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Microstructure of Neuronal Connections between the Visual Areas of the Cortex at Different Hierarchical Levels

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The direct neuronal connections of the cortical visual areas at the lower level of the hierarchy with the areas of subsequent levels were studied by microiontophoretic administration of horseradish peroxidase into individual vertical columns in areas 19 and 21a and the distribution of retrograde labeled neurons in areas 17 and 18 was analyzed in cats. Columns in areas 19 and 21a, as compared with the eye-dominant columns of area 18, receive additional cortical inputs from the ipsilateral transition zone 17/18, which indicates a more complex structure of neuronal connections. The locations of input neurons from the transition zones 17/18 of different hemispheres were found to be mirror symmetrical, such that neurons in areas 19 and 21a columns can be tuned to loci located in the central sagittal plane of three-dimensional space. Inputs from areas 17 and 18 of the ipsilateral hemisphere, located outside the transition zone 17/18, were also identified, and these, in combination with inputs from both transition zones, can enable neurons in areas 19 and 21a columns to encode more complex stereo-features of objects.

Keywords: cat, neuronal connections, areas 17 and 18, areas 19 and 21a, transition zone 17/18, symmetry.

Introduction. Since the 1950s, microelectrode studies have described the functional properties of individual neurons in many visual areas of the cortex [Hubel and Wiesel, 2005]. Formation of the selective properties of neurons is largely due to the structure of their connections. Direct – not mediated by interneurons – connections within and between cortical areas form the basic framework of neuronal networks in the brain. Differences in the layered organization of such connections between different areas of the cortex led to the idea that they have a hierarchical organization in primates and cats [Felleman and Van Essen, 1991; Scanel et al., 1995; Hubel and Wiesel, 2005]. The lower level of the hierarchy includes visual areas receiving direct afferentation from the dorsal lateral geniculate nucleus (LGNd), which in primates is cortical area V1 and in cats areas 17 and 18. These locations discriminate simple features of the visual environment. Neurons in the vertical columns of these areas have similarities in the positions of the centers of their receptive fields on the retina, inputs from the eyes, and preference for the orientation or direction of movement of stimuli. To date, direct intra- and interhemispheric connections of neurons in the ocular dominance columns have been studied in areas 17 and 18 in cats. These structural and functional units of the cortex have been shown to receive afferentation from neurons in elongated zones in these areas, oriented in area (A)17 along the projection of the horizontal meridian of the visual field, and in A18 along the projection of the vertical meridian [Alekseenko et al., 2005], which is consistent with the anisotropy of the magnification factor in these areas [Tusa et al., 1981]. Direct interhemispheric connections in these areas have also been found to be eye-specific; they combine neurons innervated from a single eye, from the zone of nasotemporal overlap represented in the cortex of both hemispheres [Olavarría, 2001; Alekseenko et al., 2002].

Areas 19 and 21a of the cat cortex are components of subsequent hierarchical levels; they do not have inputs from the LGNd and receive afferentation from areas 17 and 18, as well as from the complex of subcortical nuclei [Dreher, 1986]. The aim of the present work was to study the structure of the direct intra- and interhemispheric neuronal con-

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nections of the columns of areas 19 and 21a with areas 17 and 18. The data have been published in part elsewhere [Alekseenko and Shkorbatova, 2021].

Methods. Experiments were performed using seven adult cats weighing 2.5–3.5 kg, each of which received injections of the retrograde transported marker of neuronal connections, horseradish peroxidase (HRP), into a single vertical column in A19 or A21a of the cortex. The experimental protocol and the method of introducing marker into A19 and A21a were as described in [Alekseenko et al., 2002] to ensure that the data could be compared with previous results on tracing neuronal connections with horseradish peroxidase in columns in areas 17 and 18. All experiments were carried out in compliance with the requirements of the Directives of the Council of the European Parliament on the protection of animals used for experimental and other scientific purposes (2010/63EU) and were approved by the Care and Use of Laboratory Animals Monitoring Commission at the Pavlov Institute of Physiology, Russian Academy of Sciences (Resolution No. 01/18 of January 18, 2021).

Animals were anesthetized with a mixture of Zoletil 100 (zolazepam + tiletamine, Virbac, France) at a dose of 5 mg/kg and 2% xylazine (Interchemie Werken "De Adelaar" BV, Netherlands) at a dose of 2 mg/kg. Craniotomy, dissection of the dura mater, and administration of the connections marker were performed in animals in a stereotaxic apparatus. HRP (8% solution in phosphate buffer, pH 6.2; Boehringer, Germany) was introduced into columns of areas 19 and 21a by microiontophoresis at a constant current of +0.5 μA. A glass microelectrode (internal tip diameter 10–20 μm) filled with marker was oriented perpendicular to the cortical surface and inserted to a depth of 1500–1800 μm using a stepper motor and then raised by 200–400 μm; iontophoresis was performed for 20 min. The reference electrode was attached over the other cerebral hemisphere. After terminating the current, the microelectrode was raised to a depth of 600–800 μm and left for 10 min. After 36–48 hours, cats were subjected to deep Nembutal anesthesia (100 mg/kg) and underwent transcardiac perfusional fixation of the brain (0.9% NaCl saline solution, followed by fixative containing 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4), followed by 10% sucrose solution in phosphate buffer). Extracted brains were immersed in 30% sucrose solution in phosphate buffer. The next day, a continuous series of frontal brain sections of thickness 50 μm were cut on a cryomicrotome. HRP was detected by the Mesulam method and sections were counterstained with safranin. HRP injection zones were intensely staining areas on brain sections in the form of strips 200–300 μm in diameter, passing through all six layers of the cortex. Within this zone, the marker is taken up through the synaptic boutons of axons and undergoes retrograde transport to the bodies of the neurons giving rise to the axons.

Labeled cells (LC) were detected on brain sections in areas 17 and 18 of both hemispheres using an NU-2E light microscope (Jenaval, Netherlands). Sections containing LC were digitized using a Wild Heerbrugg Type 308700 binocular attachment connected via a video camera (Baumer Optronic, Germany) to a computer. The outlines of frontal sections and LC locations were marked in Adobe Photoshop. The resulting slice images were saved in JPEG format. The main purpose of this analysis was to reconstruct the positions of LC zones on the flattened surface of the cortex. ImageJ was used to project the location of each LC, at ×20 magnification, in the section onto the surface of the cortex (or the border of layer VI with the white matter when the LC was in the depth of the sulcus), after which the distance from the LC to the injected column or its projection on the slice was measured. The series of successive brain sections was used to construct two-dimensional point diagrams of the distribution of LC on the tangential surface of the cortex in Microsoft Excel. The locations of callosal LC were determined by mirroring the corresponding sections of the two hemispheres.

The stereotaxic coordinates of the columns studied in areas 19 and 21a along the caudorostral axis of the brain [Horsley-Clark levels] were in the range from P3 to P6.5. The visual coordinates of the columns (azimuth and elevation), as well as the afferent LC in areas 17 and 18, were determined from their positions on brain sections using detailed projection maps of cortical areas [Tusa et al., 1981]. An additional indicator of differences in the degree of remoteness of the columns from the projection of the central (zero) vertical meridian (CVM) was the assessment of distances between afferent LC zones in areas 17 and 18. Given the retinotopic ordering of these areas and their mirror-symmetrical positioning relative to the projection of the CVM, as well as the known spatial concordance of the neuronal connections between these areas [Salin et al., 1992], LC zones in areas 17 and 18 were located closer to each other in columns in A19 and A21a, which are closer to the projection of the CVM, than in columns which are more distant.

Results. Horseradish peroxidase was injected into five cortical columns in A19 and two columns in A21a; three columns were located in the left hemisphere and four in the right. These columns were located on the suprasylvian gyrus of the brain in the zone of visual field projection from –3° to +15° along the vertical meridian and from 2° to 15° along the horizontal meridian.

The vast majority of the LC afferenting these columns were located in the superficial (supragranular) layers of areas 17 and 18, and only occasional LC (1–3) were located in the infragranular layers.

Examples of locations of LC in areas 17 and 18, projected onto the flattened cortical surface, are shown for three injected columns in Fig. 1. Two were in the left hemisphere and one in the right (Fig. 1, *a*), so the data for the latter are shown in the plot in mirror image. In addition, the locations of interhemispheric (callosal) LC are shown in mirror image on the LC distribution plot of the hemisphere in which the injected column was located.

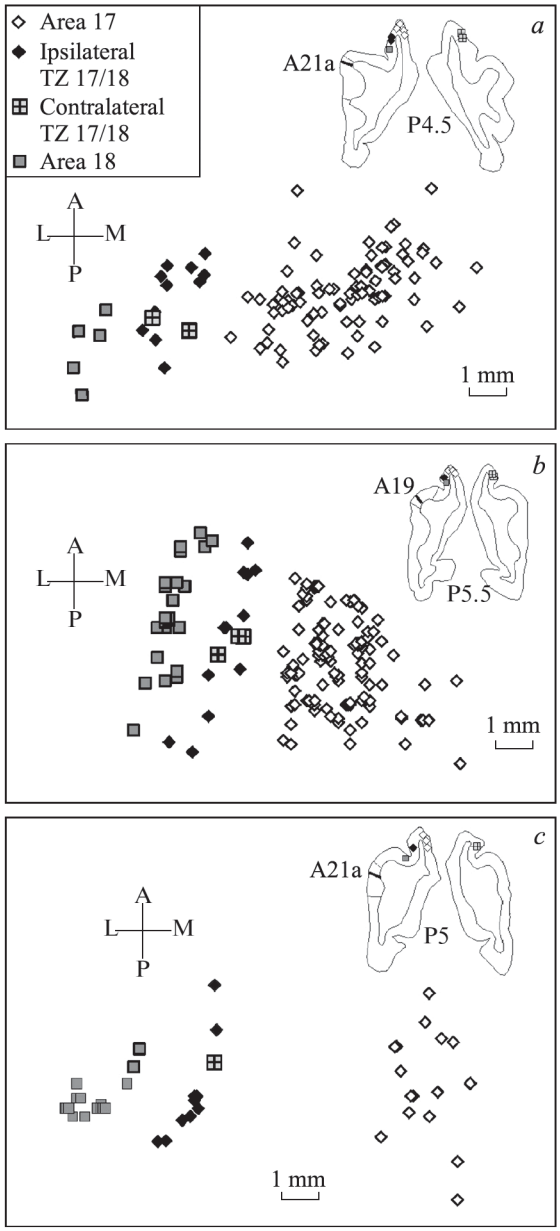

Fig. 1. Distribution of labeled cells on the flattened surface of the cortex in areas 17 and 18 of the cat brain after the application of HRP to neuron columns in area 19 (*b*) and area 21a (*a*, *c*). Column coordinates in the visual field (azimuth/ elevation): *a*) 2/–1°; *b*) 3/+5°; *c*) 7/+5°. TZ – transition zone 17/18. Top: brain sections with labeled cells in areas 17 and 18, along with the injected column and its Horsley–Clark coordinates (P). The location of the callosal inputs to the column is superimposed on the distribution of the intrahemispheric inputs in a mirror image.

Grouping of LC in areas 17 and 18 was observed. The presence of regions in these areas in which there were no LC facilitated the task of assigning LC groups to A17 and A18. This also took account of the gradual shift in the medial direction of the border between these areas during the transition from caudal to rostral frontal sections of the brain (P–A), i.e., towards the projection of the lower part of the visual field [Tusa et al., 1981].

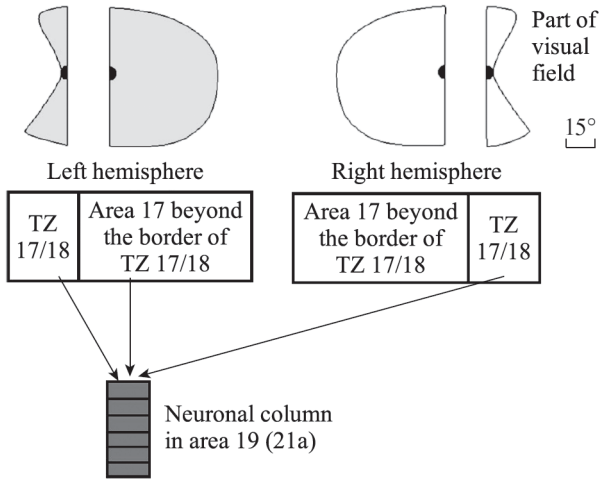

Fig. 2. Schematic showing the inputs identified from area 17 to columns in area 19 (21a). At top: parts of the visual field represented in the transition zone 17/18 and beyond its border.

Columns having callosal inputs were found to produce LC located in the transition zones between areas 17 and 18 (TZ 17/18) in both hemispheres, as well as in subzones of areas 17 and 18 located on both sides of TZ 17/18 in the hemisphere ipsilateral to the injected column. Fig. 2 schematically shows the afferent inputs from A17 for columns in A19 or A21a.

Intrahemispheric inputs of A19 and A21a columns. All seven injected columns received afferentation from regions in A17(white rhomboids in Fig. 1) and A18(gray squares), which are located on either side of TZ 17/18. These subzones of input neurons were located in the projection of the contralateral visual field in both cortical areas (Fig. 2). The distance between the subzones depended on the distance (azimuth) of the column from the projection of the CVM. For example, the distance between the LC subzones in A17 and in A18 in columns that are located 2–3° away from the projection of the CVM (Fig. 1, *a*, *b*) was less than that of the column 7° away (Fig. 1, *c*). Use of projection maps [Tusa et al., 1981] showed an approximate coincidence of the azimuth of the column with the azimuth of the center of the LC zone in A17. In A18, the LC subzone was elongated and oriented parallel to the boundary between A17 and A18, which runs inside TZ 17/18; its orientation corresponds to the orientation of the zone of intrinsic connections of columns in this area [Toporova et al., 2001]. However, the LC subzone in A17, in comparison with the zones of intrinsic connections of this area, as well as the zones of connections of A18 columns with A17, elongated along the projection of the horizontal meridian of the visual field [Alekseenko et al., 2002], is expanded mainly along the projection of the vertical meridian (A–P), indicating summation of the inputs.

Another area of intrahemispheric inputs to columns in areas 19 and 21a was located in TZ 17/18 (Fig. 1, black rhomboids). As shown earlier for A17 [Payne, 1990], TZ 17/18 includes part of the ipsilateral visual field projection,

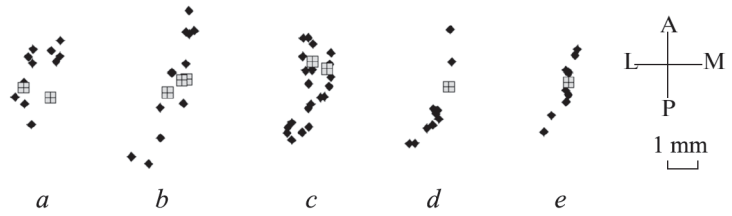

Fig. 3. Locations of labeled cells in the transition zones 17/18 of both hemispheres in cats after application of HRP to neuronal columns in areas 19 and 21a. Column coordinates (azimuth/ elevation): *a*) 2/–1°; *b*) 3/+5°; *c*) 3/–1°, *d*) 7/+5°; *e*) 10/–3°. Black rhomboids show cells in the hemisphere ipsilateral to the column; squares with crosses show callosal cells plotted on the chart as mirror image.

which expands upward and downward to 20–25° from 3.6° at the level of the zero horizontal meridian projection of the visual field (Fig. 2, upper part). Later, studies of interhemispheric connections in areas 17 and 18 by local marker application [Olavarría 2001; Alekseenko et al., 2002; Alekseenko et al., 2005] revealed the presence of two subzones in TZ 17/18, belonging to A17 and A18. In addition, spatiotemporal differences between these subzones were detected using a method for optical visualization of activity [Rochefort et al., 2007]. Consequently, the CVM is represented at both borders of TZ 17/18, beyond which are the projections of the contralateral visual hemifield in the mirror-symmetrically located areas 17 and 18 of the hemisphere.

One or two rows of LC were found in the TZ 17/18 of the hemisphere ipsilateral to columns in A19 and A21a; the orientation of these was parallel to the LC subzone in A18 outside TZ 17/18 (Fig. 1). The position of the LC in the rows gradually shifted to the medial (M) side on the cerebral gyrus as it moved away from the projection of the area centralis to the lower part of the visual field, towards A (Fig. 1, also Fig. 3, black rhomboids), which is due to the deviation of the projection of the vertical meridian of the visual field from the mid (sagittal) plane of the brain (P–A).

The data obtained here indicate that LC in individual rows have the same azimuth values for their positions in the projection of the visual field at different elevations (heights). The distribution of LC in one or two rows in TZ 17/18 depended on the coordinates of the column of areas 19 and 21a relative to the CVM. Two rows of LC (Fig. 3, *a*, *b*, *c*) were observed for columns in areas 19 and 21a, located near the projection of the CVM (azimuth 2–3° in the projection of the contralateral visual hemifield). Rows of input LC for these columns were located at a distance of less than 1 mm, i.e., they were located in TZ 17/18 near its borders, in the projections of the part of the ipsilateral visual field related to A17 and A18. For more distant columns in areas 19 and 21a (azimuth 7–10°), LC were arranged in a single row (Fig. 3, *d*, *e*), indicating their position at the center of TZ 17/18, i.e., where the border parts of the ipsilateral visual hemifield are represented in areas 17 and 18 and the border between these areas is located. Thus, data on the disposition in TZ 17/18 of LC innervating columns in areas 19 and 21a confirm the idea that this zone is divided into two subzones belonging to different areas (17 and 18).

Interhemispheric inputs of A19 and A21a columns. LC were found in TZ 17/18 in the hemisphere opposite to the injected columns in areas 19 and 21a but were not detected in regions of areas 17 and 18 located outside this zone. The positions of these callosal cells are marked by squares with crosses in Fig. 1, as well as in Fig. 3, where only the LC in transition zones 17/18 of both hemispheres are shown for the three A19 columns (Fig. 3. *b*, *c*, *e*) and for two A21a columns (Fig. 3, *a*, *c*).

On mirroring the frontal sections of different hemispheres, it was found that the locations of callosal LC in TZ 17/18 coincided with the positions of LC from one or two rows of TZ 17/18 on the corresponding sections of the opposite hemisphere. This indicates that the spatial coordinates of the positions of these inputs from the TZ 17/18 of different hemispheres are the same both in azimuth and in elevation. These symmetrically located inputs from opposite visual hemifields are located in the projection of the same horizontal meridian.

Despite significant differences in the numbers of inputs from the transition zones 17/18 of different hemispheres, the patterns of LC localization showed similar dependence on the distance of the injected column from the projection of the CVM. In columns closer to the projection of the CVM, inputs from two rows of LC in the TZ 17/18 of the ipsilateral hemisphere were located near both of its borders; inputs from two portions of callosal LC were also detected, these also being located near the borders of the TZ 17/18 (Fig. 3, a, *b*, *c*). For columns more distant from the projection of the CVM, inputs were found from one row of LC in the TZ 17/18 of the ipsilateral hemisphere, as well as in one TZ 17/18 portion of the opposite hemisphere (Fig. 3 *c*, *e*).

We note that callosal inputs from TZ 17/18 were not found in one of the most distant injected columns in A19, which was located in the projection of the visual field at a distance of more than 15° from the CVM; it also lacked intrahemispheric inputs from TZ 17/18. For technical reasons, no data were obtained on interhemispheric connections of one further column of A19 with coordinates 7/+10°, which had one row of LC in the TZ 17/18 of the hemisphere ipsilateral to the column.

Thus, the present study found that columns of neurons in A19 and A21a, located in the projection area of the visual field from 2° to 10° along the horizontal meridian and from

–3° to +5° along the vertical meridian, received afferentation from neurons in three separate subzones in A17, as well as in A18. Input neurons were located in the transition zones 17/18 of both hemispheres, as well as in regions of areas 17 and 18 located outside the transition zone 17/18 of the hemisphere ipsilateral to the column.

Discussion. A19 and A21a in cats occupy an intermediate position in the hierarchy of cortical areas between areas A17, A18 nd areas at higher levels, which are divided into channels for transmitting "what?" and where?" information. Data from electrophysiological and behavioral studies have shown that A19 and A21a belong to the channel analyzing the shape and texture of images, i.e., to the "what?" channel [Dreher, 1986; Khayat et al., 2000; Harutiunian-Kozak et al., 2008; Villeneuve et al., 2009; Kim et al., 2019]. Our studies, on a relatively small experimental group, found no fundamental difference between A19 and A21a in terms of the structure of their afferent inputs from areas 17 and 18. This is probably due to common patterns in the innervation of different cortical areas from the two retinas, while the known differences in the properties of neurons in these areas are due to local connections between neurons receiving inputs from the retina of a single eye.

The studies reported here showed that columns in areas 19 and 21a, located in the projection of the visual field up to 10 ° from the CVM, receive direct inputs from three area 17 subzones and three area 18 subzones. Two subzones are located in the hemisphere ipsilateral to the column (in TZ 17/18 and the part beyond its border) and one in the TZ 17/18 of the opposite hemisphere (Fig. 1). These data provide evidence of an increase in the complexity of the structure of neuronal connections in the transition from areas of the lower hierarchical level (17 and 18) to areas of subsequent levels (19 and 21a). The locations of input neurons in the upper layers of areas 17 and 18 for the columns of areas 19 and 21a confirm that these areas belong to different levels in the hierarchy of cortical areas [Felleman and Van Essen, 1991; Scanel et al., 1995]. At the same time, in cats, areas 17 and 18 belong to the same hierarchical level, in contrast to areas V1 and V2 in primates [Felleman and Van Essen, 1991], as they receive inputs from the LGNd and, besides, connections between areas 17 and 18, and the intrinsic connections in these areas are provided by neurons not restricted to those in the upper layers [Houzel et al., 1994; Toporova et al., 2001; Alekseenko et al. 2005; Innocenti, 2017].

Comparison of the results obtained in our studies with data from investigations of inputs from A17 to columns in A18 and inputs from A18 to columns in A17, which were also located in the area of interhemispheric connections [Alekseenko et al., 2005], makes it clear that columns in areas 19 and 21a receive additional inputs from the TZ 17/18 of the ipsilateral hemisphere. These inputs come from neurons located in the projection of the opposite visual hemifield, as compared with the inputs from neurons in the other two subzones (Fig. 2). Due to the fact that the inputs from the additional subzone in TZ 17/18 are arranged in one or two rows located along the vertical in projection of the visual field, they can provide neurons in columns in areas 19 and 21a with sensitivity to the orientational component of images [Dreher, 1986; Wimborne and Henry, 1992; Harutiunian-Kozak et al., 2008].

The columns of areas 19 and 21a, like the ocular dominance columns in areas 17 and 18, have few callosal inputs from areas 17 and 18 [Alekseenko et al., 2005]. There were significantly fewer such callosal inputs from TZ 17/18 in columns 19 and 21a than from the TZ 17/18 in the ipsilateral hemisphere, but their distances from the projection of the CVM in different hemispheres and, accordingly, in different visual hemifields, were identical. The positions of these input neurons within the transition zones 17/18 correlated with the distances of the columns in areas 19 and 21a from the projection of the CVM. These TZ 17/18 neurons of both hemispheres, equidistant from the CVM projection, are activated when symmetrically located images or their fragments appear in the nasal hemifields of the different eyes. This is due to the fact that the source of inputs to the TZ 17/18 is the nasotemporal overlap zone on the retina, which in cats is located in its temporal half. As the TZ 17/18 of each hemisphere is dominated by monocular neurons running from the contralateral eye [Berman et al., 1982], neurons in columns in areas 19 and 21a receiving inputs from neurons in both TZ 17/18 acquire binocular properties and tuning to loci in three-dimensional space. The convergence of these input neurons, equidistant from the projection of the CVM and located in the projection of the same horizontal meridian of the visual field, provides the neurons in columns with tuning to the spatial loci in the central sagittal plane in front of the fixation point [Barlow et al., 1967]. Information from such binocular neurons can be transmitted to the vergent eye movement centers and used in implementation of the psychophysical process of fusing the two images of objects.

Important information regarding the organization of interhemispheric connections is provided by our finding that columns of areas 19 and 21a have no callosal inputs from the regions of areas 17 and 18 located beyond the TZ 17/18. In areas 17 and 18, the neurons in these areas have direct interhemispheric connections with neurons in the TZ 17/18 of the opposite hemisphere [Olavarría, 2001; Alekseenko et al., 2002]. However, columns in areas 19 and 21a receive inputs from two other interhemispherically connected areas in areas 17 and 18: these are neurons in the TZ 17/18 of the hemisphere opposite to the column and neurons located in the ipsilateral hemisphere beyond the border of the TZ 17/18 (Fig. 1). Consequently, neurons in some but not all parts of the area of interhemispheric connections in areas 17 and 18 have outputs to columns in areas 19 and 21a. Based on available morphological data from tracing the trajectories of axons and their collaterals in the cortex [Houzel et al., 1994; Innocenti, 2017; Rockland, 2018], as well as the data obtained in this work, we can suggest that the axon collaterals of neurons in the three subzones identified in ar-

eas 17 and 18, which have interhemispheric connections in these areas, provide inputs to columns in areas 19 and 21a.

Binocular neurons account for 34–42% of neurons in A19 and 70% in A21a[Duysens et al., 1982; Guillemot et al., 1993]. Most of the neurons providing inputs to these areas from areas 17 and 18 are also binocular [Barlow et al., 1967; Hubel and Wiesel, 2005]; they encode absolute disparity, i.e., they are tuned to the positions of loci in three-dimensional space relative to the fixation point [Cumming and Parker, 1999] and their responses are modulated by callosal inputs [Wunderle et al., 2015; Ramachandra et al., 2020]. Recent studies of area V1 in macaques [Parker et al., 2016] identified functional modules encoding the range of disparities preferred by binocular neurons. Module size (3–4 mm) is greater than the diameter of ocular dominance columns and approximately corresponds to the length of internal neuronal connections in this area. A similar isotropic modular structure may also exist in cats in areas 17 and 18, with similarities to the organization of orientational modules [Ivanov et al., 2006]. We suggest that the module consisting of disparity selective neurons may be a subzone of neurons located in area 17, outside the TZ 17/18, which innervate separate columns in areas 19 and 21a. The convergence of inputs from the binocular neurons of this module and the neurons of both TZ 17/18 may provide the neurons of the columns in areas 19 and 21a with tuning to the relative disparity between different visual features [Thomas et al., 2002], as well as encoding more complex stereo-features of objects, as described in primates: the positions and slopes of stereoscopic planes, the boundaries between them, and surface configurations [Bakin et al., 2000; Li et al., 2017; Lu et al., 2018; Li and Shigemasu, 2019; Pettine et al., 2019; Parker, 2020; Pasupathy et al., 2020].

Conclusions. The structure of the afferent inputs from areas 17 and 18 to neuronal columns in areas 19 and 21a, as compared with the inputs of the ocular dominance columns of area 18 (17) from area 17 (18) found in the cat, may support identification of the more complex stereo features of objects.

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