PHGY 314
Diana Lin
Dr. Pack

Topic 2: The Inferotemporal Cortex

The inferotemporal cortex (IT cortex) is the highest visual processing area, consisting the anterior inferotemporal cortex (TE) and the posterior inferotemporal cortex (TEO), as illustrated in **Figure 1**. It is the part of the visual cortex located in the temporal lobe. The IT cortex has many anatomical connections with other cortical areas, both receiving and projecting, leading to its critical role in visual perception, cognition and visual memory, shown in **Figure 5** (Gross, 2008).

The IT cortex has many outward projections. It projects to limbic system, specifically to the perirhinal cortex (PR), parahippocampal gyrus (PH) and the amygdala (Gross, 2008), as well as the superior temporal sulcus, illustrated in **Figures 2 and 3** (Ichinohe, 2016). Projections to the amygdala suggest that the amygdala attaches the emotion and motivation to the neutral visual information, such as memories, that the IT cortex processes. The information is then sent back to the IT cortex to be re-processed, where the TEO consciously perceives it, and the TE recognizes and memorizes it meaningfully (Iwai et al., 1990). The information in the IT cortex now has been encoded with motivation and emotion by the amygdala. When the TE of the IT cortex is bilaterally removed in infant monkeys, the projection from TEO to the dorsal part of the lateral basal nucleus of the amygdala extends to occupy the areas in which TE projections usually terminate. Thus, the anatomical connection between the IT cortex and amygdala is maintained, and visual memory ability in monkeys is still preserved (Webster et al., 1991). The IT cortex also projects to the superior colliculus, the lateral frontal cortex, prefrontal cortex, striatum of basal ganglia, and other multimodal brain areas (Tanaka, 2003).

The IT cortex receives input from other cortical areas, such as projections from extrastriate cortex via the corpus callosum or forebrain commissures, as demonstrated in **Figure 4**, as well as input from the inferior pulvinar (of the thalamus in **Figure 5**), where the pulvinar neurons respond to visual stimuli (Gross et al., 1974). The ventral pathway of the visual stream, shown in **Figures 1 and 4**, responsible for processing form and colour, starts from V1 to V2 to V4 and finally to the TEO of the IT cortex (Yamasaki et al, 2012). Many connections are received from V4, suggesting an important role in visual memory and learning (Dubuc, 2002). A deficit in visual learning of pattern discrimination can be produced via inferotemporal lesions.

While the entire IT cortex has these connections, the sub-areas TEO and TE have different connections. TEO has more extensive connections with the parietal brain areas, whereas TE has more with the prefrontal areas. The TEO is connected to the dorsal and ventral intraparietal cortex in the intraparietal sulcus. On the other hand, TE has more connections with the dorsal intraparietal cortex than the ventral intraparietal cortex. In the intraparietal sulcus, projections from the TEO are restricted to areas 8, 45 and 12. Both TEO and TE projections in the prefrontal cortex terminate in areas 8 and 45, but in different layers; TE terminates in all layers whereas TEO only terminates in layers 1, and 5 or 6 (Webster et al., 1994). Furthermore, the IT cortex receives thalamic afferents from the aforementioned pulvinar complex. Both TEO and TE receive input from the lateral pulvinar but TE has stronger connections to the medial pulvinar than to the lateral pulvinar (Baleydier et al., 1992).

IT neurons, like other neurons in the striate cortex, also have different types of stimulus selectivity. IT neurons only respond to visual stimuli, and have receptive fields in the fovea and the center of gaze (Gross, 2008). If an IT neuron receptive field is exposed to an auditory, somatic or olfactory stimuli, there is no firing. IT receptive fields are larger than those of the striate cortex,

and they extend across the midline in both visual fields (Rocha-Miranda et al., 1975). IT neurons are selective for shape and/or colour, but respond better to complex shapes than simple ones.

There is a small percentage of IT neurons (and some neurons in the superior temporal sulcus) selective for faces, specifically emotional expression and eye gaze. Faces and other shapes are encoded by activity patterns across the IT neurons. Face responsive neurons are specifically selective, having the cumulative selectivity from the preceding striate cortex (V1) and extrastriate cortex (V2, V4, etc.) in the ventral visual pathway. For example, in the macaque monkey, there is an area called the middle face patch (MFS), located in the superior temporal sulcus, that responds vigorously and exclusively to faces.

IT neurons that are selective for specific stimuli are still selective regardless of changes in stimulus size, contrast, colour and location, but can be affected by attention or experience; they are tuned to a certain shape with sharp selectivity. In **Figure 6**, on the right side of the arrow is the backbone of the shape to trigger the receptive field, and on the left side the corresponding complex shape. These neurons tend to respond to similar shapes with differences in luminosity, texture direction and coarseness (due to projections from V2), since IT neurons are maximally activated by moderately complex features (Tanaka, 2003). Selectivity in IT neurons can be developed if the subject is trained to finely discriminate similar objects.

Selectivity also exists for two dimensional and three dimensional objects. Detection of two dimensional objects is executed through selectivity for horizontal disparity, while detection of three dimensional objects through gradient of luminosity, that is selectivity for depth of structure. This selectivity also allows for neurons to recognize different perspectives of the same three-dimensional object, as shown in **Figure 7**. Some neurons respond to a linear gradient of depth, but some to combination of gradients and others to concave or convex curvatures. IT neurons can be

sensitive to a variety of parameters that encode many aspects of a stimulus, such as contrast, wavelength, size, shape, orientation or direction of movement, with some neurons sensitive to all parameters, and others only a fraction; however, most neurons are more responsive to a moving stimulus as opposed to a stationary one, with the most vigorous response with receptive fields in the fovea. For example, a minority of IT neurons have extremely specific and complex stimuli, where the receptive fields are triggered by specific instances, such as a hand, shadow of a thermostat, bottle brush, or specific curvature (Gross et al., 1974). Due to the complexity and specificity of certain trigger features, certain selectivities may never be discovered unless thorough experimentation is carried out.

Like the striate cortex (V1), the IT cortex also has topographical clustering of neuronal selectivity. In the IT cortex, selectivity is grouped through columns, demonstrated in **Figure 8.** IT cells cluster in columns perpendicular to the cortical surface, and cells within the same column respond similarly to one another but not identical. Neighbouring columns have non-discrete borders, allowing for continuous mapping; partially overlapping columns allow for the detection of the same object from different angles or from under different lighting (Tanaka, 1996). Selectivities of two cells are different in the sense that different stimuli will evoke maximal response in each cell. These different selectivities work to extract common features but ignore certain differences within a category of objects, allowing for the categorization of objects.

When cells were recorded along penetrations vertical or oblique to the cortical surface, the optimal stimulus and variations for the cell located at the middle of the penetration also evoked strong responses in surrounding cells which span almost the entire cortical thickness, along the vertical penetration; however, along the penetrations oblique to the cortical surface, cells were only responsive to the middle cell optimal stimulus and variations within a short span around it,

averaging 400 μm (Tanaka, 2003). Cells outside this span did not respond to the optimal stimulus and variations; these cells responded strongly to stimuli which were ineffective in evoking the middle cell.

Although cells with similar selectivities are clustered into columns, non-selective columns exist; these columns are activated by any stimuli. Some cells, however, are excited by a stimulus but also inhibited by the simultaneous exposure to a second stimulus. This indicates that the selectivity of a stimulus consists of the features that activates it maximally (the optimal feature), and the features that inhibit activation. While adjacent columns might have the same optimal feature, each column could have different features that inhibit activation. This accounts for the diversity and complexity of stimulus selectivity varying from column to column, supporting the idea that a column is activated by an object's global features rather than its local features, as exhibited in **Figure 6** (Tanaka, 2003). For example, a cell in a column responds to star-like shapes; a cell in the same column responds to star-like shapes with a different size or number of protrusions, shown in **Figure 9**. These horizontal connections of inhibitory neurons between columns can span up to 8mm. These neuron projection terminals are within 1 mm from the origin, arranged in patches in more distant regions; however, longer neurons are excitatory. If a GABA antagonist is injected, stimulus selectivity in IT cells are reduced; when inhibition is blocked for a cell of interest, optimal stimuli for adjacent cells, which normally do not evoke a response, instead evoke an excitatory response in the cell of interest. This demonstrates that these inhibitory horizontal connections help form stimulus selectivity, whereas excitatory horizontal connections link together columns that respond to similar features.

There are multiple categories of objects recognized by these columns, but most common objects are small man-made objects. The selectivity for these objects evolves based on biological

significance, and may vary between species. In humans, face and object selectivity are widely distributed (Haxby et al., 2001). Other objects such as houses, chairs, animals and tools also have consistent topography across individuals, and the topographic clustering consistent within a single subject.

The inferotemporal cortex processes all the information from its anatomical connections from other cortical areas to accumulate the various selectivities of its own neurons, those of which have similar selectivities are clustered in columns. This relay and organization of visual information confers the role of the IT cortex in complex visual object recognition, as the highest visual processing center and the final stage of the ventral visual pathway.

Figures

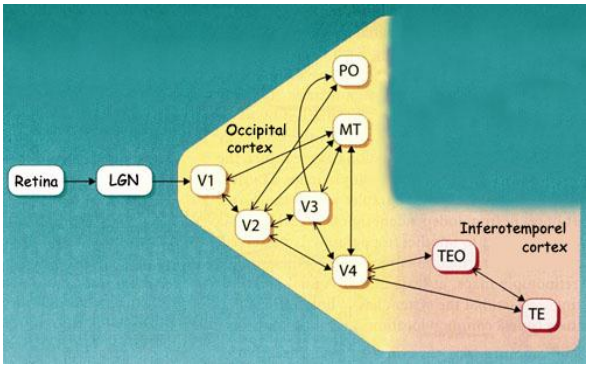

Figure 1. Dubuc, 2002.

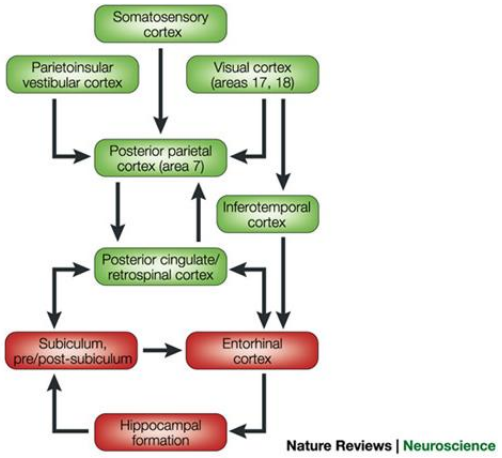

Figure 2. Corkin, 2002.

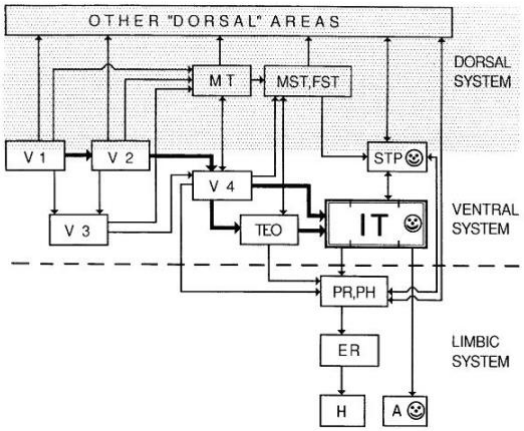

Figure 3. Gross, 2008.

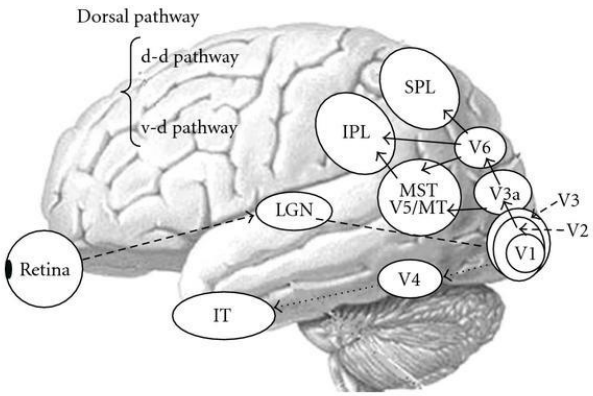

Figure 4. Yamasaki et al., 2012.

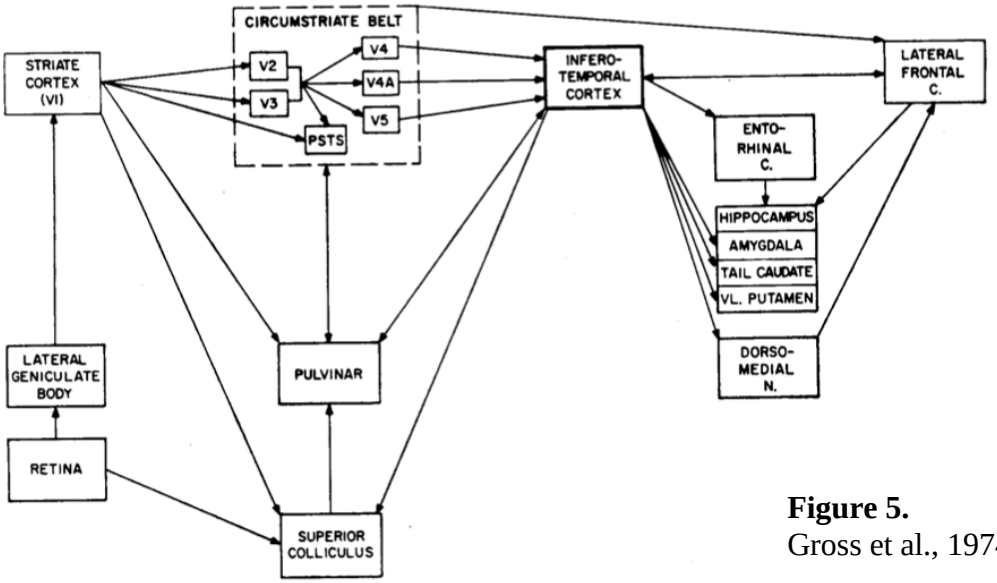

Figure 5.
Gross et al., 1974.

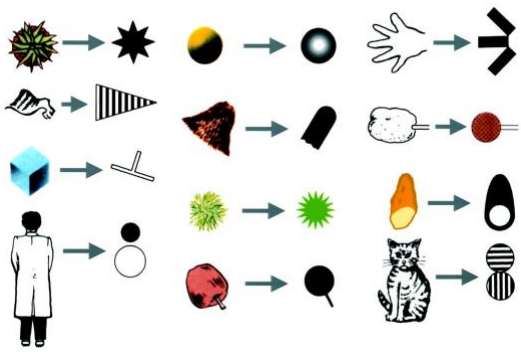

Figure 6. Tanaka, 2003.

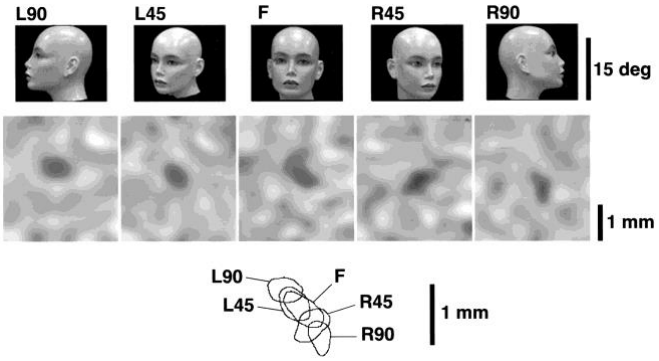

Figure 7. Tanaka, 2003.

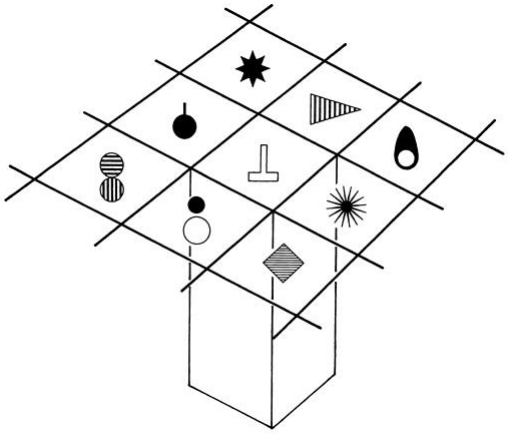

Figure 8. Tanaka, 2003.

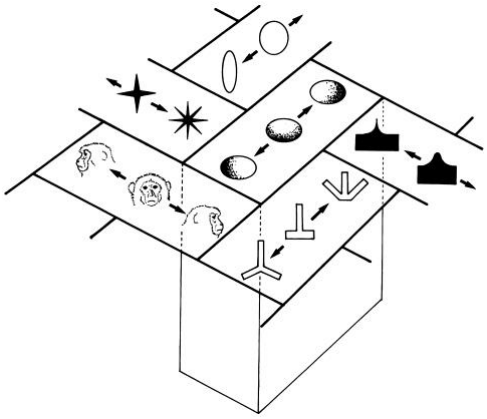

Figure 9. Tanaka, 2003.

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