural scene images, such as image contours.

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Abbreviations

area V1, primary visual cortex; CRF, classical receptive field; FP, fixation point; RMS, root-mean-square.

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