Comparative study on direction selectivity and functional organization of the primary visual cortical cells in monkeys and cats

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Abstract Although the directionally selective cells in many visual cortical areas are organized in columnar manner, the functional organization of direction selectivity of area Vl in the monkey still remains unclear. We quantitatively studied the proportion of directionally selective cells, direction selectivity and the functional organization of the striate cortical cells in the monkey and compared those with the cat. The results show that the direction selectivity and directional organization of striate cortical cells in the monkey are significantly weaker than those in the cat, suggesting that the species difference between the two kinds of animal is related to their different anatomic pathways.

Keywords: direction selectivity, visual cortex, functional organization, monkey, cat.

Orientation and direction selectivities are two important properties of the visual cortical cells in mammals. Direction selectivity is usually tightly related to orientation selectivity. In fact, many cortical cells, especially in the primate, only respond to moving stimulus at a preferred direction and orientation[1,2]. In areas 17 and 18 of the cat, cells that prefer similar directions of motion tend to cluster, and the clusters are separated by sudden discontinuities of 180 degrees. This pattern is seen with electrode penetrations within column as well as within layers[3,4]. The optical imaging showed that cells within the same orientation patch in cat area 18 were often divided into two subpatches with opposite directions[5]. In the area MT (middle temporal) of the monkey, physiological and optical imaging studies have showed that directionally selective cells are organized into columns which are often separated by columns with opposite direction preferences[6,7]. Our previous results showed that relay cells in the cat dorsal lateral geniculate nucleus (dLGN) tended to cluster together according to preferred direction[8]. However, the functional organization of directionally selective cells in Vl of the monkey remains unclear. The purpose of this study is to evaluate the degree of direction selectivity and functional organization of Vl cells in the monkey quantitatively, and compare these with the same properties in the cat. The results show that direction selectivity and its neuronal organization in V1 in the monkey are

weaker than in the cat, reflecting a species-related difference.

1 Materials and methods

1.1 Surgical preparation

Animals (6 monkeys and 5 cats) were prepared for electrophysiological recording as described previously[9]. They were sedated with ketamine, and intravenous and tracheal cannulae were inserted. Animals were placed in a stereotaxic apparatus and an acrylic chamber secured with dental cement was positioned over area 17 or V1. Animals were artificially ventilated continuously with a mixture of nitrous oxide (75%) and oxygen (25%) containing halothane (1%). All pressure points and incisions were infiltrated with a long-acting anesthetic (1% Lidocaine HCl). A mixture of d-tubocurarine (0. 4 mg/kg/h) and gallamine triethiodide (7 mg/kg/h) was continuously infused intravenously to induce and maintain paralysis. Body temperature was maintained at 38℃. The electrocardiogram and electroencephalogram were monitored. Depth of anesthesia was assessed with monitoring EEG. Expired CO_2 was monitored and maintained at approximately 4%. The histology and the electrode track reconstruction were as same as previously reported[9].

1.2 Receptive field mapping procedure

Visual stimuli were generated on a Tektronix 608 display driven by a Picasso (Innisfree, USA) image synthesizer controlled with a computer. The cell's receptive field of the dominant eye was plotted on a tangential screen with a handle target. Overlapping at each visual receptive field position, the center of the display screen was located at 171 cm from the monkey's eye and 57 cm from the cat's eye, respectively. The spatial frequency tuning, receptive field size, response tonicity, response to moving and flashing bars and spots, and sluggishness of response were studied, and the cells were determined to be simple, complex, and special complex cells using the general criteria[2].

1.3 Determination of orientation and direction sensitivity

The sinusoidal drifting gratings were employed to study the orientation and direction sensitivities at a variety of spatial frequencies. Fifteen presentations of each grating (temporal frequency of 2—4 Hz) at each of 24—36 orientations were used to compile the tuning curves for the cells. Orientation and direction orientation preferences and sensitivities were calculated for each cell using the statistical methods of Batschelet[10]. Briefly, the values of each cell's responses to the stimulus gratings presented at different directions were stored in the computer as a series of vectors. The length and polar angle of each vector represent the magnitude of fundamental Fourier component of the cell's post-stimuli time histogram and the stimulus grating moving direction to which the cell responds, respectively. The vectors were added and divided by the sum of the absolute values of the vectors. The angle of the resultant vector gives the preferred orientation or direction of the cell. The length of the resultant vector, termed orientation or direction bias, provides a quantitative measure of the orientation or direction sensitivity of the cell. Because the

periodicity of orientation is 180°, the angles of the direction of the stimulus grating are multiplied by a factor of two when calculating orientation preferences. However, direction is cyclic over 360°, therefore the actual direction of the stimulus gratings is used to calculate the direction preferences of the cell. Orientation and direction biases range from 0 to 1, with 0 being completely insensitive to orientation or direction and l responding to only one orientation or only one direction. For many cells, multiple tuning curves were compiled at a variety of spatial frequencies. According to the circular statistics, an orientation or direction bias of 0.1 or greater is significant and shows that the circular distribution of the cells' responses to moving stimuli is nonrandom (Rayleigh test, $p<0.005$) [10].

1.4 Data analysis

Paired and unpaired *t* tests were used to compare distributions of biases. Also, several statistical techniques designed specifically to analyze distributions of angles (circular statistics) were used to help us interpret our data[10]. The Rayleigh test determines if a distribution of angles differs significantly from a random distribution; that is, whether the angles are clustered about some value. If a certain angle is expected, then the *V* test is a more powerful test of whether a distribution of angles is peaked about the expected value. Watson's U^2 test compares two distributions of angles in order to determine whether the two samples differ significantly.

2 Results

2.1 Direction selectivity

The visual responses to grating stimuli of 312 neurons in the striate cortex (V1) of 6 monkeys were recorded extracellularly and studied quantitatively. Using the identical techniques, we also studied 129 cells in the area 17 of 5 cats. As previously reported, we found that the orientation and direction selectivity of most striate cortical cells were spatial frequency-dependent. In general but not always, orientation selectivity was the clearest when testing with gratings of relatively high spatial frequency, and direction selectivity was the clearest when relatively low spatial frequency was used[11,12]. In our experiments, each cell was tested with several gratings of various spatial frequencies and only the best resulting direction bias was used to construct the histogram.

Fig. l illustrates the distribution histograms of direction biases, which were calculated according to circular statistics. In the monkey 84. 6% of the cells studied (264 cells in 312) exhibited statistically significant direction selectivity due to their direction biases of 0.1 or greater (Rayleigh test, $p<0.005$) as shown in fig. 1(a). This proportion in the monkey is less than that in the cat (95. 3%, 123 cells in 129) as shown in fig. 1(b). Furthermore, the proportion of cells having strong direction biases higher than 0. 2 in the monkey (39%) is much lower than that in the cat (78%). Moreover, the mean direction bias of the monkey cortical cells (bias = 0.19) is significantly less than that of the cat (bias = 0.32) (*t* test, $p<0.005$).

2.2 Topography of preferred direction

We found a topographic relationship between the monkey cortical cells' direction preference and their receptive field's position relative to the retinal fovea. In fig. 2(a), the cell number is represented as a function of the difference between each cell's preferred direction and its polar angle of the receptive field. A cell preferring a direction pointing from the center of its receptive field to the fovea (or the area centralis) exhibits a difference of 0 degree. The opposite preferred direction leaving the fovea toward the cell's receptive field center means 180 degree difference; and 90 degrees indicate that the cell's preferred direction is orthogonal to the line joining the fovea and its receptive field center. Fig. 2(a) shows a smooth peak, but not random distribution

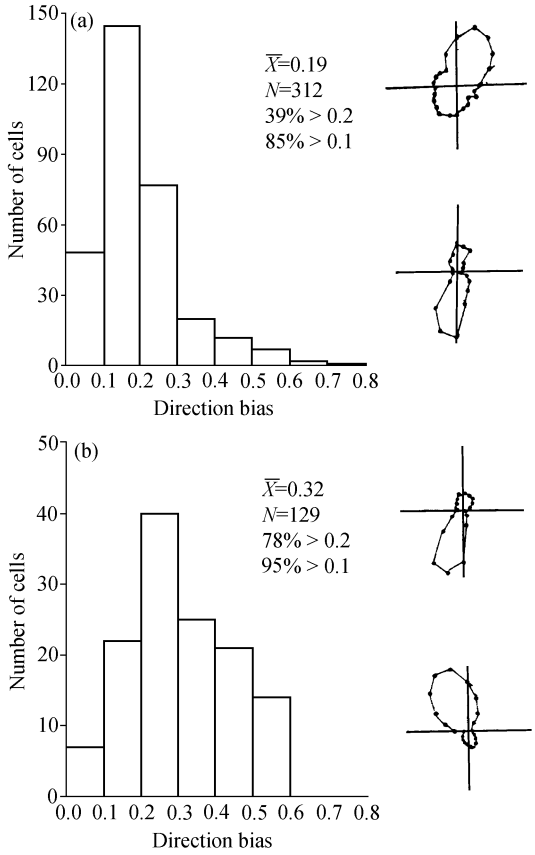

Fig. 1. Histograms illustrating the distribution of the direction biases of cortical cells in V1 of the monkey (a) and in area 17 of the cat (b). *X*, The mean direction biases; *N*, total number of cells studied. The proportions of cells (%) having direction biases greater than 0.1 and 0.2 are shown, respectively. Polar plots of direction tuning curves of four cells are also shown on the right, from top to bottom: (a) a simple cell (direction bias 0.19) and a complex cell (direction bias 0.36); (b) a simple cell (direction bias 0.38) and a complex cell (direction bias 0.59). Each point in the polar plots represents the cell's response to a moving stimulus direction along that polar angle.

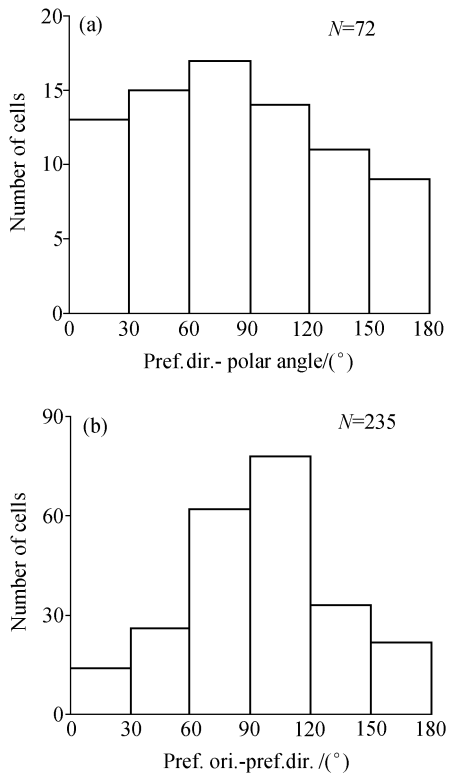

Fig. 2. (a) Topographic relation between the monkey V1 cell's preference direction and the retinal position of its receptive field center shown with the distribution of angle difference, which is an angle between cells' preferred direction and polar angle of receptive fields. Note that more cells tended to respond best to motion direction orthogonal to the line joining the fovea and their receptive fields. (b) Distribution of angle difference between the preferred orientations and preferred directions of the V1 cells in the monkey. Note that most cells' preferred directions were approximately orthogonal to their preferred orientations.

(Rayleigh test, $p<0.001$) at about 90 degrees (V test, $p<0.0005$), showing that more cells tended to respond best to tangentially moving gratings on the retina.

Fig. 2(b) illustrates the difference between the preferred orientations and preferred directions of the V1 cells in our sample of monkeys that exhibited both orientation and direction selectivity. A difference of 0 or 180 degrees indicates that the cell's preferred orientation and preferred direction were parallel, whereas a difference of 90 degrees indicates that the cell's preferred direction was orthogonal to its orientation. We found that most cortical cells in the monkey preferred to respond best to gratings with moving directions orthogonal to their preferred orientations (Rayleigh test, $p<0.000\,01$, mean difference = 92 degrees). However, it should be noted that some cortical cells preferred other directions, even approximately parallel directions. Similar orthogonal relationship between the orientation and direction preference has been reported in cells in the dLGN and retina of the cat[11,12].

2.3 Clustering of cells with similar preferred direction

In the primary visual cortex, cells having similar preferred orientations are organized into columns from the pial surface to the white matter, and the preferred orientations change gradually when the microelectrode penetrates along a track roughly parallel to the pial surface[1,2]. Because we have observed that the preferred directions of most cells in Vl area in the monkey were orthogonal to their preferred orientations, it could be theoretically predicted that neighboring directionally sensitive cells in each orientation column should mostly tend to exhibit either similar or opposite preferred directions. Fig. 3(b) and (c) show the examples obtained from long penetrations through V1 of the monkey which were approximately parallel (b) and orthogonal (c) to the pial surface. The plots show the preferred directions of the successively encountered cells along the electrode penetrations. The neighboring cells tend to exhibit similar preferred directions

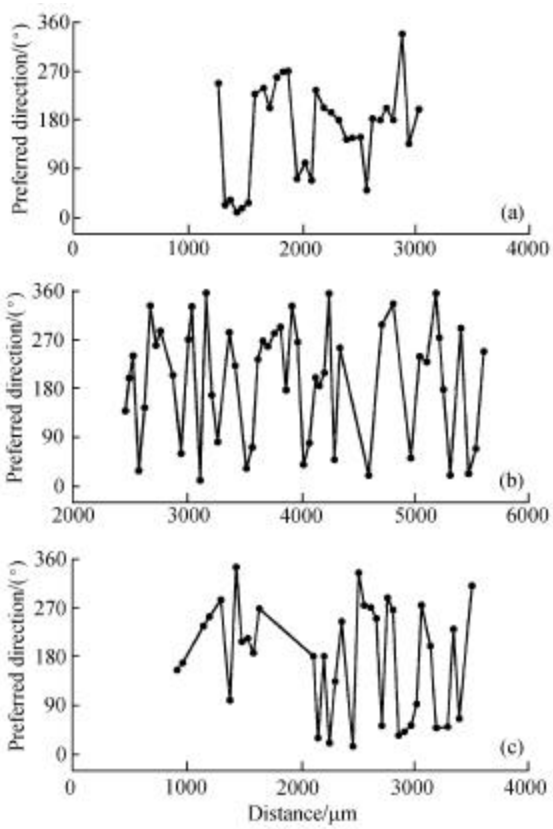

Fig. 3. Plots illustrating the change in cortical cells' preferred direction with the distance along microelectrode penetrations. (a) A penetration vertically through area 17 of a cat; (b) a penetration horizontally through V1 of a monkey; (c) a penetration vertically through V1 of a monkey. Note that in general, preferred directions of successively recorded cells were similar, but often interspersed with many reversals of approximately 180 degrees in between. This phenomenon was more significant in monkeys than in cats.

although discontinuations, an approximately 180 degree reversal, were often found either in the vertical or in the tangential penetrations. For comparison, the preferred orientations of successively recorded cortical cells in the cat's area 17 along the track are shown in fig. 3(a). It is clear that the discontinuities of preferred direction in neighboring cells of the visual cortex of the monkey appear to be more frequent than the cat. However, we did find neither columnar nor laminar organization of directionality within the primary visual cortex in all electrode penetrations both in the monkey and in the cat.

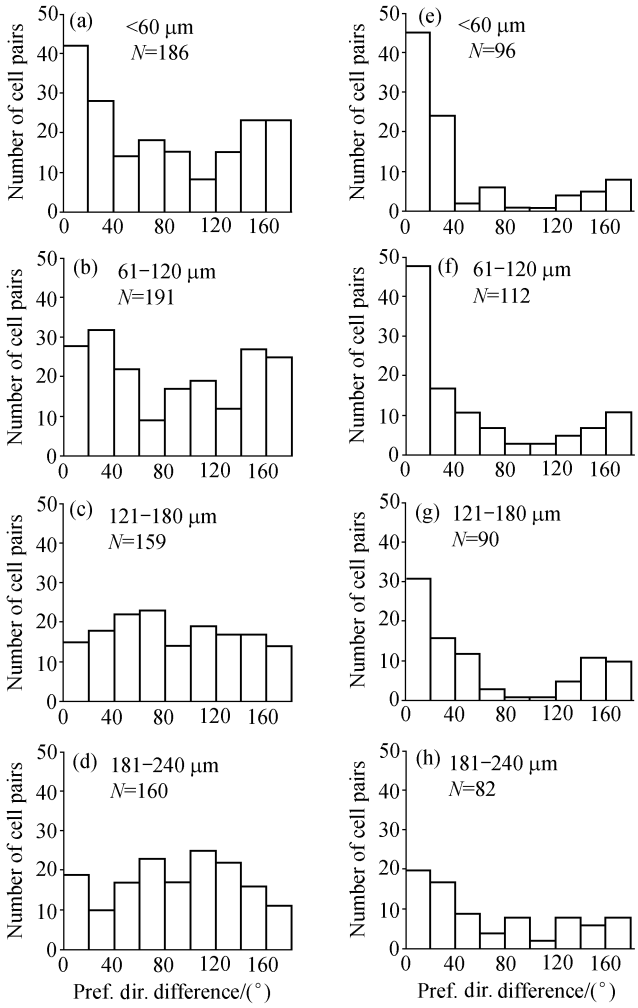

Fig. 4. Distributions of preferred direction difference of cell pairs separated by various intervals in visual cortical area V1 of the monkey ((a)—(d)) and area 17 of the cat ((e)—(h)). The interval distances between cell pairs studied: (a) and (e), less than 60 micrometers; (b) and (f) 61—120 micrometers; (c) and (g) 121—180 micrometers; (d) and (h) 181—240 micrometers, respectively. Note that the proportion of cell pairs with similar preferred directions in the striate cortex of the cat is much greater than that of the monkey, whereas the proportion of cell pairs with opposite preferred directions in the cats less than in the monkey.

2.4 Quantitative comparison

To quantify and compare the tendency of organized direction selectivity, the distributions of preferred direction difference of cell pairs separated by various spatial intervals in the striate cortex are shown in fig. 4 for monkeys ((a)—(d)) and cats ((e)—(h)). Qualitatively, there was some similarity between the monkey and the cat. For both animals, the cell pairs within the range of 60 micrometers showed two peaks in distribution of their preferred direction differences (fig. 4(a) and (e)). However, quantitative analysis indicates that the distributions of preferred direction difference of cell pairs in the cat were significantly different from that of the monkey (Watson's U^2 test, $p<0.01$). The main peaks are located from 0 to 40 degrees and show that 38% of neighboring cell pairs in the monkey (fig. 4(a), peaked at 0 degree, Rayleigh test, $p<0.001$; V test, $p<0.005$) and 71% of cell pairs in the cat (fig. 4(e), peaked at 0 degree, Rayleigh test, $p<0.001$; V test, $p<$

0.000 5) tend to have similar preferred directions. The second peaks are located from 140 degrees to 180 degrees and indicate that 25% of neighboring cells pairs in the monkeys (fig. 4(a), peaked at 180 degree, Rayleigh test, $p<0.001$; V test, $p<0.005$) and only l3. 5% of cell pairs in the cat (fig. 4(e), peaked at l80 degree, Rayleigh test, $p<0.001$; V test, $p<0.0005$) tend to have opposite preferred directions. This main peak is much more evident in the cat than in the monkey (Watson's U^2 test, $p<0.000\ 5$). This difference remains when comparing the preferred direction difference distributions for cell pairs with larger intervals between cells. In the cat, 58% of the cells separated by 61—120 micrometers exhibit their preferred direction differences within 40 degrees (fig. 4(f)), whereas only 31% of the cells in the monkey exhibit their preferred direction differences less than 40 degrees (fig. 4(b)). The difference is very significant (Watson's U^2 test, $p<0.001$). When increasing the spatial interval between cells to more than 120 micrometers, the distribution becomes flat for the monkey (fig. 4(c) and (d)), whereas the main peak in the distribution still remains clear for the cat (fig. 4(g) and (h)).

3 Discussion

Using the identical experimental and data analysis techniques in this quantitative study, we have demonstrated that the proportion of the directionally selective cells and the degree of direction selectivity of the striate cortex in the monkey are significantly less than those of area 17 in the cat, even though the large majority of cortical cells in the monkey are selective to motion direction of drifting gratings. The present results also show that in V1 of the monkey, cortical cells having similar preferred directions cluster and are often interspersed with cells having opposite preferred directions. The direction selective organization of the monkey is qualitatively similar to, but quantitatively much weaker than that of the cat. Perhaps, this is why there are few papers on quantitative analysis of direction selectivity and its functional organization of the monkey's V1 cells, while many papers on cat area 17 in scientific literature. Many previous studies have reported on the organization of direction selectivity in areas 17 and 18[3,4] and PMLS of the cat[13,14], MT and the area in the posterior bank of the superior temporal sulcus in the monkey[6,7,15], as well as area 17 in the ferret[16]. However, to our best knowledge, we are unaware of quantitative study of functional organization of directionally selective cells in area V1 of monkeys and its comparison with cats.

In such a quantitative comparison of direction selectivity of striate cortical cells between monkeys and cats, it is important to use comparably strong stimuli to reveal cells' direction selectivity and appropriate statistics to assess directional preferences. In this study, grating stimuli were employed since they are stronger stimuli than moving bars for revealing orientation and direction selectivity in cortical cells[9,17]. The circular statistics was used as a precise method to access direction and orientation sensitivity for different species of animals in quantitative studies, as employed previously for retinal ganglion cells[12], relay cells in the lateral geniculate

nucleus[11,18], and visual cortical cells[9]. In addition, we only compared the cell's direction preferences and biases at the spatial frequency to which the cell exhibited the best direction-selective responses. This makes the data of the two species animals more comparable.

The finding that the preferred direction of monkey cortical cells is orthogonal to either the cell's polar angle of receptive field or preferred orientation should logically lead to a conclusion that most cortical cells prefer to respond to gratings of radial orientation on the retina. In fact, it is true that the radial distribution of preferred orientation was also reported in cells of the visual cortex[19], dLGN[18] and retina[12].

As previously reported[9], no significant difference in functional organization of direction selectivity among cells in different layers was found in our experiments although more directionally selective cells were found in layer 4B[20,21].

The proportion of direction selective cells, the selectivity and organization are quantitatively stronger in cats than in monkeys. Perhaps this is related to the apparently more elaborate organization of extrastriate visual areas in the monkey. That is, the monkey may have more extrastriate areas, such as MT, uniquely devoted to motion than does the cat. Thus, more specific organization for directional properties is processed earlier (i. e. striate cortex) in the cat than in the monkey. This may facilitate the cat with shorter latency to find moving animals as food. Perhaps the weaker directional organization in area V1 of the monkey may play an organizing role in establishing the more orderly directional organization in MT[6,7,22].

The differences we see between monkeys and cats with regard to directional preferences in area V1 or 17 may relate to other species difference in organization of the visual pathways. For instance, nearly all of the geniculo-cortical pathways in monkeys terminate in area V1, and V1 then distributes this information to various extrastriate areas. In the cat, there are extensive geniculate projections to extrastriate areas, as well as striate cortex[4,5]. Because V1 in the monkey plays such a key role in distributing visual information to other cortical areas[20,21], it may have evolved a less specific organization for direction selectivity. More detailed directional organization may have appeared in the cat, because not as much of its striate cortex circuitry is devoted to relaying visual information to other areas.

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