

2D PHYSICAL PROPERTIES IN THE RESPONSES OF THE
MACAQUE INFEROTEMPORAL CORTEX

DOCTORAL THESIS

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The ventral visual pathway is composed of a set of posterior cortical areas extending from the primary visual cortex (V1) to the inferotemporal (IT) cortex. It can be characterised by a hierarchical architecture in which neurons in higher areas code for progressively more complex representations by pooling information from lower areas. Neurons in V1 code relatively simple features, such as local contours and colours, whereas neurons in IT fire in response to whole complex objects. (see for example Lee 2003, Tanaka 1996, Logothetis and Sheinberg 1996) In this hierarchical organization the size of the receptive fields (RF, the area of the visual field to which a neuron responds) changes characteristically. Whereas in V1 neurons have small RFs thus being able to provide precise spatial information about the position and details of the stimulus in the visual field (Lee 2003), in the most anterior part of IT cortex, the TE, where neurons receive massive convergent inputs from lower areas, the RF's are large (Gross et al 1972, Gross 1994). This feature can underlie our capacity to recognize objects independently of their size and position. (Tanaka 1996, Logothetis and Sheinberg 1996) The retinotopic organization becomes coarser along the pathway. No sign of retinotopy has been reported in TE (Tanaka, 1997), although in humans a kind of center-periphery organization has been revealed in corresponding areas by fMRI experiments. (Levy 2001).

The anterior part of the inferotemporal cortex is thought to be essential for object recognition. Multiple streams of evidence support this idea. First, cortical ablation studies have demonstrated that lesions of the IT produce selective impairments in object recognition (Dean, 1976; Logothetis and Sheinberg, 1996). Second, IT neurons respond in a highly selective manner to complex stimuli from objects differing in shape, colour and/or texture (for reviews see Logothetis and Sheinberg, 1996; Tanaka, 1996). The shape selectivity of these neurons parallels the invariances of object perception in several ways: shape preference of IT neurons is largely unaffected by changes in the position and size of an object (Schwartz et al., 1983; but see Ito et al., 1995, Cox et al 2005), by the defining cue (Sáry et al., 1993; Tanaka et al 2001) and by partial occlusion (Kovács et al. 1995).

Despite the considerable amount of work done in the field it is still unclear what features are important for the TE neurons and how they shape the responses.

To reveal the role of two-dimensional surface features in the visual processing in the object area TE, we planned a series of experiments in non-human primates.

In our experiments, we systematically examined whether the shape selectivity of IT neurons is dependent on changes in retinal input caused by variations of the surface attributes of the presented objects.

MATERIALS & METHODS

a) Subjects Three adult macaque monkeys (two *Macaca mulatta*, monkey C and Ch and one *Macaca nemestrina*, monkey K) were used as subjects. We used the „controlled water access” paradigm.

b) Surgery

A scleral search coil was implanted into one eye and a stainless steel peg cemented to the skull for head fixation. A recording chamber was next implanted the skull of the animals.

All procedures conformed to the guidelines of the NIH for the care and use of laboratory animals and were approved by the Ethical Committee of the University of Szeged.

c) Apparatus During the recording sessions, the monkey sat in a primate chair with its head fixed. A standard 17-inch monitor was placed in front of the animal 57 cm from the eye. A PC recorded eye movements, delivered the reward and controlled the animals' behaviour. Other computers presented stimuli and collected electrophysiological data.

Sterile tungsten electrodes, driven by a hydraulic microdrive, were used for single-cell recordings.

d) Stimuli

A set of chromatic stimuli (COL) composed of 20 figures was used. Half of the figures were simple geometrical shapes filled with a coloured, textured pattern, created by a commercial image processing software. We made transformations of the stimuli as described in the appropriate sections below.

e) Stimulus sequence and behavioural paradigms

During recordings monkeys performed a simple fixation task or a discrimination task. In the latter case they had to respond appropriately to the presentation of the object, by moving their gaze to the right or to the left.

Single cell responses were assessed by spike separator systems and recorded. From the recorded activity we evaluated offline the IT cell's responsivity and selectivity by a two-way ANOVA. We compared the selectivities using another two

way ANOVA. Responsivity and selectivity indices were used to compare the responses.

To compare the time courses of the spike trains in response to two conditions in selected cases, we used a paired t-test on a fine-resolution population histogram generated from the averaged responses to the first ranked stimuli. The areas under the curves were compared.

The trialwise median of the onset times of the first activations was used as latency.

Statistics

In our third study we used the following additional statistics on our data:

1. Cluster analysis (Ward method) to classify the responses into groups (clusters) on the basis of their similarity (i.e. correlation, variance) or distance.

2. Factor analysis to identify underlying variables (factors) that explain the pattern of correlations within the responses.

3. Multidimensional scaling (MDS) to detect meaningful underlying dimensions that allow explaining observed similarities or dissimilarities (distances) between the investigated objects (stimuli).

We also studied the **4. Physical features of the images**. Since our stimuli did not differ in the obvious features such as mean luminance or surface area, we looked for “non-obvious” characteristics, still in the physical domain. The following parameters were assigned to each stimulus: the surface area (SA), the perimeter length (PL), the total length of all the lines on the perimeter and also inside (AL), the perimeter length over the surface area (PL/SA) and the total length of all lines over the surface area (AL/SA).

Chromatic features were also analysed and the amount of colour information in the images was characterized in two ways.

5. Sparseness index To quantify the stimulus selectivity measure of the tested neurons we used the sparseness (SP) introduced by Rolls & Treves (1990).

INTRODUCTIONS

Study I. The discrimination of colours is an important, though not mandatory feature of the ability to recognize objects. (Gegenfurtner & Sharpe 1999). As the last unimodal part of the ventral visual pathway (Mishkin & Ungerleider 1982) the IT is

connected to areas proved to possess colour-sensitive cells (Saleem et al 2000, Tamura & Tanaka 2001) and its output (ie. amygdala, rhinal cortex etc.) requires a modestly sophisticated level of processing, which might include colour information, (Cheng et al 1997 Saleem & Tanaka 1996) The crucial role of the IT in the recognition of objects (Gross CG 1994, Tanaka 2000) makes it likely to comprise an important part of the colour-processing system.

Livingstone & Hubel (1987, 1988) have demonstrated that colour and form (altogether with motion) are processed separately in early visual areas. It is still an open question as to whether these types of information are combined or remain separate in the representation of objects in higher areas. The possibility of the existence of independent channels for shape and colour in the ventral visual pathway (Komatsu 1998) requires a closer investigation of the effects of colour on the IT neuronal responses.

A number of studies have previously been published in this field. A majority of them concluded that the IT cells play a role in colour discrimination (Fuster & Jervey 1982, Komatsu et al 1992, Komatsu 1993, Horel 1994, Heywood et al 1995, Buckley et al 1997, Takechi et al 1997, Edwards et al 2000, Tamura & Tanaka 2001, Edwards et al. 2003, a review: Komatsu 1998).

On the other hand, colour is not always of crucial importance in object recognition (Biederman & Ju 1988, Delorme et al 2000). This has also been demonstrated by a few studies as reflected in the activity of IT cells (Nakamura et al 1994, Booth & Rolls 1998, Vogels 1999).

We have conducted a study in which we tested shape-selective IT neurons for chromatic and achromatic figures. We compared the shape preferences of the cells in the two conditions and found rather similar response characteristics.

Study II. Our everyday experience teaches us that object recognition is to a large extent independent of a range of changes in the retinal image, i.e. the change (and also reduction) in the surface detail of the object. We do not find more difficult to recognize the same object when seen in reality, on a coloured or greyscale photograph, or even depicted as a line drawing. This phenomenon has been widely used in the arts and by professional illustrators (e.g. pictograms). Indeed, in a human psychophysical experiment, Biederman and Ju (1988) found that the naming latencies of masked objects presented as coloured photographs or as line drawings were

essentially the same. A series of experiments revealed no benefits for chromatic over achromatic representations (Ostergaard and Davidoff, 1985) or over line drawing representations (Davidoff and Ostergaard, 1988) in different classification tasks. This suggests that surface characteristics such as colour, texture and shading play only a secondary role in object recognition once contour information is available. This finding is in line with edge-based theories of object recognition (Biederman, 1987; Grossberg and Mingolla, 1985; Ullman, 1989).

(Cavanagh, 1991). Four different stimulus transformations of these 20 images were carried out. To remove all texture and shading information, we generated line drawings with a uniform surface brighter (BLD) or darker (DLD) than the background. These images retained their inner contours and the contrast between the inner object surfaces and the background with the two opposite polarities intact. Lines, bordering these main parts and falling inside the shapes are defined as inner contours of the stimuli. Line drawings (LDs) were generated by filling the inner surface of the objects with the background uniform grey and by removing all contrast from the images, except at the outer and inner contours, which were drawn with lines identical to those in the BLDs and DLDs. (4) Silhouettes (SILs) were obtained by filling the objects with the uniform dark-grey used in the DLDs and removing all surface detail, leaving only the occluding contours and the contrast present in the image. The DLDs and SILs differ only in the presence/absence of the black lines corresponding to the inner contours of the objects.

Study III Previous studies have indicated that IT neurones respond differentially to complex visual stimuli (Gross et al., 1972, Desimone et al., 1984, Richmond et al., 1987, Eskandar et al., 1992).

It has also been shown that there exists a “complexity” gradient in the IT, the more anterior regions respond to more complex features (Tanaka et al., 1991, Tanaka 1996).

Tanaka et al., (1991) suggested that cells are clustered in cellular columns (modules) in the IT, containing cells selective for moderately complex features. They proved this idea by gradually reducing the images in their experiments to the simplest configuration, the critical features, which could still drive the neighbouring units. They hypothesized that general classes of objects are represented not by the activity of a single cell, but by the activity across different IT modules. Detailed

discrimination would require the detection of small differences in activity of the neurones within the modules. Thus, IT cells form ensembles, involving different modules depending on the visual stimulus. New stimuli require a new recruitment of modules, which gives an infinite variability for coding novel stimuli using a relative small number of modules.

On the other hand, Sigala and Logothetis (2002) suggested that stimulus features important for visual categorization for instance, are represented in the activity of single units (neurones) in the primate IT cortex. In their opinion, neurones in the IT signal the diagnostic features for categorization via their firing rate, thereby, being especially selective for them.

One of the open questions concerning coding in IT is: how are objects similar to each other coded in the neuronal responses?

The present study is based on the further analysis of the experiments detailed above. During the experiments we presented 20 non-parameterised images similar in size and luminance but having different complexity, either geometrical shapes (GI) or photos of real objects (RI). The monkeys performed a fixation task while neuronal activity was recorded from the IT. The responses were subjected to cluster analysis, factor analysis and multidimensional scaling and the images were analysed regarding the physical features. Our results suggest that a given neuronal population in the IT may code simple and complex stimuli in different ways and similarity between images is manifested by the clustering of the neuronal responses given to them.

Results and Discussion

Study I.

Our results support the notion that colour information is not a crucial cue in the processing of object information for most of the IT cells. Not only did a majority of the recorded cells retain their response amplitude (mean firing rate) for their preferred stimuli, but the overall selectivity also remained the same. The population response curves for the preferred stimuli in the 2 conditions overlap fully.

The mean response rates and the peak response amplitude in response to the COL and BW stimuli did not differ in either animal. However, a difference was noted between the 2 animals. While the peak response amplitudes were the same, in the case of the

discriminating animal the response had a more sustained character. The differences observed might be attributed to the difference in the tasks, since one of the monkeys was only involved in a fixation task, whereas the other actively discriminated the stimuli. Similar attention-related differences have been described elsewhere (Super et al 2001). Despite this, since the animals were presented with the same stimulus set, we believe that our argumentation about coding COL and BW stimuli in the IT are not affected by this difference.

However, our results do not indicate that the IT does not have a role in colour processing. It might be the case that colour-sensitive cells are clustered in the cortex. This possibility is suggested by Komatsu et al (1992) whose recording technique includes a search for colour-sensitive cortical areas and the implantation of chronic guiding tubes for electrodes. A clustering of colour-sensitive cells in the cerebral cortex would not be unique: blobs are thought to be such clustered colour-sensitive cells in v1 (Livingstone & Hubel 1988).

Study II.

Our results of the surface-reduction study can be summarised as follows. 1) Shape selective IT neurons remain selective for objects without texture and shading information. The responsiveness of the neurons, however, is affected by removal of these surface attributes. 2) IT neurons respond highly similarly to stimuli with opposite signs of contrast. Selectivity for shapes is also preserved over contrast reversal of the images. 3) Deletion of the inner contours has only mild effects on the responses and selectivity of the IT neurons 4) processing of the line drawing representation of the objects differ characteristically according to the responses of IT neurons. Both the responsivity and selectivity are changed.

Texture and shading

This stimulus variation affected the shape sensitivity of the IT neurons only weakly, suggesting the relatively low importance of texture in IT stimulus selectivity.

However, the response rate did decrease under the texture-removed conditions, suggesting some degree of interaction of texture and shading with shape.

Silhouettes

At a neuronal population level, we observed similarly decreased firing rates for the objects containing the inner contours (DLDs) and for the SILs as compared to the

chromatic versions, a result supported by another study (Vogels, 1999). This suggests that inner contours are not necessary for the selective response of these neurons.

Contrast

The comparison of our line drawing stimuli having higher (BLD) or lower (DLD) luminance values than that of the background showed no differences in either neural response rate or shape selectivity. This indicates that the responses of IT neurons do not reflect the contrast sign of the stimuli, suggesting that the IT may play a role in the contrast-invariant recognition of objects.

LD

Removal of all contrast from within the objects and generating line drawings resulted in significantly lower response rates and changed selectivity

However, if the hunting stimuli are the LDs themselves, then the response given to the preferred stimuli is of the same amplitude as it was for the COL ones in the other case. This suggests that by searching the cells using coloured stimuli (which are supposedly preferred by IT cells) we introduce a bias. In other words we find a subpopulation of IT cells preferring coloured complex objects, and to some extent miss a possible other subpopulation, namely that of those cells which are tuned to line-drawn representations. Eventually the data suggest the (co)existence of (at least) two subpopulations of IT neurons

Study III

Similarities of the responses from 217 cells in the IT given to 20 images were analysed by factor analysis, by cluster analysis and by MDS. A common result of each method was that on the basis of an analysis of the net cellular responses given to our image set, the geometrical shapes could be distinguished from those containing photos of real-world objects.

We report that cells in the IT might code stimuli with different complexities in other ways than just the amplitude of the mean firing rate.

We hypothesized the presence of non-obvious, higher-order differences between the images .

An attempt was made to identify some of the factors, which could explain the clustering of the responses to our stimuli. Our images differed both in the length of the perimeter and also in the total length of the lines visible in the stimuli.

Since these parameters add to the complexity of the images, we suggest, that IT neurones code images in a different way if the images differ in these characteristics. Our two stimulus groups differed in colourfulness index (2.52 and 1.45 for GI and RI, respectively), it seems that colour might be another clustering factor.

In both animals, there were stimulus pairs, which grouped consistently in the dendrogram. It is tempting to speculate that this grouping was a result of some implicit categorization mechanism, and that the images were situated close together in the dendrogram because of some semantical or higher-order categorisation process. We think that this is unlikely since the animals were required to perform a simple fixation task and the reward was probably associated more with the successful fixation than with the stimulus content. It is plausible to suggest that exemplars belonging in the same category share similar physical features (colourfulness, internal pattern, building elements colours etc.).

Our results suggest that there might be separate coding in the monkey inferotemporal cortex for the processing of simple and complex images at a single cell level. Single cells might code the complexity of images reliably, even if they do not differ in simple physical features. Since the results from the two monkeys were highly similar, there might be general rules that determine the responses of IT cells to stimuli that differ in complexity.

CONCLUSION AND SUMMARY

In our work we have shown that the invariances experienced in the IT are indeed extended to most of the stimulus-reduced conditions – a result which is in line with the new dynamic view of the cortex, where the “early” areas provide a fine-grained buffer for the representation, and the higher ones (like IT or TE) are responsible for the immediate pre-categorization representation, regardless of the individual differences in the actual presentation. It remains a question if these invariances are acquired through training or are hard-wired. We found however an interesting exception to that rule – namely the depiction by lines: the line-drawn contours. It seems according to our results, that these (edge-defined) representations are dealt with by a separate population of cells in the IT. This on its turn suggests that there is a separate machinery in the visual system to process surface-defined and edge-defined representations, and this separation is present still in the IT. The same holds true to

the color processing: we showed that at least for a considerable population of cells in the anterior IT, color does not add more information to what is already processed by the cell. This finding challenges the putative role of the inferior temporal cortex as a “colour center” in the macaque brain.

In our further investigations however it became clear that the population response of the IT cells indeed carries more information about the stimuli than what is evident from the study of the spike trains. The information we found seems to be contained in the difference of the variances in the neuronal responses across the area. The information we extracted turned out to be about the complexity of the given stimuli. Thus although the individual responses do not allow any fine-grained representation of the stimulus (it is not even needed: the representation is supposed to be given by the “active blackboard” or “buffer” of the “early” areas), the population response contains more information than provided simply by the frequency code.

Our further efforts shall be aimed to address the question of the reduction of our stimuli. Responses in the physical absence of the contours (illusory contours) will help us to elucidate the question of the surface-edge processing in the IT. We will also challenge the phenomenon detected in the first (“colour”) study: namely the putative task dependence of the responses of the IT neurones.

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PUBLICATIONS RELATED TO THE THESIS

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Invariances of shape-processing for reduced surface cues: how IT neurons and psychophysics correlate in the macaque
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