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ORIGINAL ARTICLE

Structure and function of neural circuit related to gloss perception in the macaque inferior temporal cortex: a case report

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Abstract

The inferior temporal (IT) cortex of the macaque monkey plays a pivotal role in the visual recognition of objects. In the IT cortex, a feature-selective network formed by connecting subregions specialized for common visual features seems to be a basic strategy for processing biologically important visual features. Gloss perception plays an important role in the judgment of materials and conditions of objects and is a biologically significant visual function. In the present study, we attempted to determine whether a neural circuit specialized for processing information related to gloss perception exists in the IT cortex in one monkey. We injected retrograde tracer into a gloss-selective subregion in the IT cortex where gloss-selective neurons were clustered in the neural recording experiment, and anatomically examined its neural connections. We observed that retrogradely labeled neurons were densely accumulated in multiple locations in the posterior and anterior IT cortices. Based on the results of this case study, we will discuss the possibility that, together with the injection site, the sites with a dense cluster of labeled neurons form feature-selective neural circuits for the processing of gloss information in the IT cortex.

Keywords Gloss perception · Neural circuit · Neuroanatomy · Macaque · IT cortex

Functional architecture of the inferior temporal cortex

It is generally agreed that the inferior temporal (IT) cortex of the macaque monkey plays a pivotal role in the visual recognition of objects (Ungerleider and Mishkin 1982; Logothetis and Sheinberg 1996; Tanaka 1996; Rolls 2000; DiCarlo et al. 2012). Many studies have examined how visual information of objects is represented in the IT cortex. At a small scale, neurons that are sensitive to similar visual features align in a direction perpendicular to the IT cortical surface (Fujita et al. 1992). At a larger scale, however, there are many unclear points about how columns expressing visual features of objects are gathered to represent objects. Certain classes of biologically important categories of visual information, such as face, body parts, location, depth, and color, evoke strong activities in restricted regions in the IT cortex that are common across individual subjects and species (macaques and humans) (Zeki et al. 1991; Kanwisher et al. 1997; Epstein and Kanwisher 1998; Downing et al. 2001; Tsao et al. 2003, 2008; Pinsk et al. 2005; Conway et al. 2007; Bell et al. 2008; Harada et al. 2009; Verhoef et al. 2015). Other visual features may be represented in a distributed fashion across wide regions in the IT cortex, but a recent report suggests that the IT cortex is topographically organized such that a more general class of objects may also be represented in a spatially regular fashion that is common across individual subjects (Rajalingham and DiCarlo 2019).

In the IT cortex, neural circuits connecting multiple patches involved in the representation of the same class of visual attributes have been reported for face and color. Multiple face patches were identified as regions strongly responsive to face images, and neural recordings targeting face patches have shown that neurons selectively responsive to face images are densely clustered in these regions (Tsao et al. 2006). Experiments combining electrical microstimulation and functional magnetic resonance imaging (fMRI) have suggested that different face patches are mutually connected (Moeller et al. 2008). Multiple face patches in the

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IT cortex are thought to form a functional circuit that is specialized for processing face information. Different face patches are thought to contribute to different aspects of face processing (Freiwald and Tsao 2010). With regard to color, electrophysiological experiments and fMRI experiments have identified multiple color patches in the IT cortex with varying properties (Harada et al. 2009; Lafer-Sousa and Conway 2013; Namima et al. 2014; Chang et al. 2017). An experiment combining electrophysiological and neuroanatomical techniques has shown that the color patches in the AIT and PIT cortex are mutually connected (Banno et al. 2011). Feature-selective networks formed by mutually connected subregions specialized for common visual features, such as face and color, can be considered as one of the basic ways to process biologically important visual features in the IT cortex.

Gloss perception and the IT cortex

Gloss perception plays an important role in the judgment of materials and conditions of objects and is a biologically significant visual function (Motoyoshi et al. 2007; Fleming, 2014; Fleming et al. 2015; Komatsu and Goda 2018). Psychophysical studies suggest that gloss perception involves complicated interactions between the processing of various visual features, including those related to 3D shape and illumination. Neural mechanisms of gloss perception have been studied in humans and monkeys in recent years, and neural responses that are possibly related to gloss perception have been observed in various areas of the visual cortex (Okazawa et al. 2012; Wada et al. 2014). In particular, neural responses are consistently detected in the ventral higher visual cortex, and it is likely that this cortical area plays an important role in gloss perception. Neurons selectively responsive to the glossiness of objects are observed in the central IT (CIT) cortex of macaque monkeys (Nishio et al. 2012, 2014). These neurons are clustered in the posterior bank of the superior temporal sulcus (STS) and are observed in a similar position across individual animals (Baba et al. 2021). These gloss-selective neurons accurately represent visual parameters that are important for gloss perception (Nishio el al. 2014), and they are thought to be strongly related to gloss perception. Neurons that are strongly responsive to glossy objects are also observed in the posterior part of the STS in marmosets (Miyakawa et al. 2017). Interestingly, the same group observed that neurons sensitive to glossy objects were also recorded in area MTc, from which this part of the STS receives inputs. As noted in the previous section, there exist multiple subregions in the IT cortex where neurons selective for specific features such as face and color are clustered, and there is some evidence that these subregions are anatomically connected to form functionally specialized neural circuits within the IT cortex. A feature-selective network formed by connecting subregions specialized for common visual features is presumably a basic strategy to process biologically important visual features in the IT cortex. In the present study, we attempted to study the possibility that such functionally specialized circuits may exist in the IT cortex for gloss information processing, which is also a biologically important visual feature. For this purpose, we injected a retrograde tracer into the site in the CIT cortex where gloss-selective neurons were clustered in the neural recording experiment in a macaque monkey, and we anatomically examined the neural connection. Retrogradely labeled neurons were widely distributed in the IT cortex, but these neurons were densely accumulated in multiple locations more posteriorly and anteriorly to the injected site. We will discuss the possibility that sites with dense clusters of labeled neurons together with the injection site form a neural circuit specialized for the processing of gloss information in the IT cortex.

Anatomical connections of the gloss selective region in CIT

Procedures of neuroanatomical experiment

Gloss-selective neurons were concentrated in a restricted region (gloss-selective region) extending 2–3 mm in the lower bank of the STS in the CIT cortex (Nishio et al. 2012; Baba et al. 2021). In the present study, we examined the anatomical connection of the gloss-selective region in one of the monkeys (AQ) used in the previous recording experiment (Nishio et al. 2012, 2014). The procedure of the recording experiment and testing the gloss selectivity of neurons is reported in these papers. Recording sites and the localization of gloss-selective neurons in the left hemisphere of monkey AQ are shown in Fig. 1A. After the recording experiments were completed, we injected a retrograde tracer into the gloss-selective regions identified in the left and right hemispheres of the monkey AQ. We targeted the coordinates where the gloss-selective neurons were clustered in each hemisphere ('injection site' in Fig. 1A).

On the day of tracer injection, we first fixed a stainless-steel guide tube (outer diameter of 800 μm) in the hole of the plastic grid attached to the recording chamber. A tungsten microelectrode (FHC) was vertically inserted into the brain and neuronal activity was recorded. After confirming the depth of the target cortical area, the monkey's head was held with a stereotaxic apparatus under general anesthesia. A micro-syringe (KH PT-2, 25-G needle; Hamilton, Reno, NV) was inserted vertically into the target cortical area through the guide tube. A micro-syringe was placed in reference to the depth of the target cortex determined by

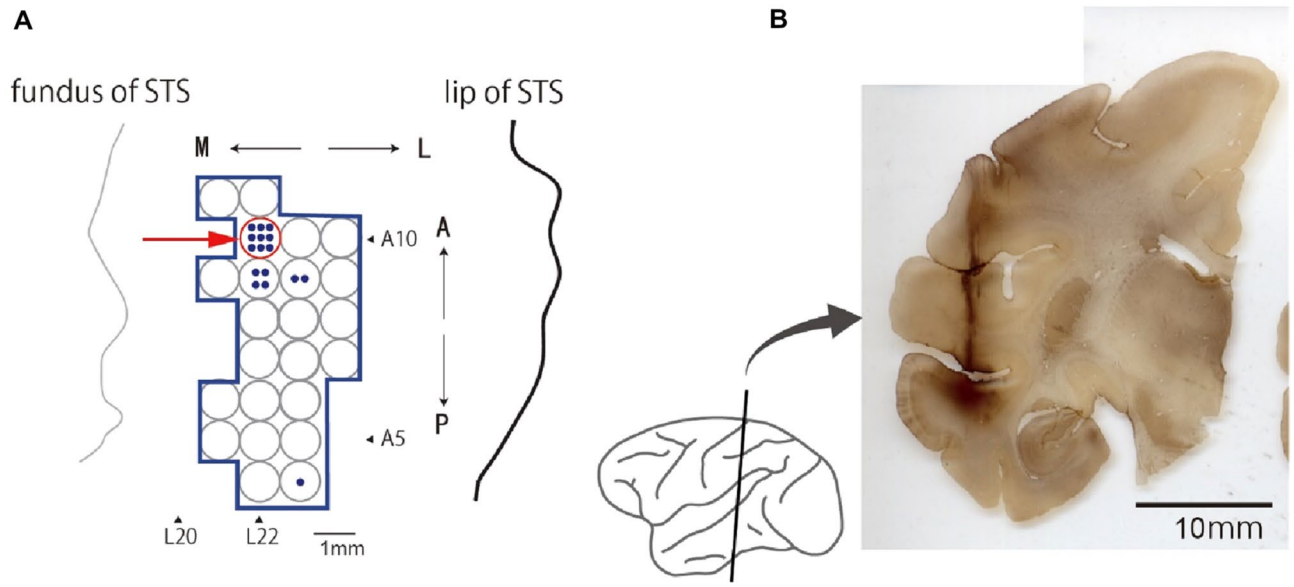

Fig. 1 Location of the gloss-selective region in the superior temporal sulcus and injection site of the retrograde tracer. **A** Top view of the areas of electrode penetration in the lower bank of the superior temporal sulcus (STS) in the left hemisphere of monkey AQ (same as in Nishio et al. 2012) with stereotaxic coordinates. Within the blue contour, open circles indicate the positions of the grid holes for electrode penetration, and the blue dots represent gloss-selective neurons recorded at that locus. They were concentrated in a restricted region in the anterior part of the mapped area (gloss-selective region). The red circle indicates the coordinates where the tracer injection was made in this hemisphere (injection site). **B** Schematic drawing of the coronal section of this hemisphere (left) and a photograph (right) of the brain section at the level of tracer injection

the neural recordings. We first slowly injected 1 µL of retrograde tracer (CTB Alexa 555; Thermo Fisher Scientific, Waltham, MA) into the target cortical area in the left hemisphere using an automatic injection device (0.1 µL/min). The syringe was positioned at the same depth for 3 min to avoid tracers going up along the needle track, and then the micro-syringe was drawn up slowly. After the injection to the left hemisphere was completed, the same procedure was repeated to inject a retrograde tracer (CTB Alexa 488) in the right hemisphere. One week after tracer injection, the monkeys were perfused with 4% paraformaldehyde in 0.1 M phosphate buffer (PB) under deep anesthesia, and the brains were removed, trimmed, and placed in 30% sucrose in PB solution at 4 °C for a few days until they sank. After the brains sank, the brain blocks were coronally sectioned on a freezing microtome at a thickness of 50 µm. The sections were divided into seven series. The first series was stained for Nissl by thionin, the second for myelin, the third was reacted with mouse anti-Cy3/Cy5(1:2000) (SIGMA), and the fourth was reacted with CTB Alexa 488 (Thermo Fisher Scientific), respectively, by immunoperoxidase using 3–3'-diaminobenzidine (DAB) and H_2O_2. The remaining samples were discarded. We used an anti-Cy3/Cy5 antibody to visualize Alexa 555 in this experiment because the molecular structures of these fluorescent dyes are similar to each other. We have confirmed that this Cy3/Cy5 antibody can detect Alexa 555, but does not cross-react with Alexa 488. Histological procedures have been described in detail in our previous paper (Banno et al. 2011). All procedures for animal care and experimentation were performed in accordance with the U.S. National Institutes of Health (NIH) Guide for the Care and Use of Laboratory Animals (1996) and were approved by our institutional animal experimentation committee.

Results of the neuroanatomical experiment

Retrogradely labeled cells were visualized using DAB and peroxidase. The injection site and labeled cells were clearly identified in the left hemisphere, but they were not detected in the right hemisphere. This is likely due to an error in the placement of the micro-syringe such that the tip of the syringe was within the STS and the tracer was not injected into the gray/white matter of the cortex. In the following section, only the results of the injection in the left hemisphere are described. Figure 1A shows the distribution of the gloss-selective neurons in the posterior bank of the STS in this hemisphere (left hemisphere of monkey AQ) and the coordinates where the tracer was injected (red arrow). Figure 1B shows the brain slice in which the track of the microsyringe can be clearly seen. A dense halo due to the spread of the tracer is mainly observed in

the posterior bank of the STS and the underlying white matter, but not in the inferior temporal gyrus. We determined the extent of injection site as the area in which the tracers filled the entire neuropil. In areas surrounding the injection site, the tracers labeled only cell somas, but not glial cells. Accordingly, we can interpret that the retrogradely labeled neurons described in the following section had axons that terminate in the posterior bank of the STS where the gloss-selective neurons were recorded.

Retrogradely labeled neurons were observed over a wide area in the IT cortex. We mapped the positions of the labeled neurons in each slice under microscopic observation using a camera lucida, and the mapping results were quantified using a custom MATLAB program (MathWorks, Natick, MA) that computes the density of the labeled cells for each 250 μm × 250 μm block on the slice. Figure 2 illustrates an example of a slice with retrogradely labeled neurons (A) and the result of the quantification of the distribution of the labeled neurons (B) in which the density of the labeled cells is indicated by the shading of the red color. We also drew the boundary between the gray and white matter as well as the contour of the middle of the gray matter around layer 4 (layer 4 contour) based on the Nissl-stained sections. After mapping the labeled cells across the entire temporal lobe, we reconstructed 3D images of the brain and plotted the density of the labeled cells on the cortical surface by projecting the position of the labeled cells onto the layer 4 contour using CARET software (Fig. 3A). We also flattened the cortical surface to show the density of the labeled cells in both the IT gyrus and within the STS (Fig. 3B).

Labeled neurons were densely observed in the STS region surrounding the injection site, but were also observed in a wide region in the IT gyrus and in the posterior bank of the STS both anterior and posterior to the injection site. Within these cortical regions, the labeled neurons were not uniformly distributed. Discontinuity of the labeled cells can be clearly seen in the representative sections shown in Fig. 2C (b, c). Notably, we found that labeled neurons were densely clustered in three regions. One of these regions was located in the IT gyrus dorsal to the anterior end of the posterior middle temporal sulcus (PMTS) (marked as site I in Fig. 3B). Another region with dense clustering of labeled cells was located at the lip of the STS in the PIT cortex (marked as site II in Fig. 3B). We also observed dense clustering of labeled cells in the region dorsal and posterior to the anterior middle temporal sulcus (AMTS) (marked as site III in Fig. 3B) in the AIT cortex. This third region is more widespread than the former two regions (sites I and II) in the PIT cortex, and the boundary is difficult to define. Contours of the regions with clustering of labeled neurons determined by a quantitative criterion (density > 75 cells/block, cluster area > 4mm^2) is indicated as blue contours in Fig. 3B: one contour is located in a region surrounding the injection site, one corresponds to site I, the other to site II, and two contours can be seen for site III. Numbers and positions

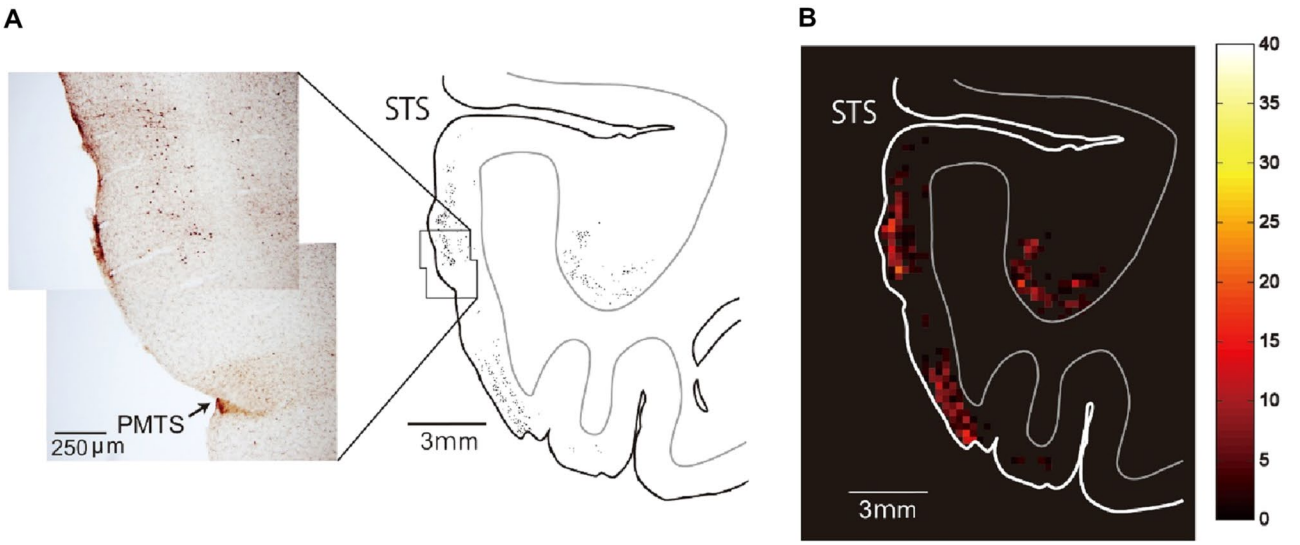

Fig. 2 Distribution of the retrogradely labeled neurons in an example section in the posterior inferior temporal cortex. **A** A micrograph (left) of a part of a section in the posterior inferior temporal (PIT) cortex around the anterior end of the posterior middle temporal sulcus. Clusters of labeled cells are viewed as dark brown dots in the upper half of the micrograph. Contour drawing (right) of the inferior temporal (IT) cortex with a box showing the position of the micrograph shown in the left panel. **B** Distribution of the labeled cells shown as the density of labeled cells computed in every 0.25 mm × 0.25 mm grid. The density is color-coded with a brighter color indicating higher density. The cluster of labeled neurons in the IT gyrus below the lip of the superior temporal sulcus corresponds to site I in Fig. 3. The color scale indicates the number of retrogradely labeled neurons in every 0.25 mm × 0.25 mm grid

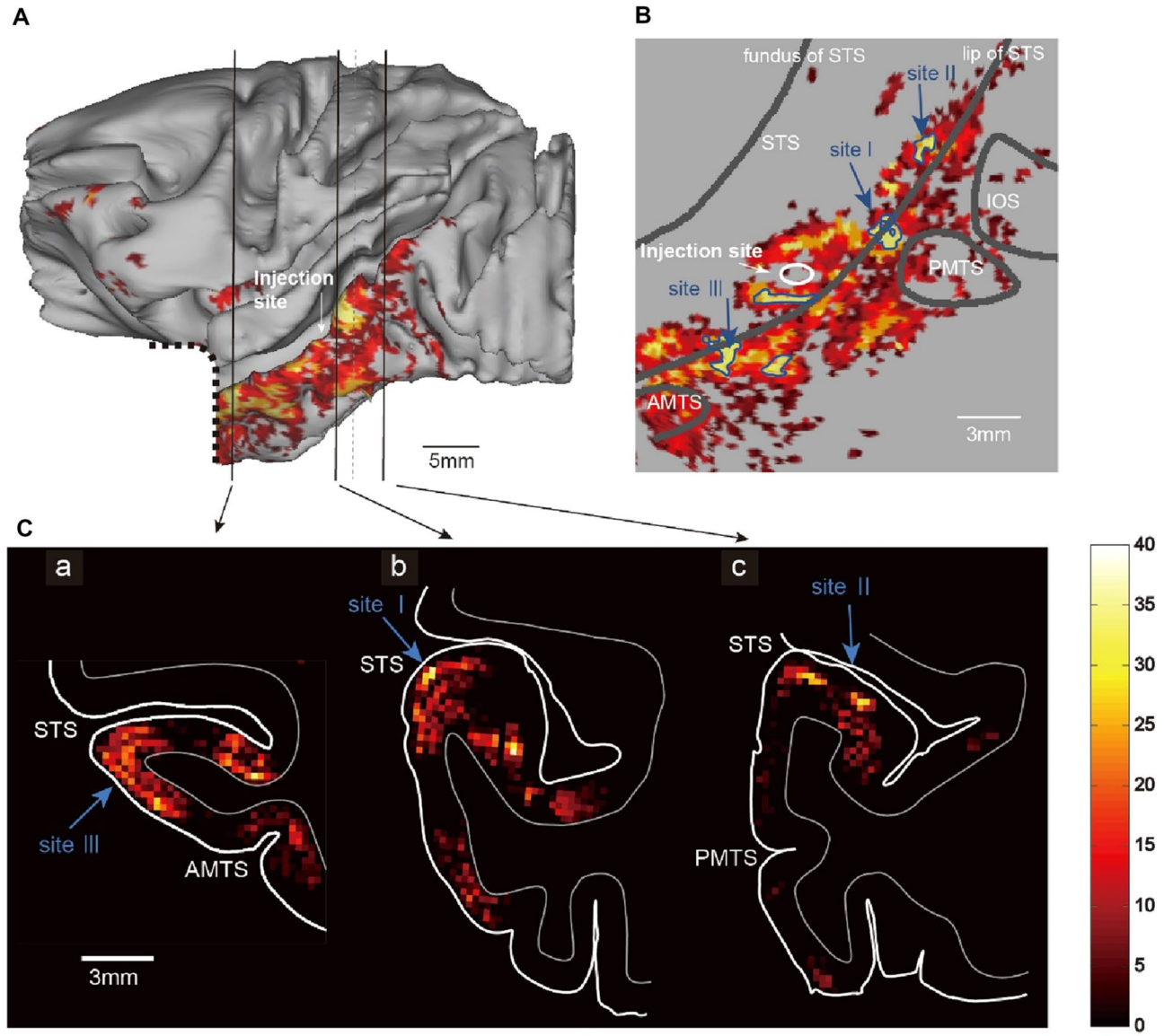

Fig. 3 Distribution of the retrogradely labeled neurons. **A** Location of the labeled cells plotted on the surface of the 3D reconstructed left hemisphere of the monkey AQ. The dotted line at the bottom left corner of the brain corresponds to the temporal pole where reconstruction failed because of the detachment of the brain sections. The scale indicates the number of retrogradely labeled neurons in every 0.5 mm × 0.5 mm grid on the cortical surface. For clarity, regions where the number > = 5 are shown. **B** Distribution of labeled neurons in the inferior temporal (IT) cortex shown in the sulcus-unfolded representation of the IT cortex. Positions of three locations where labeled neurons were densely clustered (sites I, II, and III) are indicated by blue arrows. Blue contours indicate the boundary of the quantitively defined clusters (see text for more detail). Sulci: AMTS: anterior middle temporal sulcus, IOS: inferior occipital sulcus, PMTS: posterior middle temporal sulcus, STS: superior temporal sulcus. **C** Distribution of labeled cells in three coronal sections of the IT cortex. The anterior–posterior level of each section is indicated as a vertical line in A. The positions of three clusters (sites I–III) are indicated by blue arrows. The other formats are the same as those in Fig. 2B

of the contour depend on the criteria to some extent but are largely stable. These results suggest that, first, neurons in the gloss-selective region in the posterior bank of the STS in the CIT cortex are connected with and receive inputs from wide regions in the IT cortex. Second, these neurons have especially strong connections with three regions within the IT cortex: one region is located more anteriorly and the other two regions are located more posteriorly. Presumably, these regions with strong connections form neural networks that are involved in the processing of information related to gloss perception. In the following section, we will evaluate evidence that supports the presence of neural networks for gloss processing in the IT cortex.

Structure and function of neural network for gloss processing

An fMRI study in macaques examining the distribution of the responses evoked by glossy stimuli support the idea that gloss information is not uniformly distributed in the IT cortex (Okazawa et al. 2012). In this fMRI study, brain activity was measured while the monkeys performed a visual fixation task, and the responses to a rotating glossy object were compared with those to a rotating matte object. Figure 4 shows the results obtained for one hemisphere, where strong responses to the glossy object image are observed in a wide region in the visual cortical areas along the ventral visual pathway. Interestingly, strong responses to the glossy object were observed at three sites. One of these sites (Fig. 4, red arrow) was located in the posterior bank of the STS in the CIT cortex, and this location seems to correspond well with the site where gloss-selective neurons were recorded and tracer was injected in the present study (Fig. 3A, B, white arrow). One of the remaining two regions was located in the posterior bank of the STS in the PIT cortex around the lip of the STS (Fig. 4, green arrow), where strong responses to the glossy object were consistently observed. Judging from the relative position of the STS and the inferior occipital sulcus (IOS), the location seems to coincide with one of the clusters of retrogradely labeled neurons (site II) in the present study (Fig. 3B and Cc). The other region where strong responses to the glossy object were observed was in the area around the anterior end of the PMTS (Fig. 4, blue arrow). Anatomical experiments also showed a region with a dense cluster of labeled neurons (site I) around the anterior end of the PMTS (Fig. 3B and Cb), and this region may correspond to the region with a strong response to the glossy object in the fMRI experiment.

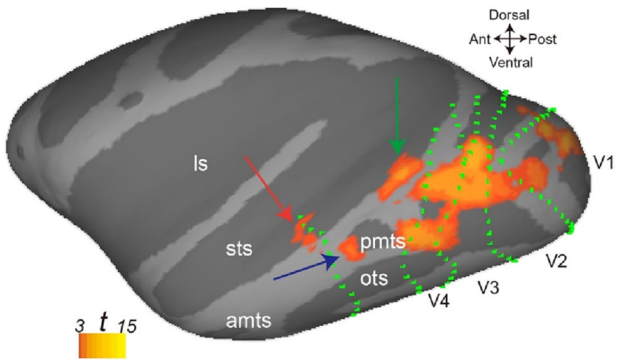

Fig. 4 Results of functional magnetic resonance imaging showing regions responsive to glossy object image. The color scale indicates the t-score of visual responses. The green dashed lines indicate the area boundaries of V1, V2, V3, V4, posterior inferior temporal (PIT) cortex, and central inferior temporal (CIT) cortex. Arrows indicate where responses to glossy object images were observed in the inferior temporal (IT) cortex. Sulci: ls, lateral sulcus; sts, superior temporal sulcus; amts, anterior middle temporal sulcus; pmts, posterior middle temporal sulcus; ots, occipitotemporal sulcus. Reproduced with permission from Fig. 2A of Okazawa et al. 2012)

In the region more anterior to the injection site, although clustering of labeled neurons was observed (site III), fMRI experiments did not reveal corresponding activity in the AIT cortex. We must be cautious when interpreting this negative result because, in this region of the cortex, the lack of activity may be due to the effect of susceptibility artifacts that make the sensitivity of blood-oxygen-level-dependent signals low in this part of the cortex (e.g., Fig. 3 of Harada et al. 2009). An alternative possibility is that more anterior regions play a role in processing gloss information that is different from more posterior regions. In the following section, we will consider the possibility that regions anatomically connected with the injection site are related to gloss perception and their potential roles in gloss perception.

In the PIT cortex, we observed two regions connected to the injection site (sites I and II). One of these regions (site I) was located near the anterior end of the PMTS. Neural recordings around this region have found visual responses that are selective to luminance contrast or shading, and neurons sensitive to such visual features form columns in this region of the cortex (Fujita et al. 1992). We have also observed clustering of neurons that are selective for the direction and magnitude of the luminance gradient in this region of the cortex (Komatsu et al. annual meeting of the Japan Neuroscience Society, 2007). Many of these neurons preferred stimuli with a large luminance gradient. Another region with the clustering of labelled cells (site II) was located at the lip of STS in the PIT. An fMRI study using macaque monkeys that compared responses between images of 3D objects defined by texture and luminance gradients revealed that a small region at the lip of STS in the PIT cortex exhibited stronger responses to stimuli with luminance gradients (Nelissen et al. 2009). Therefore, both sites I and II seem to be related to the processing of luminance gradient information. In addition, an fMRI study has shown that regions including the lip of the STS in the PIT cortex are sensitive to low-spatial-frequency components of visual images (Rajimehr et al. 2011).

Then, how is the information of luminance gradient related to gloss perception? Ferwerda et al. (2001) showed that one of the main axes of the perceptual gloss space corresponds to the contrast of highlight (c), and this parameter roughly corresponds to the difference between the luminance inside and outside of the highlight, which is strongly related to the magnitude of the luminance contrast. On the other hand, the direction of the luminance gradient is related to the orientation of the highlight, and, together with the contour and shading of the object image, this information plays an important role in the occurrence of gloss perception by

interpreting whether the bright spot is a highlight or due to the change in albedo (Blake and Bülthoff 1990; Anderson and Kim 2009). Recently, Sawayama and Nishida (2018) also showed that the direction and rank order of the luminance gradient is related to 3D-shape perception, the magnitude of the luminance gradient is related to gloss perception, and both are related to the estimation of albedo and illumination.

Based on these findings, we speculate that the two clusters of retrogradely labeled neurons observed in the PIT cortex are related to gloss perception in different ways. The region located around the anterior end of the PMTS (site I) possibly represents the information needed to compute the contrast of highlights and sends this information to the gloss-selective region on the posterior bank of the STS in the CIT cortex. Meanwhile, information on the luminance gradient represented in the region around the lip of the STS in the PIT cortex (site II) can be used to compute the 3D shape and albedo of objects as well as their glossiness. It has been shown that neurons in the gloss-selective region in the CIT cortex accurately represent information on albedo, and many neurons also have 3D-shape selectivity (Nishio et al. 2012, 2014). Presumably, information about the luminance gradient from site II is integrated with the information about highlights transmitted from site I in the CIT cortex to give rise to the glossiness of objects with specific shapes and lightness. These considerations lead us to predict that neurons selectively responsive to the glossiness of objects exist in both sites I and II, but the properties of these neurons should be different in various aspects. We expect that neurons that are highly sensitive to the magnitude and orientation of highlights exist at site I, whereas those that are sensitive to shading and lightness as well as to specularity exist in site II. These predictions should be tested in future recording experiments. We should note that, because neurons in the gloss-selective region in the CIT (injection site) have mixed properties, it is likely that neurons selective for gloss are mixed with those not selective for gloss in both sites I and II.

Finally, we will speculate on the possible function of the cluster of labeled neurons in the AIT cortex (site III). As can be seen in the flattened map (Fig. 3B), retrogradely labeled neurons in this region are distributed over a relatively wide area extending several millimeters, and it is possible that this region contains multiple subregions with heterogeneous properties. Because no significant response to glossy object images was observed in this region of the cortex in the fMRI experiment, it is unlikely that this region simply represents the glossiness of objects, although there is a possibility that the fMRI experiment yielded false-negative results due to potential signal dropout. Recently, an experiment to examine the effects of electrical microstimulation on the gloss judgment behavior of monkeys has shown an interesting result that may help interpret the role of the labeled neurons in the AIT cortex (Baba et al. 2021). In this experiment, electrical microstimulation was applied to the area inside and the surrounding area of the gloss-selective region in the CIT cortex, and it was shown that behavioral bias tended to be more frequently observed when microstimulation was applied in the region more anterior to the gloss-selective region. This suggests the presence of a region in the AIT cortex that is strongly related to the performance of gloss judgment behavior. This cortical region is mutually connected with the prefrontal cortex and should be more strongly related to the control and execution of behavioral tasks. Information on the glossiness of an object is related to a number of behaviors such as object discrimination, the judgment of the freshness of food, and control of grasping objects through the judgment of an object's smoothness. Presumably, the AIT cortex contributes to these various behaviors by exchanging signals with the gloss-selective region in the CIT cortex through feed-forward and feedback connections. The relatively wide distribution of labeled neurons in the AIT cortex may be related to the range of behaviors using the gloss information involved together with the fact that feedback projections tend to be more dispersed than feed-forward projections.

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Availability of data and materials Data used in the present study can be made available upon request to the primary contact author.

Code availability Code used in the study can be requested by emailing the primary contact author.

Declarations

Ethical statement All procedures for animal care and experimentation were performed in accordance with the U.S. National Institutes of Health (NIH) Guide for the Care and Use of Laboratory Animals (1996) and were approved by our institutional animal experimentation committee.

Conflict of interests There are no relevant financial or non-financial conflicts of interest among the authors to disclose.

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