Neuroscience 138 (2006) 1397–1406

PRIMARY VISUAL CORTEX NEURONS THAT CONTRIBUTE TO RESOLVE THE APERTURE PROBLEM

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Abstract—It is traditional to believe that neurons in primary visual cortex are sensitive only or principally to stimulation within a spatially restricted receptive field (classical receptive field). It follows from this that they should only be capable of encoding the direction of stimulus movement orthogonal to the local contour, since this is the only information available in their classical receptive field "aperture." This direction is not necessarily the same as the motion of the entire object, as the direction cue within an aperture is ambiguous to the global direction of motion, which can only be derived by integrating with unambiguous components of the object. Recent results, however, show that primary visual cortex neurons can integrate spatially and temporally distributed cues outside the classical receptive field, and so we reexamined whether primary visual cortex neurons suffer the "aperture problem." With the stimulation of an optimally oriented bar drifting across the classical receptive field in different global directions, here we show that a subpopulation of primary visual cortex neurons (25/81) recorded from anesthetized and paralyzed marmosets is capable of integrating informative unambiguous direction cues presented by the bar ends, well outside their classical receptive fields, to encode global motion direction. Although the stimuli within the classical receptive field were identical, their directional responses were significantly modulated according to the global direction of stimulus movement. Hence, some primary visual cortex neurons are not local motion energy filters, but may encode signals that contribute directly to global motion processing.

Key words: direction selectivity, aperture problem, motion, primary visual cortex, monkey.

Individual measurements of local contour direction are inherently ambiguous (Wallach, 1976). One striking example is the so-called "aperture problem" (Marr, 1982), the motion of a featureless line seen behind a circular aperture is perceptually ambiguous: for any global direction of motion, the perceived direction is perpendicular to the orientation of the line. To overcome this "aperture problem," the visual system must have the capability of computing unambiguous directional cues derived from "line terminators," and weighting them more than ambiguous signals produced by line interior.

Traditionally, vision is viewed as hierarchical analysis of the retinal input (Livingstone and Hubel, 1988; Felleman and Van Essen, 1991; Lennie, 1998). Specifically, visual information is conceived to be amplified and conveyed at high gain and fidelity to and through a hierarchically organized visual cortex by feed-forward connections, where the information is successively extracted by receptive fields of increasing size and sophistication, each effectively a local filter, situated at each successive stage. In this bottom-up "vision-as-analysis" framework, neurons in the primary visual cortex (area V1) are sensitive only or principally to stimulation within spatially restricted receptive fields (classical receptive fields, CRFs). They would invariably suffer the "aperture problem," and would only encode the component of stimulus movement orthogonal to the local contour presented within their CRFs (Movshon et al., 1985; Snowden, 1994; Andersen, 1997), since this is the only information available in their CRF "aperture." This direction is not necessarily the same as the motion of entire object or surface of which the neuron's preferred contour is only a small component. The "true" direction of motion could presumably only be determined by neurons with CRFs lying over unambiguous components of the object, such as end-points of the line, or corners in a more complex shape. Pack et al. (2003) showed that end-stopped V1 neurons could certainly signal (apparent) motion unambiguously, when the end-points of a line intersect their CRFs.

The activities of V1 neurons are not only determined by feed-forward inputs (reviewed in Gilbert, 1998; Lamme et al., 1998; Angelucci and Bullier, 2003; Lorenceau, 2003; Chisum and Fitzpatrick, 2004). In fact, only a small portion of excitatory synapses (<5%) on V1 neurons is from lateral geniculate nucleus, the principal relay between the eye and the visual cortex (e.g. Peters and Payne, 1993). Consequently, over 95% of the excitatory synapses, even in geniculo-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 (Young, 2000). Indeed, neurophysiological studies have demonstrated that V1 neurons can integrate orientation, contrast, luminance and relative motion information from regions beyond their CRFs, and can contribute to perceptual pop-out, contour integration, surface perception

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Abbreviations: CRF, classical receptive field; DI, direction index; MI, modulation index; MT, middle temporal visual cortex; V1, primary visual cortex; 1-ANOVA, one-way analysis of variance; 2-ANOVA, two-way analysis of variance.

0306-4522/06$30.00+0.00 © 2005 Published by Elsevier Ltd on behalf of IBRO.
doi:10.1016/j.neuroscience.2005.12.016

and figure-ground segregation (reviewed in Gilbert, 1998; Fitzpatrick, 2000; Albright and Stoner, 2002; Lee, 2003; Chisum and Fitzpatrick, 2004). It is intriguing to speculate that V1 neurons behaving in this way would not view the world through an aperture, and consequently would not suffer the "aperture problem." They could be capable of signaling information about global motion direction through integrating informative unambiguous motion cues presented outside their CRFs. To examine this, we compared the directional responses of V1 neurons, sampled in anesthetized and paralyzed marmosets, to an optimally oriented bar, with length extending beyond the CRF, drifted across the CRF in a variety of global directions.

EXPERIMENTAL PROCEDURES

Animal preparation

Standard electrophysiological techniques for extracellular recording were used for four adult marmosets (*Callitrix jacchus*, 350–500 g) (Guo et al., 2004a). The number of animals used and their suffering were minimized, and all procedures complied with the "Principles of laboratory animal care" (NIH publication no. 86–23, revised 1985) and UK Home Office regulations on animal experimentation (Animals (Scientific Procedures) Act, 1986). Briefly, the animals were anesthetized with halothane (0.8–2%) and a 70:30 mixture of N_2O and O_2, and alfentanil (30 μg/kg/h). During the recording, they were paralyzed with a continuous i.v. infusion of vecuronium bromide (0.1 mg/kg/h) in glucose–saline and artificially ventilated. The rectal temperature (~38 °C), expired CO_2 (3.5–4.5%), blood pressure and electrocardiogram were continuously monitored and maintained. A small craniotomy was positioned over the central visual field representation of area V1.

Pupils were dilated with atropine. The corneas were protected with zero-power contact lenses, and artificial pupils (3 mm diameter) were positioned in front of each eye. The refractive state of each eye was measured by direct ophthalmoscopy, and additional lenses were used to focus the eyes on the stimulus monitor.

Visual stimuli, recording and data analysis

Visual stimuli were generated by VSG 2/3 graphics system (Cambridge Research Systems, Cambridge, UK) and displayed on a gamma-corrected high frequency non-interlaced color monitor (110 Hz, Sony GDM-F500T9; Sony, Tokyo, Japan) with the resolution of 1024×768 pixels. At a viewing distance of 57 cm the monitor subtended a visual angle of 40×30°. The mean luminance of uniform gray background was 6.0 cd/m^2.

The activity of V1 neurons was recorded using glass-coated tungsten microelectrodes (1–2 MΩ impedance), and was amplified and sampled through CED1401 plus digital interface (Cambridge Electronic Design, Cambridge, 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 program (Spike2, Cambridge Electronic Design) 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 non-orientation selective, high spontaneous activity and brisk "on" and "off" responses). No attempt was made to select neurons from a particular layer of cortex.

Having isolated a neuron and determined the dominant eye (non-dominant eye was covered with a black disk during the recording), the CRF was carefully mapped using a sweeping bar and a sinusoidal grating patch moving across the screen with variable length, width and velocity. Within the patch, the optimal grating drifted continuously in the neuron's preferred direction. In this way, we estimated CRF width and breadth profiles (Guo et al., 2004a). To avoid underestimating the size of the CRF, the CRF was further covered with a uniform gray background and an annular window was centered on the CRF. A drifting sinusoidal grating with moderately high contrast (~70%) 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 drifting sinusoidal grating with the size of the CRF was then placed at the center of the CRF. The grating's orientation/direction, spatial and temporal frequency were systematically varied to quantitatively determine the neuron's preferred tuning characteristics. For all neurons reported in this experiment, their CRF locations were within central 10° and CRF diameters ranged from 0.6° to 1.5°.

The CRF of each neuron recorded was classified as "simple" or "complex" on the basis of the spatial arrangement of "on" and "off" regions and the presence of spatial summation within each region (Hubel and Wiesel, 1968). These classifications were later confirmed by the frequency component of their responses to the optimal drifting sinusoidal grating (Skottun et al., 1991). We recorded preferentially from complex cells for the reasons that complex cells tend to be more direction selective than simple cells (Hubel and Wiesel, 1968; Conway and Livingstone, 2003).

The neuron's direction selectivity, tested with the drifting grating, was characterized by a direction index (DI), expressed as $1-N/P$, where P and N are the neuron's firing rate to motion in its preferred and opposite directions (each minus spontaneous firing rate). Neurons with no direction preference will give a DI of 0. A unidirectional neuron gives an index near 1, and a neuron inhibited by motion in the null direction gives a value >1 (DeValois et al., 1982; Hawken et al., 1988; Chaudhuri and Albright, 1997).

To investigate whether V1 neurons can integrate unambiguous directional cues presented outside their CRFs, an optimally oriented bar (±70% contrast) was drifted across the CRF in one of nine different global directions (±40° around the preferred direction in 10° intervals; Fig. 1). The component velocity, orthogonal to the preferred orientation and determined by neuron's preferred

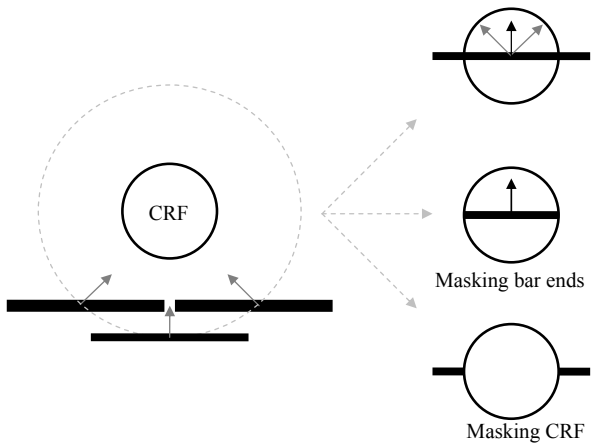

Fig. 1. Stimulus conditions. An optimally oriented bar was drifted across the neuron's CRF in one of nine different global directions (±40° around the preferred direction in 10° intervals, indicated by gray arrow lines). The component velocity, orthogonal to the neuron's preferred orientation (indicated by black arrow line), was constant and determined by the neuron's preferred temporal frequency. The dotted circle line around the CRF indicates the start and finish positions of the bar movement. Control conditions include the bar being masked either outside (masking bar ends) or inside (masking CRF) the CRF of the recorded neuron.

temporal frequency, was kept constant for different global motion directions. The width of the bar was determined by the neuron's preferred spatial frequency, and the length of the bar was varied from two to eight times CRF diameter. The start and finish positions of the drifting bar were also adjusted according to the global direction to ensure that the center of the bar was in the center of the CRF when it was drifted halfway across the CRF, and the total drifting distance was three times CRF diameter. During the stimulus presentation, therefore, the movements of the bar segment within the CRF were identical for different global directions.

Control conditions involved the bar being masked either outside (masking bar ends) or inside (masking CRF) the CRF of the recorded neuron (Fig. 1). In the masking bar ends condition, the movement of the bar was restricted within the CRF and looked identical although the global directions were varied. In the masking CRF condition, the neuron's CRF did not receive any direct visual stimulation while the bar segments outside the CRF were drifted across both sides of the CRF.

Each stimulus condition was presented to the dominant eye for 15–30 repetitions in randomized order. The inter-stimulus interval was 1000 ms.

As this experimental design comprised nine levels of global motion direction (±40° around the preferred direction in 10° intervals) and three levels of bar length (two, four, and eight times CRF diameter), two-way analysis of variance (2-ANOVA) was carried out after averaging the neuron's discharge for the duration of CRF stimulus presentation (from the bar entering the CRF till the bar leaving the CRF, same duration for the drifting bars with different directions and velocities). Appropriate post hoc testing of differences between levels of global direction (Tukey's least significant procedure) was carried out following detection of significant overall variable ratios. One-way analysis of variance (1-ANOVA) and post hoc test (Tukey's least significant procedure) were also carried out for the test condition of masking CRF to detect whether the neuronal responses were statistically different for the different global directions of the bar ends movement and the spontaneous activity (sampled during the inter-stimulus interval between −250 ms and 0 ms before the presentation of the bar), and for the test condition of masking bar ends to detect whether the neuronal responses were statistically different for the different invisible global directions of the bar movement.

RESULTS

Eighty-one V1 neurons (14 simple cells and 67 complex cells) were recorded from four anesthetized and paralyzed marmosets. Consonant with processing information from a spatially restricted small CRF, most of the recorded neurons (69%, 56/81) suffered the "aperture problem." Their responses to the component motion of the bar segment within the CRF were indistinguishable, although the global motion direction of the entire bar was varied (2-ANOVA, direction: $P>0.05$). These neurons thus appear only to signal the direction of stimulus movement orthogonal to the orientation, even when this direction is not the same as the motion of entire object.

A substantial group of neurons (31%, 25/81; 4 simple cells and 21 complex cells), however, was significantly modulated by the global direction of the stimulus movement. Fig. 2 shows two examples. These neurons showed clear direction selectivity to the drifting gratings presented within their CRFs (DI=0.76 and 0.5 for cells 3–20 and 1–4). When a single bar with the neuron's preferred orientation and length of two times CRF diameter was drifted across the CRF in the preferred direction (indicated as 0° in Fig. 2A and B), the neurons had maximum firing rates. When the global drifting directions were shifted up to 40° away from the preferred direction, their responses gradually decreased although the movements of the bar segment within the CRF were identical for different global directions (ANOVA, $P<0.05$; black curve with solid circle symbols in Fig. 2A and B). For cells 3–20, its response reduced up to 55% when the global direction was 20° away from its preferred direction; for cells 1–4, the firing rate reduced up to 39% for the global direction 40° away from its preferred direction.

When the bar ends outside the CRF were masked (masking bar ends, see Fig. 1 for an example), the movement of the bar segment inside the CRF was always perceived as drifting in the neuron's preferred direction as invisible bar ends presented outside the CRF could not provide unambiguous global directional cues. Consequently, with this masking, the responses of the two neurons in Fig. 2 were statistically indistinguishable among the different global directions of the bar movement (1-ANOVA, $P>0.05$; gray curve with solid triangle symbols in Fig. 2A and B). When the bar segment inside the CRF was masked (masking CRF, see Fig. 1 for an example), the neurons did not receive any direct CRF stimulation, although the global directional cues were clearly presented by the bar ends outside the CRF. For this pattern of masking, the responses of two neurons were not significant different from their spontaneous activities (1-ANOVA, $P>0.05$; thin black curve with open circle symbols in Fig. 2A and B).

Despite the local directions of the bar movement within the CRF being identical, the responses of some V1 neurons were modulated by the global motion directions, and this modulation is likely derived from the unambiguous directional information provided by the bar ends outside the CRF region. To further investigate how far the V1 neurons can integrate these global directional cues, we systematically varied the length of the bar as two, four and eight times the CRF diameter, and compared the neuronal responses to the bars with different lengths and drifting in various global directions. Although its response was significantly modulated by the global direction of a short bar (2× CRF diameter), cells 3–20 failed to integrate the directional cues from the bar ends of longer bars (4 and 8× CRF diameter). Its responses were statistically indistinguishable for the different global motion directions (ANOVA, $P>0.05$; Fig. 2C). Cells 1–4, on the other hand, integrated the global directional cues provided by the ends of the longest bar tested (8× CRF diameter, Fig. 2D). Its responses to the identical CRF stimuli were systematically modulated by the global directions no matter the length of the bar used (2-way ANOVA, direction: $P<0.05$; length: $P>0.05$), up to the limit tested.

Generally, V1 neurons' capability of computing global directions of movement gradually decreased with increasing distance between the global directional cues (bar ends) and the center of the CRF. Population analysis showed that out of 25 neurons whose direction selectivity was modulated by the global motion directions, 24 could integrate unambiguous directional cues from the bar ends

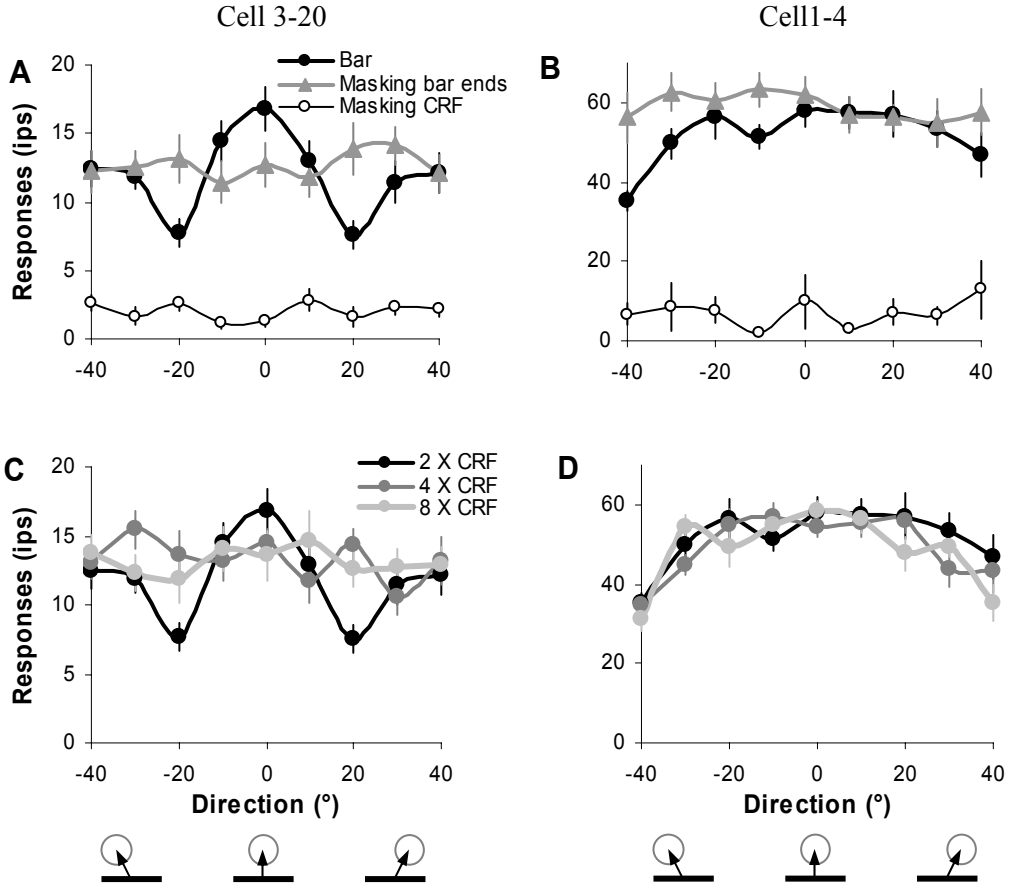

Fig. 2. Example of two neurons (cells 3–20: A and C; cells 1–4: B and D) whose directional responses were systematically modulated by the global directions of an optimally oriented bar drifting across their CRFs. A and B show neuronal responses to the optimally oriented bar with the length of two times CRF diameter drifting across the CRF in various global directions (±40° around the preferred direction in 10° intervals), the bar was either intact or masked at the bar segments inside or outside the CRF (masking CRF or bar ends). C and D show neuronal responses to the optimally oriented bar with various length (two, four, and eight times CRF diameter) drifting across the CRF in various global directions. Error bars indicate standard error of the mean.

presented close to their CRFs (bar length=2× CRF diameter), while 19 and 10 neurons could still integrate these directional cues presented relatively far away from their CRFs (bar length=4 and 8× CRF diameter; Fig. 3A). We

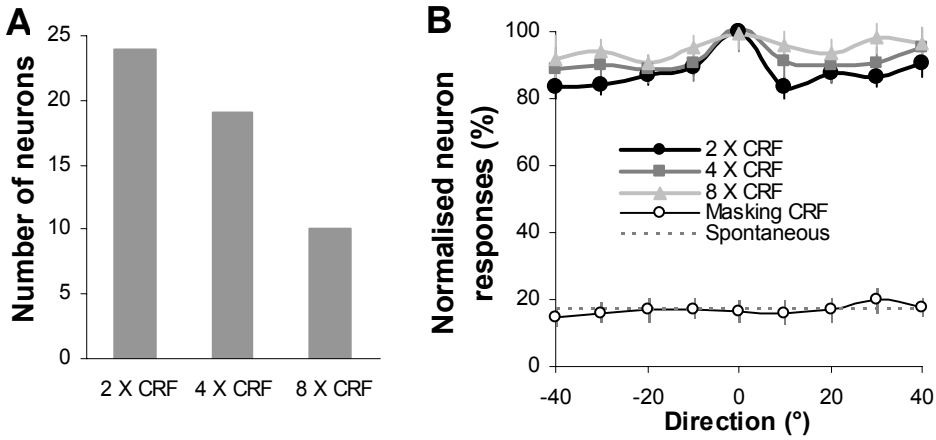

Fig. 3. (A) The frequency distribution of V1 neurons whose directional responses to the identical CRF stimuli were modulated by the global directions of the drifting bar with the length of two, four, and eight times CRF diameter. (B) Normalized responses to the global directions of the drifting bar with the length of two, four, and eight times CRF diameter for the population of 25 V1 neurons. The response to the shortest bar drifted in the neuron's preferred direction was treated as 100%. Error bars indicate standard error of the mean.

also directly compared neuronal responses to various global directions generated by the bars with different lengths for these 25 neurons (neuronal discharge to the shortest bar drifting in the preferred direction was treated as 100%; Fig. 3B). The normalized directional response was most significantly modulated by the shortest bar, and the tuning curve became broader and flatter with increasing bar length. In the control condition of masking CRF, although the global directional cues were clearly presented by the bar ends outside the CRF, the responses of these 25 neurons were statistically indistinguishable for the different directions of the bar ends movement, and were not significantly different from their spontaneous activities (1-ANOVA, $P>0.05$; Fig. 3B).

The majority of V1 neurons show effects of spatial summation, normally suppression, to stimuli extended beyond their CRFs (for reviews see Gilbert, 1998; Fitzpatrick, 2000), and therefore have some measure of end-stopping (DeAngelis et al., 1994; Jones et al., 2001; Sceniak et al., 2001) as demonstrated by Hubel and Wiesel (1965). Recently, Pack et al. (2003) have suggested that only end-stopped neurons in monkey V1 can encode global direction signals in a manner that is largely independent of the orientation of the CRF stimulus. Our results, however, suggest that V1 neurons' capability of computing global directions seems not to be strictly restricted by the size of the CRF or summation field. We measured the neuron's length tuning function by presenting optimally oriented bars drifting across the CRF in the preferred direction; the length of the bar was varied as one, two, four, or eight times CRF diameter. Fig. 4A shows the length tuning responses of two neurons whose directional responses were modulated by the global motion directions as demonstrated in Fig. 2. These two neurons did not show any end-stopped tuning properties within the range of bar length tested. Their responses were not significant different for the drifting bars with various lengths (1-ANOVA, $P>0.05$).

To further examine how the property of length tuning relates to the capability of integrating global motion direction, we calculated a modulation index (MI), defined as the neuronal response (minus spontaneous activity) to the longest bar (8× CRF diameter) divided by the response to the shortest bar (1× CRF diameter), for each neuron, and we plotted the frequency of their MI distribution with 0.2 bin width (Fig. 4B). If a neuron's response to the CRF presentation was suppressed by the longer bar, its MI should be less than 1. If its response was facilitated by the longer bar, on the other hand, its MI should be larger than 1. Out of the 81 neurons we sampled (gray curve with solid circles in Fig. 4B), only 14 neurons showed significant length tuning for the bar length up to eight times CRF diameter (1-ANOVA, $P<0.05$; thin black curve with open circles in Fig. 4B); while 25 neurons showed modulated responses to the global motion directions (black curve with solid circles in Fig. 4B). Most of these neurons (16/25) did not show any length tuning effect to the longer bars. However, there was a tendency for those neurons showing length tuning to have a higher probability of responding to the global motion signals. Out of 14 neurons showing length tuning effect, nine had modulated responses to the global directions of the bar movement. For 67 neurons not showing length tuning responses within our test range, only 16 had modulated responses to the global motion directions.

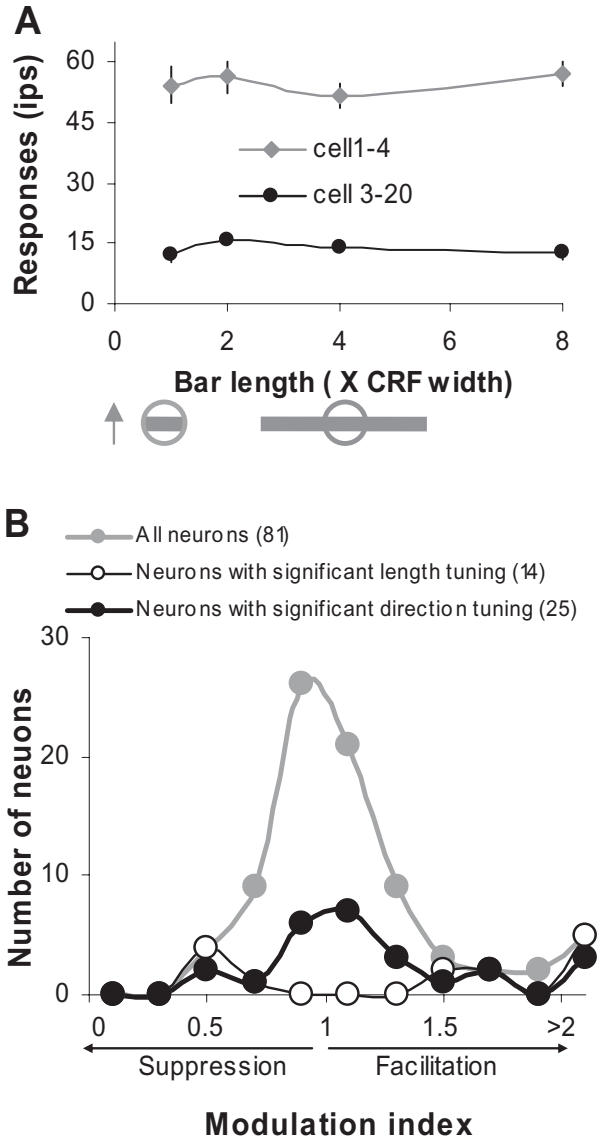

Fig. 4. (A) The length tuning responses of two example neurons. The optimally oriented bar was drifted across the CRF in the neuron's preferred direction with various length (from one to eight times CRF diameter). Error bars represent standard error of the mean. (B) Frequency distributions of MI for all tested V1 neurons, for neurons showing significant length tuning responses, and for neurons responding to the global motion directions.

In our experiments, although the length of the entire bar was fixed for a given trial, the portion of the (single) bar falling on either side of the CRF changed when the bar drifted across the CRF in the non-preferred directions. Fig. 5A shows one example. In this trial the bar with the neuron's preferred orientation drifted across the CRF in its non-preferred direction. For the two portions of the bar falling outside the CRF, the right portion was longer than

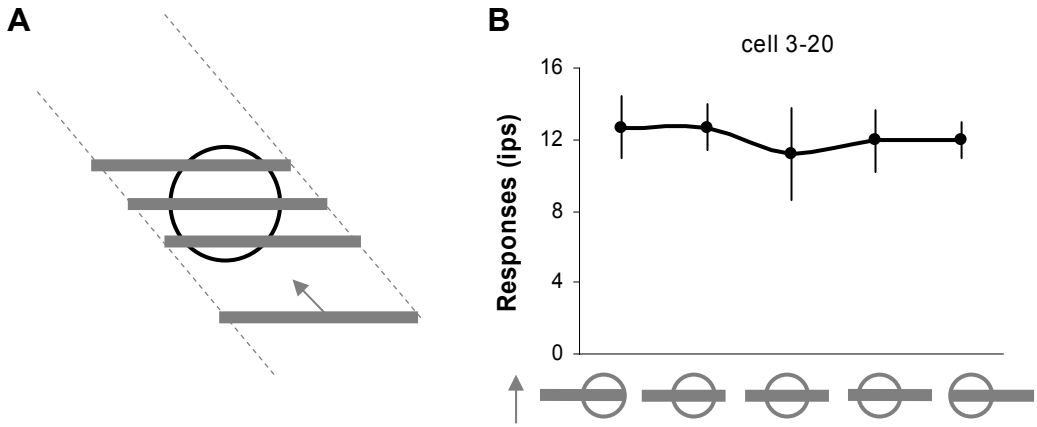

Fig. 5. (A) Stimulus example. When a single bar drifted across the CRF in the non-preferred directions, the portion of the bar falling on either side of the CRF changed systematically. (B) Example of a neuronal responses to the bar drifting across the CRF in its preferred direction. The distribution of the length of bar segments on both sides of the CRF was systematically manipulated (see bottom inset, arrow line on the left indicates the motion direction). Error bars indicate standard error of the mean.

the left portion before the bar reached the center of the CRF; and then it was shorter than the left portion after the bar passed the center of the CRF. To exclude the unlikely possibility that this dynamic change of the bar length on either side of the CRF could modulate neuronal responses (i.e. non-linear integration from regions outside the CRF), we carried out an additional experiment, where we systematically manipulated the distribution of the bar length on both side of the CRF while keeping the total bar length constant, and compared the neuronal responses to these bars drifting in the preferred direction for those neurons showing sensitivity to the global motion directions. The bar segments outside the CRF were either located on one side of CRF, or 75% of the length was presented on one side while 25% on the other side of the CRF, or were equally distributed on both side of the CRF (see Fig. 5B for an example). For cells 3–20, there was no significant response difference to these test conditions (1-ANOVA, $P>0.05$; Fig. 5B). Therefore, its reduced response to the non-preferred directions was most likely due to the integration of the global directional cues available outside its CRF (see also Figs. 2 and 3). Out of 22 neurons tested with these control stimuli, 21 showed indistinguishable responses to the various bar length distributions outside their CRFs (1-ANOVA, $P>0.05$).

When a field of short bars or a plaid pattern containing conflicting local and global motion signals is presented within the CRF, neurons in the middle temporal visual cortex (MT), a specific motion selective area in monkey visual cortex where the neurons are capable of encoding the global motion cues, appear initially to respond primarily to the component of motion perpendicular to the contour's orientation. After a short period, responses gradually shift to encode the global motion direction (Pack and Born, 2001; Pack et al., 2001; Smith et al., 2005). To investigate whether there is a similar temporal evolution of the shift in V1 response properties while integrating the global directional cues presented outside the CRFs, we compared time-courses of neuronal responses to the preferred and the least preferred global motion directions. Although in our experiments the starting and ending positions of the bar movement for a given trial were varied according to the global bar directions, the entering and leaving points of the CRF, and the duration of the bar movement within the CRF were identical for various global directions (see Fig. 1 for an example). In this time-course analysis, we only compared neuronal responses to the bar movements within the CRF. For two neuron examples showing modulated responses to different global directions (see Fig. 2), their discharges were plotted as peristimulus time histograms (PSTHs) with 10 ms bins; time 0 indicates the time when the bar entered the CRF (Fig. 6A and B). Compared with the response to the preferred direction, the response to the least preferred direction was clearly delayed and suppressed at the earliest stage of the neuronal response. We further calculated each neuron's response latency using cumulative sum analysis (Maunsell and Gibson, 1992; Raiguel et al., 1999). The latency was taken to be the time corresponding to the first bin after the bar entering the CRF where the bin exceeded the spontaneous firing rate by two standard deviations and which was followed by at least two successively increasing bins. The difference of response latencies between the preferred and the least preferred global directions was 40 and 30 ms for cells 3–20 and 1–4, respectively.

For the population analysis of 25 neurons showing sensitivity to the global motion directions, we chose the time when the bar entered the CRF as time 0 and accordingly averaged and normalized neuronal responses to the preferred and the least preferred global motion directions. As shown in Fig. 6C, compared with the response to the preferred global direction, the response to the least preferred direction was delayed by 20 ms$\pm$3 (mean$\pm$S.E.M.), and the peak response was suppressed by 36%$\pm$5. These delayed and suppressed responses to the non-preferred global directions are probably due to the result of resolving conflicting local motion signals (Nowlan and Sejnowski, 1995; Grossberg et al., 2001) rather than simple suppression introduced by the bar segments presented outside the CRF, as the total bar length was identical for various global

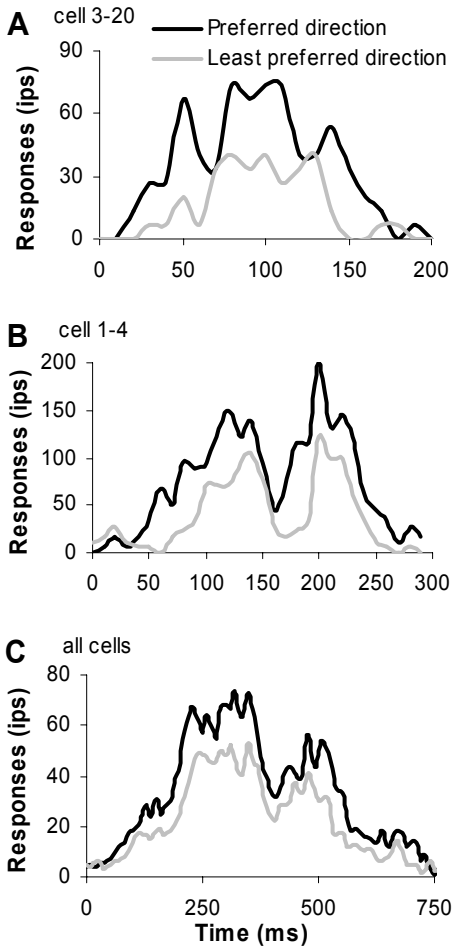

Fig. 6. Directional responses to the preferred and the least preferred global direction of the bar movement as a function of time for cells 3–20 (A), cells 1–4 (B) and the population of 25 V1 neurons (C).

directions and most of the neurons did not show modulated responses to different bar length or different distribution of bar length on both side of the CRF (see Figs. 4 and 5).

In our V1 sample, the neuron's DI, measured with a drifting sinusoidal grating whose direction was always perpendicular to the orientation, ranged from 0.02–1.04 with the mean value of 0.44±0.03. To examine how the property of direction selectivity relates to the capability of integrating global directional cues, we calculated the DI for each of the 81 neurons, and plotted the percentage of neurons showing modulated responses to the global directions as a function of their DI (0.1 bin width, Fig. 7). There was a tendency for neurons with higher sensitivity to motion stimuli (higher DI) to have a higher probability of responding to the global direction of the bar movement (linear regression: correlation coefficient $r=0.75$, $P=0.006$).

DISCUSSION

Research on brain mechanisms of motion processing has tended to emphasize a hierarchical pathway for motion analysis. In the primary motion detection stage (area V1), direction selective neurons act as local motion energy filters (Adelson and Bergen, 1985; Grzywacz and Yuille, 1990) and respond to the motion of image constituents within particular bandpass characteristics for orientation, spatial and temporal frequency. These neurons simply encode the motion of the oriented components comprising a complex pattern rather than the global motion of the pattern itself. Neurons in the later motion integration stage (i.e. area MT) perform more complex computations based on extensive local motion measurements provided by V1, and detect the "true" direction of global motion that is independent of the motion of contours within them (Movshon et al., 1985; Rodman and Albright, 1989; Stoner and Albright, 1994; Pack and Born, 2001; Pack et al., 2004).

In this framework, V1 neurons are simply local spatio-temporal filters, extracting local motion measurements and transmitting them to higher visual areas for further processing. They inevitably suffer the "aperture problem" while dealing with a moving contour extended beyond their CRFs. However, neurophysiological studies have revealed that some V1 neurons are capable of signaling some complex motion signals presented within their CRFs, such as pattern motion (Tinsley et al., 2003; Guo et al., 2004a) and second-order motion signals (Chaudhuri and Albright, 1997; O'Keefe and Movshon, 1998). Furthermore, the well-documented phenomenon of center-surround interaction shows that V1 neurons can integrate orientation, relative motion, contrast and luminance signals from regions beyond their CRFs (Knierim and Van Essen, 1992; Kapadia et al., 1995; Lamme, 1995; Rossi et al., 1996; Zipser et al., 1996; Kastner et al., 1997; MacEvoy et al., 1998; Jones et al., 2001; Angelucci et al., 2002; Cavanaugh et al., 2002; Levitt and Lund, 2002; Guo et al., 2005), suggesting that the function of V1 neurons is far from that of local spatio-temporal filters.

Inferential model of visual processing suggests a contrasting view of the function of V1 neurons (Knill and Richards, 1996; Young, 2000; Friston, 2002; Guo et al., 2004b). In this model, visual neurons should have access, through their embedding neural network, to information about the

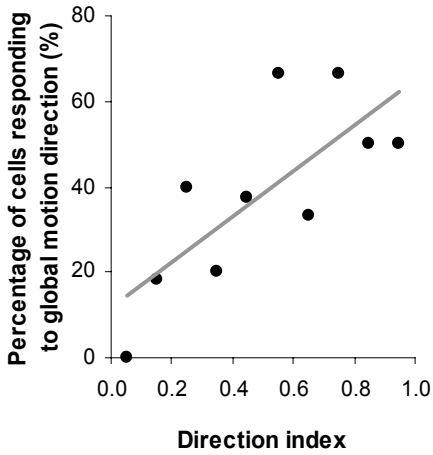

Fig. 7. The percentage of neurons showing modulated responses to the global motion directions as function of their DI.

distribution of prior probabilities of stimuli (Lee, 1995; Young, 2000), and the output of a neuron critically depends on the interaction between the likelihood function (i.e. CRF visual input) and the prior probability (i.e. extra-CRF information) rather than simply on direct visual input from its CRF (Guo and Li, 1997; Gilbert, 1998; Young, 2000; Sharma et al., 2003). In light of this, when processing the motion of a extended bar passing through the CRF, the interpretation of V1 neurons should be the result of interaction between the ambiguous direction signals derived from the bar segment inside the CRF and the unambiguous direction signals derived from the bar ends outside the CRF. Accordingly, their directional responses would be expected to be modulated by the "actual" direction of the moving bar.

In our experiment, although the component motion was identical within the CRF, the directional responses of a substantial group of V1 neuron were significantly modulated according to the global direction of the moving bar, and this response modulation is most likely derived from the unambiguous directional cues presented by the bar ends, outside the CRF region. However, it is not clear whether the observed neuronal modulations in this experiment can truly reflect recovery of the global motion. As our stimuli used to test the neurons' preferred tuning characteristics (sinusoidal gratings) and global motion modulations (drifting bars) had different direction test range (grating: 0–360°; bar: ±40° around the neuron's preferred direction) and different orientation information (grating: orientation perpendicular to its direction; bar: constant orientation), it is difficult to directly compare the direction tuning yielded in response to the gratings and bars. In our future study, it will be interesting to address this question by employing stimuli without orientation information, such as moving dot patterns. However, our observation that the peak of the modulation tuning function for the main experiment coincides with the peak of the directional tuning function for the gratings suggests that the modulated neuronal responses in area V1 are directly related to the processing of global motion information, and a substantial group of V1 neurons can contribute directly to the global motion processing rather than only perform local motion measurements.

How can some V1 neurons integrate local motion signals into global motion measurements? Some recent studies suggest that this capability of V1 neurons depends on local receptive field properties (i.e. "end-stopped" responses; Pack et al., 2003, 2004) or receptive field shape (Tinsley et al., 2003). Using two-flash apparent motion stimuli (Pack et al., 2003) and "barber pole" illusion stimuli (Pack et al., 2004), Pack et al. suggested that the computation of global motion occurs on a spatial scale that is similar to V1 CRF diameter. However, our results do not accord with this suggestion that only "end-stopped" V1 neurons can compute the global motion direction. Most of neurons showing capability of global direction integration in this study are not "end-stopped," at least within the quite extensive length summation range we tested (Fig. 4). Therefore, the capability of integrating and computing various local motion cues in area V1 seems not to be strictly restricted by the size of the CRF or summation field. It is also unlikely that the receptive field shape can fully determine the global motion selectivity of V1 neurons as the neuron's activity in computing the global directions decreased with the increasing distance between the global directional cues (bar ends) and the center of the CRF (Fig. 3). Given these considerations, it is reasonable to assume that CRF itself or feed-forward connections in V1 cannot fully account for V1 neuronal responses to global motion signals.

The lateral and feedback connections may play a critical role in V1 motion information integration. The extensive lateral/horizontal connection enables V1 neurons to integrate visual information available from regions beyond the CRFs (for reviews, see Gilbert, 1998; Chisum and Fitzpatrick, 2004). When an elongated bar is drifted through a neuron's CRF in various directions, although the direction of the bar segment within the CRF of the recorded neuron is ambiguous, the bar ends containing the unambiguous directional cues, pass through the CRF of the neighboring motion sensitive neurons. These unambiguous motion signals could be fed to the recorded neuron via lateral connections, and enable the neuron to integrate direction vectors from various part of the bar into a more global representation of the "actual" direction of the entire bar movement, provided the unambiguous motion signals from the bar ends are given much more weight than the ambiguous motion signals from the bar interior.

V1 neurons also receive feedback connections from a number of extrastriate areas (Lamme et al., 1998; Angelucci and Bullier, 2003). Those feedback influences from neurons with larger CRF and complex computation capabilities may inform V1 neurons with the processing results of higher areas, and allow them to integrate some global information (Hupé et al., 1998, 2001; Hochstein and Ahissar, 2002; Guo et al., 2004a). As MT neurons are capable of performing more complex computations based on extensive local motion measurements provided by V1, and detecting the direction of global motion (Movshon et al., 1985; Andersen, 1997; Pack et al., 2004), it is possible that some V1 neurons might receive the critical feedback information from MT and thus inherit the computed property or properties of global motion selectivity so clearly evident in MT. This feedback information may further provide the top-down priors for geometric inference in area V1 in a hierarchical Bayesian inference framework which has been demonstrated in the computation of perceptual contours, surface shapes and object saliency (reviewed in Lee, 2003).

The interaction between CRF and its surround may take time to develop (Lamme, 1995; Pack and Born, 2001; Pack et al., 2003). Generally, the early part of the neuronal responses reflects only the stimulus presented within the CRF, while the late part takes the larger stimulus context into account. When integrating motion cues, V1 (Pack et al., 2003) and MT (Pack and Born, 2001; Pack et al., 2004; Smith et al., 2005) neurons initially respond primarily to the component of motion perpendicular to a contour's orientation. After a short period (20–30 ms in

V1 and around 60 ms in MT) the response gradually shifts to encode the global motion direction, regardless of orientation. In our experiment, we also observed a clear time difference of neuronal responses to different global motion directions. Although the component motion within the CRF was kept as the neuron's preferred direction, the neuronal response was delayed and reduced when the global motion direction was less preferred (Fig. 6). However, unlike the results from Pack et al. (2001, 2003, 2004), this modulation started from the earliest part of neuronal responses. This may be due to the way we presented the stimuli. The motion onset in our experiment starts from regions outside the CRF rather than inside the CRF (see Fig. 1 for an example). Consequently, the computation of the global motion direction could start even before the bar enters the CRF of the recorded neuron. Although it may be sub-threshold, this unambiguous motion information could be passed to the recorded neuron via feedback influences or lateral interactions within V1, and the time difference we observed could be the result of resolving conflicting local motion signals (Nowlan and Sejnowski, 1995; Grossberg et al., 2001). From this study, it is difficult to differentiate the contribution from lateral interaction and feedback influence. The early surround modulation to neuronal responses may suggest that the unambiguous direction signals come from lateral interactions. However, given the existence of fast speed feedback connections from MT to V1 (e.g. Movshon and Newsome, 1996), it is possible that some higher-lever computations may also be involved in V1 directional computations (top-down interactions).

In light of our results, a natural interpretation is that neurons in area V1 are not only specialized for extracting local features and conveying information of a low-level nature, such as local motion measurements, as suggested by the classical model of "vision-as-analysis"; but also represent and communicate signals that may contribute to relatively global processing as proposed by the model of "vision-as-inference." On this interpretation, V1 is an active interpreter of the visual world, and is involved in many levels of visual computation, including global motion computation demonstrated in this study.

Acknowledgments—This work is supported by the Wellcome Trust, HFSPO and EU FP5. We thank Dr. A. Thiele, M. Roberts and W. Zinke for assistance with physiological recordings.

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(Accepted 10 December 2005)
(Available online 30 January 2006)