

# The representation of information about faces in the temporal and frontal lobes

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Available online 23 June 2006

## Abstract

Neurophysiological evidence is described showing that some neurons in the macaque inferior temporal visual cortex have responses that are invariant with respect to the position, size and view of faces and objects, and that these neurons show rapid processing and rapid learning. Which face or object is present is encoded using a distributed representation in which each neuron conveys independent information in its firing rate, with little information evident in the relative time of firing of different neurons. This ensemble encoding has the advantages of maximising the information in the representation useful for discrimination between stimuli using a simple weighted sum of the neuronal firing by the receiving neurons, generalisation and graceful degradation. These invariant representations are ideally suited to provide the inputs to brain regions such as the orbitofrontal cortex and amygdala that learn the reinforcement associations of an individual's face, for then the learning, and the appropriate social and emotional responses, generalise to other views of the same face. A theory is described of how such invariant representations may be produced in a hierarchically organised set of visual cortical areas with convergent connectivity. The theory proposes that neurons in these visual areas use a modified Hebb synaptic modification rule with a short-term memory trace to capture whatever can be captured at each stage that is invariant about objects as the objects change in retinal view, position, size and rotation. Another population of neurons in the cortex in the superior temporal sulcus encodes other aspects of faces such as face expression, eye gaze, face view and whether the head is moving. These neurons thus provide important additional inputs to parts of the brain such as the orbitofrontal cortex and amygdala that are involved in social communication and emotional behaviour.

Outputs of these systems reach the amygdala, in which face-selective neurons are found, and also the orbitofrontal cortex, in which some neurons are tuned to face identity and others to face expression. In humans, activation of the orbitofrontal cortex is found when a change of face expression acts as a social signal that behaviour should change; and damage to the orbitofrontal cortex can impair face and voice expression identification, and also the reversal of emotional behaviour that normally occurs when reinforcers are reversed.

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*Keywords:* Face expression; Face identity; Inferior temporal visual cortex; Orbitofrontal cortex

## 1. Introduction

Evidence on how information about visual stimuli is represented in the temporal cortical visual areas and on how these representations are formed is described. The neurophysiological recordings are made mainly in non-human primates, macaques, firstly because the temporal lobe, in which this processing occurs, is much more developed than in non-primates, and secondly because the findings are relevant to understanding the effects of brain damage in patients, as will be shown. In this paper, attention will be paid to neural systems involved

in processing information about faces, because with the large number of neurons devoted to this class of stimuli, this system has proved amenable to experimental analysis; because of the importance of face recognition and expression identification in primate including human social and emotional behaviour; and because of the application of understanding this neural system to understanding the effects of damage to this system in humans. It will also be shown that the temporal cortical visual areas have neuronal populations that provide invariant representations of objects. Although there is some segregation of face identity and object identity representations in different cytoarchitectonic regions, the proportion of face-selective neurons in any one region reaches only 20%, so that no region is devoted exclusively to faces (see Section 2).

In Section 2, I show that there are two main populations of face-selective neurons in the temporal cortical visual areas. The

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first population is tuned to the identity of faces, and has representations that are invariant with respect to, for example, retinal position, size and even view. These invariant representations are ideally suited to provide the inputs to brain regions such as the orbitofrontal cortex and amygdala that learn the reinforcement associations of an individual's face, for then the learning, and the appropriate social and emotional responses, generalise to other views of the same face. Moreover, these inferior temporal cortex neurons have sparse distributed representations of faces, which are shown to be well suited as inputs to the stimulus–reinforcer association learning mechanisms in the orbitofrontal cortex and amygdala which allow different emotional and social responses to be made to the faces of different individuals, depending on the reinforcers received. The properties of these neurons tuned to face identity, and how the brain may learn these invariant representations of faces, are described in Sections 3–12. Section 13 describes a second main population of neurons that are in the cortex in the superior temporal sulcus, which encode other aspects of faces such as face expression, eye gaze, face view and whether the head is moving. This second population of neurons thus provides important additional inputs to parts of the brain such as the orbitofrontal cortex and amygdala that are involved in social communication and emotional behaviour. This second population of neurons may in some cases encode reinforcement value (e.g. face expression neurons), or provide social information that is very relevant to whether reinforcers will be received, such as neurons that signal eye gaze, or whether the head is turning towards or away from the receiver. In Sections 14 and 15, I describe the responses of face-selective neurons in two areas, the amygdala and orbitofrontal cortex, to which the temporal cortical areas have direct projections. I also review evidence (in Section 15) that damage to the human orbitofrontal cortex can impair face (and voice) expression identification. The orbitofrontal cortex is also shown to be involved in the rapid reversal of behaviour to stimuli (which could be the face of an individual) when the reinforcement contingencies change, and therefore to have an important role in social and emotional behaviour. Moreover, the human orbitofrontal cortex is shown to be activated in a simple model of human social interaction when a face expression change indicates that the face of a particular individual is no longer reinforcing.

## 2. Neuronal responses found in different temporal lobe cortex visual areas

Visual pathways project by a number of cortico-cortical stages from the primary visual cortex until they reach the temporal lobe visual cortical areas (Baizer, Ungerleider, & Desimone, 1991; Maunsell & Newsome, 1987; Seltzer & Pandya, 1978) in which some neurons respond selectively to faces (Bruce, Desimone, & Gross, 1981; Desimone, 1991; Desimone, Albright, Gross, & Bruce, 1984; Desimone & Gross, 1979; Gross, Desimone, Albright, & Schwartz, 1985; Perrett, Rolls, & Caan, 1982; Rolls, 1981, 1984, 1991, 1992a, 2000a, 2005; Rolls & Deco, 2002). The inferior temporal visual cortex, area TE, is divided on the basis of cytoarchitecture, myeloarchitecture and afferent input, into areas TEa, TEm, TE3, TE2

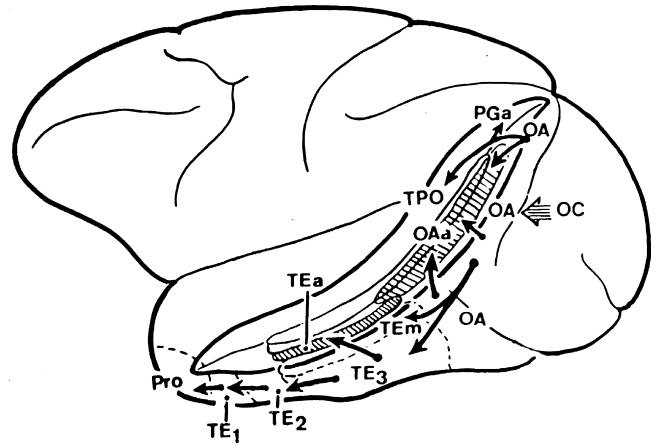


Fig. 1. Lateral view of the macaque brain (left) and coronal section (right) showing the different architectonic areas (e.g. TEm, TPO) in and bordering the anterior part of the superior temporal sulcus (STS) of the macaque (see text). (After Seltzer & Pandya, 1978.).

and TE1. In addition there is a set of different areas in the cortex in the superior temporal sulcus (Baylis, Rolls, & Leonard, 1987; Seltzer & Pandya, 1978) (see Fig. 1). Of these latter areas, TPO receives inputs from temporal, parietal and occipital cortex; PGa and IPa from parietal and temporal cortex; and TS and TAa primarily from auditory areas (Seltzer & Pandya, 1978).

Considerable specialisation of function was found in recordings made from more than 2600 neurons in these architectonically defined areas (Baylis et al., 1987). Areas TPO, PGa and IPa are multimodal, with neurons that respond to visual, auditory and/or somatosensory inputs; the inferior temporal gyrus and adjacent areas (TE3, TE2, TE1, TEa and TEm) are primarily unimodal visual areas; areas in the cortex in the anterior and dorsal part of the superior temporal sulcus (e.g. TPO, IPa and IPg) have neurons specialised for the analysis of moving visual stimuli; and neurons responsive primarily to faces are found more frequently in areas TPO, TEa and TEm, where they comprise approximately 20% of the visual neurons responsive to stationary stimuli, in contrast to the other temporal cortical areas in which they comprise 4–10%. The stimuli which activate other cells in these TE regions include simple visual patterns such as gratings, and combinations of simple stimulus features (Gross et al., 1985; Tanaka, Saito, Fukada, & Moriya, 1990). Due to the fact that face-selective neurons have a wide distribution, it might be expected that only large lesions, or lesions that interrupt outputs of these visual areas, would produce readily apparent face-processing deficits. Moreover, neurons with responses related to facial expression, movement and gesture are more likely to be found in the cortex in the superior temporal sulcus, whereas neurons with activity related to facial identity are more likely to be found in the TE areas (Hasselmo, Rolls, & Baylis, 1989).

In human fMRI studies, evidence for specialisation of function is described (Grill-Spector & Malach, 2004; Haxby, Hoffman, & Gobbini, 2002; O'Toole, Jiang, Abdi, & Haxby, 2005; Spiridon, Fischl, & Kanwisher, 2006; Spiridon & Kanwisher, 2002) related to face processing (in the fusiform

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