



Position paper

Face processing in different brain areas, and critical band masking

Edmund T. Rolls*

Department of Experimental Psychology, University of Oxford, Oxford, UK

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, view, and spatial frequency of faces and objects, and that these neurons show rapid processing and rapid learning. Critical band spatial frequency masking is shown to be a property of these face-selective neurons and of the human visual perception of faces. 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 maximizing the information in the representation useful for discrimination between stimuli using a simple weighted sum of the neuronal firing by the receiving neurons, generalization, 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 generalize to other views of the same face. A theory is described of how such invariant representations may be produced by self-organizing learning in a hierarchically organized set of visual cortical areas with convergent connectivity. The theory utilizes either temporal or spatial continuity with an associative synaptic modification rule. 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 human orbitofrontal and pregenual cingulate cortex can impair face and voice expression identification, and also the reversal of emotional behaviour that normally occurs when reinforcers are reversed.

*Correspondence should be addressed to Professor Edmund T. Rolls, Oxford Centre for Computational Neuroscience, (e-mail: Edmund.Rolls@oxcns.org; <http://www.oxcns.org>).

I. Introduction

This position paper describes evidence on how information about faces is represented by neurons in different brain areas, and on the computational processes being performed in each area. This provides a foundation for helping to understand some of the neuropsychology of face processing. The focus of the paper is not only on the different temporal lobe cortical areas with representations of faces, but also on the orbitofrontal and cingulate cortices, the amygdala, and the neuropsychological changes that follow damage to these. In addition, evidence on critical band masking of face representations and processing, which addresses questions about how faces are being processed in the brain, is described. The neurophysiological recordings are made mainly in non-human primates, macaques, firstly because the temporal and frontal lobes, in which this processing occurs, are 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 section 2, I show that there are at least two main populations of face-selective neurons in the anterior temporal cortical visual areas. The 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 generalize 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 that 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 14 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 15 and 16, 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 16) 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 that respond selectively to faces are found (Bruce, Desimone, & Gross, 1981; Desimone, 1991; Desimone, Albright, Gross, & Bruce, 1984; Desimone & Gross, 1979; Gross, Desimone, Albright, & Schwartz, 1985; Perrett, Hietanen, Oram, & Benson, 1992; Perrett, Rolls, & Caan, 1979; Perrett, Rolls, & Caan, 1982; Rolls, 1981, 1984, 1991, 1992, 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, 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 Figure 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 specialization of function was found in recordings made from more than 2,600 neurons in these architecturally 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 specialized 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, though found in high proportion in some subregions (Tsao, Freiwald, Tootell, & Livingstone, 2006), nevertheless are found in lower proportions in many temporal lobe architectonic regions (Baylis *et al.*, 1987), it might be expected that only large lesions, or lesions that

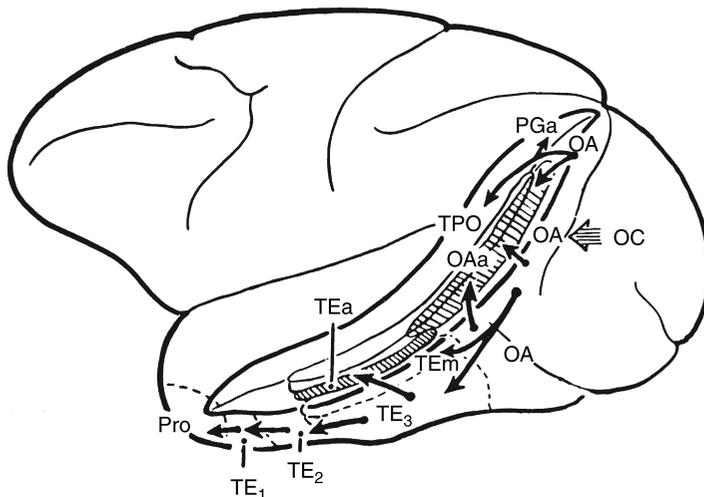


Figure 1. Lateral view of the macaque brain (left) and coronal section (right) showing the different architectonic areas (e.g. TEm, TPO) in and bordering the anterior part of the superior temporal sulcus (STS) of the macaque (see text). (After Seltzer & Pandya, 1978).

interrupt outputs of these visual areas, would produce readily apparent face-processing deficits. Moreover, neurons with responses related to facial expression, head and face 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). The face-selective temporal cortex neurons we have studied are found mainly between 7 and 3 mm posterior to the sphenoid reference, which in a 3–4 kg macaque corresponds to approximately 11–15 mm anterior to the interaural plane (Baylis *et al.*, 1987). The ‘middle face patch’ of Tsao *et al.* identified with fMRI in the macaque was at A6, which is probably part of the posterior inferior temporal cortex. Tsao *et al.* also described ‘anterior face patches’ at A15 to A22. A15 might correspond to where we have analysed face-selective neurons (it might translate to 3 mm posterior to our sphenoid reference).

In human fMRI studies, evidence for specialization 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 face area, which may correspond to parts of the macaque inferior temporal visual cortex in which face neurons are common); to face expression and gesture (i.e. moving faces; in the cortex in the superior temporal sulcus, which corresponds to the macaque cortex in the superior temporal sulcus); to objects (in an area that may correspond to the macaque inferior temporal cortex in which object but not face representations are common, as described above); and to spatial scenes (in a parahippocampal area which probably corresponds to the macaque parahippocampal gyrus areas in which neurons are tuned to spatial view and to combinations of objects and the places in which they are located (Georges-François, Rolls, & Robertson, 1999; Robertson, Rolls, & Georges-François, 1998; Rolls, 1999c; Rolls & Kesner, 2006; Rolls, Robertson, & Georges-François, 1997; Rolls, Treves, Robertson, Georges-François, & Panzeri, 1998; Rolls & Xiang, 2006; Rolls, Xiang, & Franco, 2005)). However, there is much debate arising from these human fMRI studies about how specific each region is for a different type of function, in that such studies do not provide clear evidence on whether individual neurons can be very selective for face identity versus face expression versus objects and thereby convey specific information about these different classes of object; whether any one neuron encodes information independently of other neurons or in contrast whether there is great redundancy; whether each area contains a mixture of different populations of neurons each tuned to different specific classes of visual stimuli, or neurons with relatively broad tuning that respond at least partly to different classes of stimuli; about whether temporal cortical areas without strong fMRI activations to faces nevertheless contain some face-selective neurons; and about the fine-grain topology within a cortical area. The single neuron studies in macaques described above and below do provide direct evidence on these questions. The neuronal recording studies show that individual neurons can be highly tuned in that they convey information about face identity, face expression, head movement, objects, *or* spatial view. The recording studies show that within these different classes, individual neurons by responding differently to different members of the class convey information about whose face it is, what the face expression is, etc., using a sparse-distributed code with an approximately exponential firing rate probability distribution. The neuronal recording studies also show that each cytoarchitecturally defined area contains different proportions of face identity versus object neurons, but that the proportion of face-selective neurons in any one area is not higher than 20% of the visually responsive neurons in a cytoarchitecturally defined

area, so that considerable intermixing of specifically tuned neurons is the rule (Baylis *et al.*, 1987), although there are subregions with high proportions of face-selective neurons (Tsao *et al.*, 2006). The neuronal recording studies also show that at the fine spatial scale, clusters of neurons extending for approximately 1-several mm with tuning to one aspect of stimuli are common (e.g. face identity, the visual texture of stimuli, or a particular class of head motion), and this can be understood as resulting from self-organizing mapping based on local cortical connectivity when a high-dimensional space of objects, faces, etc., must be represented on a two-dimensional cortical sheet (Rolls, 2008; Rolls & Deco, 2002). Indeed, consistent with self-organizing map principles, there is a high concentration of face-selective neurons within a patch identified by fMRI (Tsao *et al.*, 2006). However, and consistent with neuronal recording studies, mapping with activity-dependent cellular markers shows that there is a patchy distribution of areas with predominantly face-selective neurons, placed between areas with object-selective neurons, throughout the monkey inferior temporal visual cortical area, with the face-selective patches having estimated widths of several mm (Zangenehpour & Chaudhuri, 2005). Even in the human fusiform face area, there is some evidence for patches that are not very selective for faces, but instead respond to objects (Grill-Spector, Sayres, & Ress, 2006). Thus overall the evidence is consistent with a patchy distribution of face-selective neurons in the inferior temporal cortical areas, consistent with self-organizing map principles that arise because of the predominance of short-range excitatory (1 – several mm) connections in the neocortex, and the resulting minimization of wiring length between neurons that are interconnected for computational reasons (Rolls, 2008). However, the spatial topography of face-selective neurons in the inferior temporal cortical areas is not a matter of fundamental significance for the types of computation and processing that are performed in the inferior temporal cortical areas, and it is to these more fundamental issues that we now turn.

3. The selectivity of one population of neurons for faces

The inferior temporal cortex neurons described in our studies as having responses selective for faces are selective in that they respond 2–20 times more (and statistically significantly more) to faces than to a wide range of gratings, simple geometrical stimuli, or complex three-dimensional objects (Baylis, Rolls, & Leonard, 1985; Baylis *et al.*, 1987; Rolls, 1984, 1992, 1997, 2000a; Rolls & Deco, 2002). The recordings are made while the monkeys perform a visual fixation task in which after the fixation spot has disappeared, a stimulus subtending typically 8° is presented on a video monitor (or, in some earlier studies, while monkeys perform a visual discrimination task). The responses to faces are excitatory with firing rates often reaching 100 spikes/s, sustained, and have typical latencies of 80–100 ms. The neurons are typically unresponsive to auditory or tactile stimuli and to the sight of arousing or aversive stimuli. These findings indicate that explanations in terms of arousal, emotional, or motor reactions, and simple visual feature sensitivity are insufficient to account for the selective responses to faces and face features observed in this population of neurons (Baylis *et al.*, 1985; Perrett *et al.*, 1982; Rolls & Baylis, 1986). Observations consistent with these findings have been published by Desimone *et al.* (1984), who described a similar population of neurons located primarily in the cortex in the superior temporal sulcus which responded to faces but not to simpler stimuli such as edges and bars or to complex non-face stimuli (see also Gross *et al.*, 1985).

These neurons are specialized to provide information about faces in that they provide much more information (on average 0.4 bits) about which (of 20) face stimuli is being seen than about which (of 20) non-face stimuli is being seen (on average 0.07 bits) (Rolls & Tovee, 1995; Rolls, Treves, & Tovee, 1997). These information theoretic procedures provide an objective and quantitative way to show what is 'represented' by a particular neuron and by a particular population of neurons.

4. The selectivity of these neurons for individual face features or for combinations of face features

Masking out or presenting parts of the face (e.g. eyes, mouth, or hair) in isolation reveal that different cells respond to different features or subsets of features. For some cells, responses to the normal organization of cut-out or line-drawn facial features are significantly larger than to images in which the same facial features are jumbled (Perrett *et al.*, 1982; Rolls, 2008; Rolls, Tovee, Purcell, Stewart, & Azzopardi, 1994). These findings are consistent with the hypotheses developed below that by competitive self-organization some neurons in these regions respond to parts of faces by responding to combinations of simpler visual properties received from earlier stages of visual processing, and that other neurons respond to combinations of parts of faces and thus respond only to whole faces. Moreover, the finding that for some of these latter neurons the parts must be in the correct spatial configuration shows that the combinations formed can reflect not just the features present, but also their spatial arrangement. This provides a way in which binding can be implemented in neural networks (Elliffe, Rolls, & Stringer, 2002; Rolls, 2008; Rolls & Deco, 2002). Further evidence that neurons in these regions respond to combinations of features in the correct spatial configuration was found by Tanaka *et al.* (1990) using combinations of features that are used by comparable neurons to define objects.

5. Distributed encoding of face and object identity

An important question for understanding brain function is whether a particular object (or face) is represented in the brain by the firing of one or a few gnostic (or 'grandmother') cells (Barlow, 1972), or whether instead the firing of a group or ensemble of cells each with different profiles of responsiveness to the stimuli provides the representation. It has been shown that the representation of which particular object (face) is present is rather distributed. Baylis *et al.* (1985) showed this with the responses of temporal cortical neurons that typically responded to several members of a set of five faces, with each neuron having a different profile of responses to each face. In a further study using 23 faces and 45 non-face natural images, a distributed representation was again found (Rolls & Tovee, 1995), with the average sparseness being 0.65. (The sparseness of the representation provided by a neuron can be defined as

$$a = \frac{\left(\sum_{s=1,S} r_s / S\right)^2}{\sum_{s=1,S} (r_s^2 / S)}$$

where r_s is the mean firing rate of the neuron to stimulus s in the set of S stimuli, see Rolls and Treves (1998) and Franco, Rolls, Aggelopoulos, and Jerez (2007). If the neurons are binary (either firing or not to a given stimulus), then a would be 0.5 if

the neuron responded to 50% of the stimuli, and 0.1 if a neuron responded to 10% of the stimuli.) If the spontaneous firing rate was subtracted from the firing rate of the neuron to each stimulus, so that the changes of firing rate, i.e. the *active responses* of the neurons, were used in the sparseness calculation, then the 'response sparseness' had a lower value, with a mean of 0.33 for the population of neurons.

The distributed nature of the representation can be further understood by the finding that the firing rate distribution of single neurons when a wide range of natural visual stimuli are being viewed is approximately exponentially distributed, with rather few stimuli producing high firing rates, and increasingly large numbers of stimuli producing lower and lower firing rates (Baddeley *et al.*, 1997; Franco *et al.*, 2007; Rolls & Tovee, 1995; Treves, Panzeri, Rolls, Booth, & Wakeman, 1999) (see Figure 2). The sparseness of such an exponential distribution of firing rates is 0.5. It has been shown that the distribution may arise from the threshold non-linearity of neurons combined with short-term variability in the responses of neurons (Treves *et al.*, 1999).

Complementary evidence comes from applying information theory to analyse how information is represented by a population of these neurons. The information required to identify which of S equiprobable events occurred (or stimuli were shown) is $\log_2 S$ bits. (Thus, 1 bit is required to specify which of two stimuli was shown, 2 bits to specify which of four stimuli was shown, 3 bits to specify which of eight stimuli was shown, etc.) The important point for the present purposes is that if the encoding was local (or grandmother cell like), the number of stimuli encoded by a population of neurons would be expected to rise approximately linearly with the number of neurons in the population. In contrast, with distributed encoding, provided that the neuronal responses are sufficiently independent and are sufficiently reliable (not too noisy), the number of stimuli encodable by the population of neurons might be expected to rise exponentially as the number of neurons in the sample of the population was increased. The information available about which of 20 equiprobable faces had been shown that was available from the responses of different numbers of these neurons is shown in Figure 3. First, it is clear that some information is available from the responses of just one neuron – on average approximately 0.34 bits. Thus, knowing the activity of just one neuron in the population does provide some evidence about which stimulus was present. This evidence that information is available in the responses of individual neurons in this way, without having to know the state of all the other neurons in the population, indicates that information is made explicit in the firing of individual neurons in a way that will allow neurally plausible decoding, involving computing a sum of input activities each weighted by synaptic strength, to work (see below). Second, it is clear (Figure 3) that the information rises approximately linearly, and the number of stimuli encoded thus rises approximately exponentially, as the number of cells in the sample increases (Abbott, Rolls, & Tovee, 1996; Rolls & Treves, 1998; Rolls, Treves *et al.*, 1997).

It has in addition been shown that there are neurons in the inferior temporal visual cortex that encode view invariant representations of objects, and for these neurons the same type of representation is found, namely distributed encoding with independent information conveyed by different neurons (Booth & Rolls, 1998).

The analyses just described were obtained with neurons that were not simultaneously recorded, but we have more recently shown that with simultaneously recorded neurons similar results are obtained, that is the information about which stimulus was shown increases approximately linearly with the number of neurons, showing that the neurons convey information that is nearly independent (Panzeri,

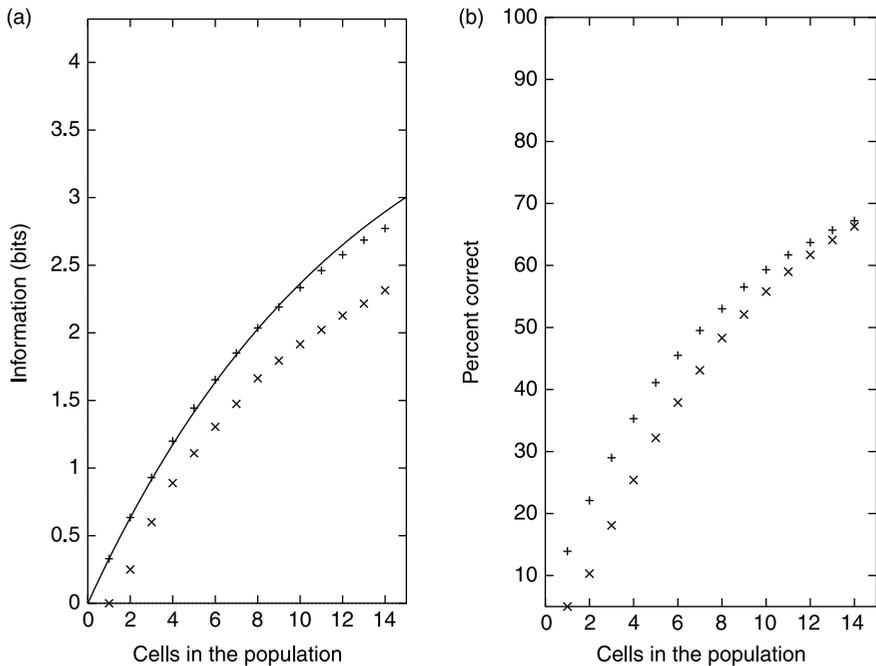


Figure 3. (a) The values for the average information available in the responses of different numbers of these neurons on each trial about which of a set of 20 face stimuli has been shown. The decoding method was dot product (DP, \times) or probability estimation (PE, $+$), and the effects obtained with cross-validation procedures utilizing 50% of the trials as test trials are shown. The remainder of the trials in the cross-validation procedure were used as training trials. (Probability estimation refers to estimating the probability from the neuronal responses for a single trial that each of the 20 faces was shown, thus utilizing the neuronal evidence available about how likely it was that each stimulus was shown, see Rolls *et al.*, 1997.) The full line indicates the amount of information expected from populations of increasing size, when assuming random correlations within the constraint given by the ceiling (the information in the stimulus set, $I = 4.32$ bits). (b) The percentage correct for the corresponding data to those shown in Figure 3a. (After Rolls, Treves, & Tovee, 1997).

Schultz, Treves, & Rolls, 1999; Rolls, Aggelopoulos, Franco, & Treves, 2004; Rolls, Franco, Aggelopoulos, & Perez, 2006). (Consistently, Gawne and Richmond (1993) showed that even adjacent pairs of neurons recorded simultaneously from the same electrode carried information that was approximately 80% independent.) In the research described by Panzeri *et al.* (1999), Rolls *et al.* (2003), and Franco, Rolls, Aggelopoulos, and Treves (2004), we developed methods for measuring the information in the relative time of firing of simultaneously recorded neurons, which might be significant if the neurons became synchronized to some but not other stimuli in a set, as postulated by Engel, Konig, Kreiter, Schillen, and Singer (1992). We found that for the set of cells currently available, almost all the information was available in the firing rates of the cells, and very little (not more than approximately 5% of the total information) was available about these static images in the relative time of firing of different simultaneously recorded neurons (Franco *et al.*, 2004; Panzeri, Schultz *et al.*, 1999; Rolls *et al.*, 2004; Rolls, Franco, Aggelopoulos, & Reece, 2003). The same result was found in natural scenes in which two test images had to be segmented from a complex

background, the features of each object had to be bound together, and the monkey had to use top-down attention to search for one of two images in a complex scene (Aggelopoulos, Franco, & Rolls, 2005). Thus the evidence is that for representations of faces and objects in the inferior temporal visual cortex (and of space in the primate hippocampus and of odours in the orbitofrontal cortex, see Rolls, Critchley, & Treves, 1996; Rolls *et al.*, 1998), most of the information is available in the firing rates of the neurons.

It is unlikely that there are further processing areas beyond those described where ensemble coding changes into grandmother cell (local) encoding. Anatomically, there does not appear to be a whole further set of visual processing areas present in the brain; and outputs from the temporal lobe visual areas such as those described, are taken to limbic and related regions such as the amygdala and orbitofrontal cortex, and via the entorhinal cortex the hippocampus, where associations between the visual stimuli and other sensory representations are formed (see Rolls, 2005; Rolls & Deco, 2002). Indeed, tracing this pathway onwards, we have found a population of neurons with face-selective responses in the amygdala (Leonard, Rolls, Wilson, & Baylis, 1985; Rolls, 2000b) and orbitofrontal cortex (Rolls, Critchley, Browning, & Inoue, 2006), and in the majority of these neurons, different responses occur to different faces, with ensemble (not local) coding still being present. The amygdala in turn projects to another structure which may be important in other behavioural responses to faces, the ventral striatum, and comparable neurons have also been found in the ventral striatum (Williams, Rolls, Leonard, & Stern, 1993).

6. Advantages of the distributed representation of objects and faces for brain processing

The advantages of the distributed encoding found are explained elsewhere (Rolls, 2005, 2007, 2008; Rolls & Deco, 2002; Rolls & Treves, 1998) and summarized briefly here.

Exponentially high coding capacity

This property arises from a combination of the encoding being sufficiently close to independent by the different neurons (i.e. factorial), and sufficiently distributed, and is illustrated by the evidence shown in Figure 3. One of the underlying themes here is the neural representation of faces and objects. How would one know that one had found a neuronal representation of faces or objects in the brain? The criterion suggested (Rolls, 2008; Rolls & Treves, 1998) is that when one can identify the face or object that is present (from a large set of stimuli, that might be thousands or more) with a realistic number of neurons, say in the order of 100, and with some invariance, then one has a useful representation of the face or object.

The properties of the representation of faces, or objects (Booth & Rolls, 1998), have been evident when the readout of the information was by measuring the *firing rate* (i.e. the number of spikes) of the neurons, typically over a 20, 50, or 500 ms period. Thus, information can be readout without taking into account any aspects of the possible temporal synchronization between neurons (Engel *et al.*, 1992), or temporal encoding within a spike train (Aggelopoulos *et al.*, 2005; Franco *et al.*, 2004; Panzeri, Schultz *et al.*, 1999; Rolls *et al.*, 2004; Rolls, Franco *et al.*, 2003; Rolls, Treves *et al.*, 1997; Tovee, Rolls, Treves, & Bellis, 1993).

Ease with which the code can be read by receiving neurons

For brain plausibility, it is also a requirement that neurons should be able to read the code. This is why when we have estimated the information from populations of neurons, we have used in addition to a probability estimating measure (optimal, in the Bayesian sense), also a dot product measure, which is a way of specifying that all that is required of decoding neurons would be the property of adding up postsynaptic potentials produced through each synapse as a result of the activity of each incoming axon (Abbott *et al.*, 1996; Rolls, Treves *et al.*, 1997). It was found that with such a neurally plausible algorithm (the Dot Product, DP, algorithm), which calculates which average response vector the neuronal response vector on a single test trial was closest to by performing a normalized dot product (equivalent to measuring the angle between the test and the average vector), the same generic results were obtained, with only a 40% reduction of information compared with the more efficient (PE) algorithm. This is an indication that the brain could utilize the exponentially increasing capacity for encoding stimuli as the number of neurons in the population increases.

Higher resistance to noise

Because the decoding of a distributed representation involves assessing the activity of a whole population of neurons, and computing a dot product or correlation, a distributed representation provides more resistance to variation in individual components than does a local encoding scheme (Panzeri, Biella, Rolls, Skaggs, & Treves, 1996; Rolls, 2008; Rolls & Deco, 2002).

Generalization

Generalization to similar stimuli is again a property that arises in neuronal networks if distributed but not if local encoding is used. The generalization arises as a result of the fact that a neuron can be thought of as computing the inner or dot product of the stimulus representation with its weight vector (see further Rolls, 2008; Rolls & Deco, 2002; Rolls & Treves, 1998).

Completion

Completion occurs in associative memory networks by a similar process. Completion is the property of recall of the whole of a pattern in response to any part of the pattern. Completion arises because any part of the stimulus representation, or pattern, is effectively correlated with the whole pattern during memory storage. Completion is thus a property of distributed representations and not of local representations. It arises, for example, in auto-association (attractor) neuronal networks, which are characterized by recurrent connectivity. It is thought that such networks are important in the cerebral cortex, where the association fibres between nearby pyramidal cells may help the cells to retrieve a representation that depends on many neurons in the network (Rolls, 2008; Rolls & Deco, 2002; Rolls & Treves, 1998).

Graceful degradation or fault tolerance

This also arises only if the input patterns have distributed representations, and not if they are local. Local encoding suffers sudden deterioration once the few neurons or synapses carrying the information about a particular stimulus are destroyed.

Speed of readout of the information

The information available in a distributed representation can be decoded by an analyser more quickly than can the information from a local representation, given comparable firing rates. Within a fraction of an interspike interval, with a distributed representation, much information can be extracted (Panzeri, Treves, Schultz, & Rolls, 1999; Rolls, Franco *et al.*, 2006; Rolls, Treves *et al.*, 1997; Treves, 1993; Treves, Rolls, & Simmen, 1997; Treves, Rolls, & Tovee, 1996). In effect, spikes from many different neurons can contribute to calculating the angle between a neuronal population and a synaptic weight vector within an interspike interval (Franco *et al.*, 2004; Rolls, 2008; Rolls & Deco, 2002). With local encoding, the speed of information readout depends on the exact model considered, but if the rate of firing needs to be taken into account, this will necessarily take time, because of the time needed for several spikes to accumulate in order to estimate the firing rate.

7. Invariance in the neuronal representation of stimuli

One of the major problems that must be solved by a visual system is the building of a representation of visual information which allows recognition to occur relatively independently of size, contrast, spatial frequency, position on the retina, angle of view, etc. This is required so that if the receiving associative networks (in, e.g. the amygdala, orbitofrontal cortex, and hippocampus) learn about one view, position, etc., of the object, generalization occurs correctly to other positions, views, etc., of the object. It has been shown that the majority of face-selective inferior temporal cortex neurons have responses that are relatively invariant with respect to the size of the stimulus (Rolls & Baylis, 1986). The median size change tolerated with a response of greater than half the maximal response was 12 times. Also, the neurons typically responded to a face when the information in it had been reduced from three-dimensional to a two-dimensional representation in grey on a monitor, with a response which was on average 0.5 of that to a real face. Another transform over which recognition is relatively invariant is spatial frequency. For example, a face can be identified when it is blurred (when it contains only low spatial frequencies), and when it is high-pass spatial frequency filtered (when it looks like a line drawing). It has been shown that if the face images to which these neurons respond are low-pass filtered in the spatial frequency domain (so that they are blurred), then many of the neurons still respond when the images contain frequencies only up to 8 cycles per face (cpf). Similarly, the neurons still respond to high-pass filtered images (with only high spatial frequency edge information) when frequencies down to only 8 cpf are included (Rolls, Baylis, & Leonard, 1985). Face recognition shows similar invariance with respect to spatial frequency (Rolls *et al.*, 1985). Further analysis of these neurons with narrow (octave) bandpass spatial frequency filtered face stimuli shows that the responses of these neurons to an unfiltered face cannot be predicted from a linear combination of their responses to the narrow band stimuli (Rolls, Baylis, & Hasselmo, 1987). This lack of linearity of these neurons, and their responsiveness to a wide range of spatial frequencies, indicates that in at least this part of the primate visual system recognition does not occur using Fourier analysis of the spatial frequency components of images.

Inferior temporal visual cortex neurons also often show considerable translation (shift) invariance, not only under anaesthesia (see Gross *et al.*, 1985), but also in the awake behaving primate (Tovee, Rolls, & Azzopardi, 1994), and selectivity between faces is maintained.

Until recently, research on translation invariance (and much visual neurophysiology) considered the case in which there is only one object or stimulus in the visual field. What happens in a cluttered, natural, environment? Do all objects that can activate an inferior temporal neuron do so whenever they are anywhere within the large receptive fields of inferior temporal cortex neurons. If so, the output of the visual system might be confusing for structures that receive inputs from the temporal cortical visual areas. It has now been shown that the receptive fields of inferior temporal cortex neurons being large (typically 70° in diameter) when a test stimulus is presented against a blank background, become much smaller, as little as several degrees in diameter, when objects are seen against a complex natural background (Rolls, Aggelopoulos, & Zheng, 2003) (cf DiCarlo & Maunsell, 2003; Op De Beeck & Vogels, 2000). Thus, the neurons provide information biased towards what is present at the fovea, and not equally about what is present anywhere in the visual field. This makes the interface to action simpler, in that what is at the fovea can be interpreted (e.g. by an associative memory in the orbitofrontal cortex or amygdala) partly independently of the surroundings, and choices and actions can be directed if appropriate to what is at the fovea (Ballard, 1993; Rolls & Deco, 2002). These findings are a step towards understanding how the visual system functions in a natural environment (Gallant, Connor, & Van Essen, 1998; Rolls, 2008; Rolls & Deco, 2002).

8. A view-independent representation of faces and objects

It has also been shown that some temporal cortical neurons reliably responded differently to the faces of two different individuals independently of viewing angle (Hasselmo, Rolls, Baylis, & Nalwa, 1989), although in most cases (16 out of 18 neurons) the response was not perfectly view independent. Mixed together in the same cortical regions there are neurons with view-dependent responses (Hasselmo, Rolls, Baylis *et al.*, 1989). Such neurons might respond, for example, to a view of a profile of a monkey but not to a full face view of the same monkey (Perrett, Smith, Potter *et al.*, 1985). These findings of view-dependent, partially view-independent, and view-independent representations in the same cortical regions are consistent with the hypothesis discussed below that view-independent representations are being built in these regions by associating together neurons that respond to different views of the same individual.

Further evidence that some neurons in the temporal cortical visual areas have object-based rather than view-based responses comes from a study of a population of neurons that responds to moving faces (Hasselmo, Rolls, Baylis *et al.*, 1989). For example, four neurons responded vigorously to a head undergoing ventral flexion, irrespective of whether the view of the head was full face, of either profile, or even of the back of the head. These different views could only be specified as equivalent in object-based coordinates. Further, for all of the 10 neurons that were tested in this way, the movement specificity was maintained across inversion, responding, for example, to ventral flexion of the head irrespective of whether the head was upright or inverted. In this procedure, retinally encoded or viewer-centred movement vectors are reversed, but the object-based description remains the same. It is an important property of these neurons that they can encode a description of an object that is based on relative motions of different parts of the object, and that is not based on flow relative to the observer. The implication of this type of encoding is that the upper eyelids closing could be encoded as the same social signal that eye-contact is being broken independently of the particular in-plane rotation (tilt, as far as being fully inverted) of the face being observed (or of the observer's head).

Also consistent with object-based encoding is the finding of a small number of neurons that respond to images of faces of a given *absolute* size, irrespective of the retinal image size or distance (Rolls & Baylis, 1986).

9. Learning of new representations in the temporal cortical visual areas

To investigate the hypothesis that visual experience might guide the formation of the responsiveness of neurons so that they provide an economical and ensemble-encoded representation of items actually present in the environment, the responses of inferior temporal cortex face-selective neurons have been analysed while a set of new faces were shown. It was found that some of the neurons studied in this way altered the relative degree to which they responded to the different members of the set of novel faces over the first few (1-2) presentations of the set (Rolls, Baylis, Hasselmo, & Nalwa, 1989b). This evidence is consistent with the categorization being performed by self-organizing competitive neuronal networks, as described below and elsewhere (Rolls, 1989a; Rolls, Baylis, Hasselmo, & Nalwa, 1989a; Rolls & Deco, 2002; Rolls & Treves, 1998).

Further evidence that these neurons can learn new representations very rapidly comes from an experiment in which binarized black and white images of faces which blended with the background were used. These did not activate face-selective neurons. Full grey-scale images of the same photographs were then shown for ten 0.5-s presentations. It was found that in a number of cases, if the neuron happened to be responsive to that face, when the binarized version of the same face was shown next, the neurons responded to it (Tovee, Rolls, & Ramachandran, 1996). This is a direct parallel to the same phenomenon that is observed psychophysically and provides dramatic evidence that these neurons are influenced by only a very few seconds (in this case 5 s) of experience with a visual stimulus. We have shown a neural correlate of this effect using similar stimuli and a similar paradigm in a PET (positron emission tomography) neuroimaging study in humans, with a region showing an effect of the learning found for faces in the right temporal lobe and for objects in the left temporal lobe (Dolan *et al.*, 1997).

Such rapid learning of representations of new objects appears to be a major type of learning in which the temporal cortical areas are involved. Ways in which this learning could occur are considered briefly below, and in detail elsewhere (Rolls, 2008; Rolls & Deco, 2002; Rolls & Stringer, 2006b).

10. The speed of processing in the temporal cortical visual areas

Given that there is a whole sequence of visual cortical processing stages including V1, V2, V4, and the posterior inferior temporal cortex to reach the anterior temporal cortical areas, and that the response latencies of neurons in V1 are about 40-50 ms, and in the anterior inferior temporal cortical areas approximately 80-100 ms, each stage may need to perform processing for only 15-30 ms before it has performed sufficient processing to start influencing the next stage. Consistent with this, response latencies between V1 and the inferior temporal cortex increase from stage to stage (Thorpe & Imbert, 1989). In a first approach to this issue, we measured the information available in short temporal epochs of the responses of temporal cortical face-selective neurons about which face had been seen. We found that if a period of the firing rate of 50 ms

was taken, then this contained 84.4% of the information available in a much longer period of 400 ms about which of four faces had been seen. If the epoch was as little as 20 ms, the information was 65% of that available from the firing rate in the 400 ms period (Tovee *et al.*, 1993). We were able to extend this finding to the case when a much larger stimulus set, of 20 faces, was used. Again, we found that the information available in short (e.g. 50 ms) epochs was a considerable proportion (e.g. 65%) of that available in a 400 ms long firing rate analysis period (Tovee & Rolls, 1995). We extended these results by showing that although there is considerable information in the first spike of each neuron that arrives after a stimulus has been shown, there is more information if the number of spikes in a short window of, for example, 20 ms is used, and that the order of arrival of the spikes from different neurons is not an important factor, whereas the number of spikes in a short window is an important factor (Rolls, Franco *et al.*, 2006). These investigations thus showed that there was considerable information about which stimulus had been seen in short-time epochs near the start of the response of temporal cortex neurons, and the way in which such systems could operate has been considered elsewhere (Rolls, 2008).

The next approach has been to use a visual backward masking paradigm. In this paradigm, there is a brief presentation of a test stimulus which is rapidly followed (within 1–100 ms) by the presentation of a second stimulus (the mask), which impairs or masks the perception of the test stimulus. It has been shown (Rolls & Tovee, 1994) that when there is no mask, inferior temporal cortex neurons respond to a 16 ms presentation of the test stimulus for 200–300 ms, far longer than the presentation time. It is suggested that this reflects the operation of a short-term memory system implemented in cortical circuitry, the importance of which in learning invariant representations is considered below in section 12. If the pattern mask followed the onset of the test face stimulus by 20 ms (a stimulus onset asynchrony of 20 ms), then face-selective neurons in the inferior temporal cortex of macaques responded for a period of 20–30 ms before their firing was interrupted by the mask (Rolls & Tovee, 1994; Rolls, Tovee, & Panzeri, 1999). We went on to show that under these conditions (a test-mask stimulus onset asynchrony of 20 ms), human observers looking at the same displays could just identify which of six faces was shown (Rolls *et al.*, 1994).

These results provide evidence that a cortical area can perform the computation necessary for the recognition of a visual stimulus in 20–30 ms (although it is true that for conscious perception, the firing needs to occur for 40–50 ms, see Rolls, 2003). This provides a fundamental constraint which must be accounted for in any theory of cortical computation. The results emphasize just how rapidly cortical circuitry can operate, a topic that is treated elsewhere (Panzeri, Rolls, Battaglia, & Lavis, 2001; Rolls, 2008; Rolls & Treves, 1998; Treves, 1993; Treves *et al.*, 1996).

11. Critical band masking of face perception and of the responses of face-selective neurons

Critical band masking occurs when the response to a test stimulus is reduced by a masking stimulus close in spatial frequency, but less by a stimulus remote in spatial frequency, from the test stimulus. It arises because of the finite width of the tuning of spatial frequency filters or channels, and because of their partial independence. Thus, detection or recognition may be based on the output of a set of channels into which a mask with a close but not with a distant frequency might intrude. It is a well-known

phenomenon in the auditory system (Scharf, 1961). It has also been shown by Harmon and Julesz (1973) to operate in the visual system, for they reported that the perception of a face low-pass filtered to 8 cycles per image (w) was disrupted more by a mask with spatial frequencies of $1-4w$ than a mask of $4-7w$. Given these psychophysical studies on face perception, and to investigate similarities between human performance and the properties of face-selective neurons, E. T. Rolls, G. C. Baylis, and T. R. Vidyasagar performed the following study. They investigated whether the responses of the face-selective neurons in the macaque cortex in the ventral lip of the anterior part of the superior temporal sulcus (areas TEa, TEm, and TPO) described above and thought to be involved in face perception are also subject to similar critical band masking as occurs psychophysically at the level of human performance. They made a direct comparison of the neuronal responses and of human psychophysical performance with a similar set of stimuli designed to investigate critical band masking.

A set of face stimuli were prepared with the basic stimulus a face low pass spatial frequency filtered at 8 cpf (LP8). This frequency was chosen because it has been shown that many face-selective neurons respond to a face filtered to this frequency well, but have smaller responses if the low-pass filter cuts off below 8 cpf (Rolls *et al.*, 1987, 1985). Further stimuli contained the LP8 face image, and band-pass filtered noise with frequencies of 8-24 cycles per image (corresponding to $1-3w$), 24-40 ($3-5w$), 40-56 ($5-7w$), and 56-72 cycles per image ($7-9w$), with examples of the complete set of images used for one face shown in Figure 4.

The responses of a face-selective neuron to the stimuli are shown in Figure 5a. It can be seen that the addition of the two closest noise bands (8-24 and 24-40 cpf) leads to a reduction in the mean response compared with the low-pass filtered face, and to an increase in the standard deviations of the neuronal responses. Addition of either of the two higher noise bands did not lead to a significant reduction in the mean response rate, but did increase the standard deviations of the neuronal responses.

Of 34 neurons tested in this way in two macaques by Rolls, Baylis and Vidyasagar, 29 showed a significant effect of the masking (as shown by the ANOVA). Of these 29 neurons, the numbers with significant decreases to the stimulus masked with 8-24 cpf noise were 22, with 24-40 cpf noise 23, with 40-56 cpf noise 12, and with 56-72 cpf noise 10. Thus, many neurons showed significant reductions of response caused by the noise masks with the two closest spatial frequency bands, but not by the two more distant noise bands. Consistent with the fact that these face-selective neurons generally have only small responses to non-face stimuli, only four neurons showed any significant increase in activity to the face stimuli to which noise had been added, and only one of these neurons responded to the noise image alone.

To facilitate comparison between neurons, and with the psychophysics, the firing rates were converted to the number of standard deviations that separated the spontaneous firing rate from the response to each of the masked images. This gives a measure of discriminability that is analogous to d' (Baylis *et al.*, 1985). Figure 5b shows the responses of the neuron shown in Figure 5a converted to discriminability in this way. Both a reduction in the mean firing rate and an increase in the variability of the neuronal response will reduce the neuronal discriminability d' .

The mean and standard error of the responses expressed in this way for the population of neurons analysed is shown in Figure 6. It is shown that the two noise bands close in spatial frequency (8-24 and 24-40 cpf) produced a greater reduction in d' than did the two noise bands remote in spatial frequency from the frequencies in the face image (ANOVA $F = 12.3$, $df = 33$, $p < .001$); Neuman-Keuls analyses showed that

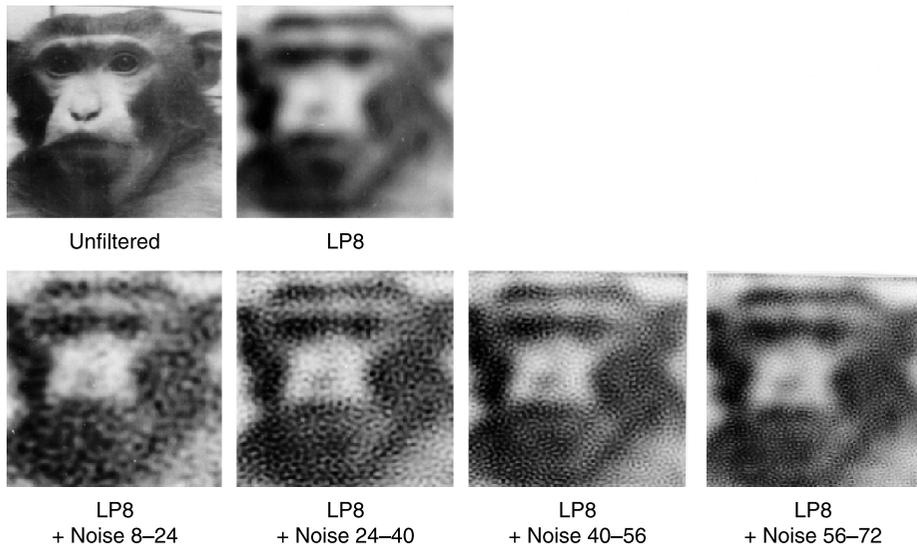


Figure 4. Critical band masking. Stimuli used in investigation of critical band masking by Rolls, Baylis and Vidyasagar. The top images are of an unfiltered face and of the same face low-pass filtered at 8 cycles per image (or face) (LP8). The lower four images show the same LP8 face to which has been added band-limited noise including the spatial frequencies of 8–24, 24–40, 40–56, and 56–72 cycles per image. The filtering was performed by a digital Fourier transform convolution with filters circularly symmetric in the spatial frequency domain. In the frequency domain, the profile of the low-pass and band-pass filters was flat with a Gaussian taper which occurred over two adjacent spatial frequency points, as described by Rolls, Baylis, and Leonard (1985). The greyscale range of the original image was divided by 2 so that when white noise also in the range 0–128 was added, the maximum grey level of the framestore (255) was not exceeded.

the responses to the low-pass face masked with 8–24 or 24–40 cpf were significantly less than to the unmasked low-pass filtered face ($p < .01$ in both cases) and were also significantly less than to the low-pass faces masked with 40–56 and 56–72 cpf noise masks (all $p < .02$). Critical band masking was thus demonstrated for the neuronal responses to a face, and the width of the critical band was shown to extend up to at least 24 cpf ($3w$) but not as far as 40 cpf ($5w$) for a face low-pass filtered at 8 cpf (w).

These neurophysiological results were complemented by psychophysical investigations with human observers with the same LP8 face stimuli, and noise masks added analogously to those above but in the bands $1-4w$ (8–32 cpf) and $4-7w$ (32–64 cpf), as these had been shown to be effective in humans by Harmon and Julesz (1973). In addition, to make the task sufficiently difficult to produce approximately 10% errors, the contrast of the LP8 face used with the humans was half that of the noise, the contrast of the screen was adjusted to levels that were between 0.075 and 0.15 for the five subjects, and the stimulus duration was 100 ms. The subjects' task was to discriminate which of four faces had been shown. Figure 7 shows d' values (calculated according to Hacker and Ratcliff (1979)) for the five subjects for the three stimulus conditions. It can be seen that for all observers, addition of the adjacent noise band (8–32 cpf) to the low-pass filtered image markedly reduced discriminability, whereas the addition of the distant noise band (32–56 cpf) had little effect. The d' across all observers was 2.164 for

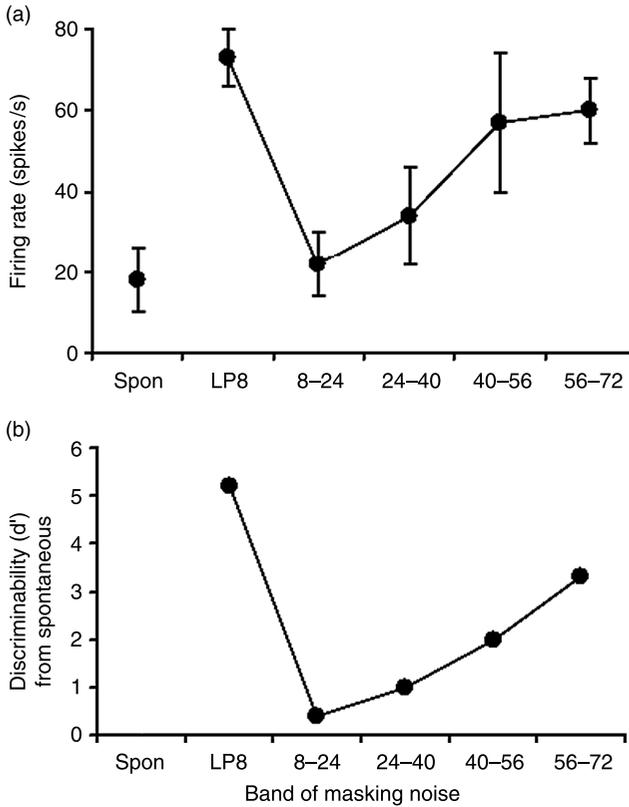


Figure 5. Critical band masking. The responses of one of the macaque face-selective neurons to the set of unmasked and masked face stimuli. (a) The responses are shown as the mean firing rate across trials measured in a 500 ms period starting 100 ms after stimulus onset, \pm the standard deviation, in 10 trials. The main effect of the stimuli in an ANOVA (calculated over the unmasked low-pass filtered and the four masked faces) was significant at the $p < .01$ level ($F = 8.2$, $df = 31$). Neuman–Keuls *post hoc* analyses showed that the responses to the low-pass face masked with the 8–24 and 24–40 cycles per image noise masks were significantly less than to the unmasked low-pass filtered face ($p < .01$ and $p < .02$, respectively), and also were significantly less than to each of the low-pass faces masked with the 40–56 and 56–72 cycle per face noise masks (all $p < .05$). (b) The values are expressed as discriminability (d') from the spontaneous firing rate (see text).

the LP8 face, 1.624 for the case with adjacent masking noise, and 2.106 for the distant masking noise. The ANOVA was significant ($p < .007$) and there were significant differences between the adjacent mask compared with the no mask and the distant mask conditions ($p < .01$ and $p < .05$, respectively), and no difference between the LP8 and the distant noise mask conditions.

The results show that critical band masking by spatial frequency noise masks occurs for the responses of face-selective neurons in the cortex in the anterior part of the superior temporal sulcus, at sites similar to those illustrated by Baylis *et al.* (1985). Critical band masking was also found with similar stimuli in humans, and d' was reduced by 0.5 more than by a mask outside the critical band. The similarity of the human and neurophysiological results is an indication that these face-selective neurons found in the

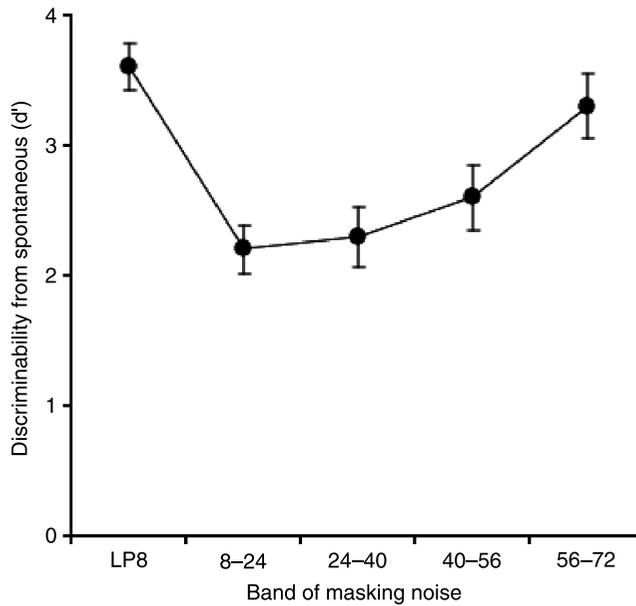


Figure 6. Critical band masking. The mean responses (\pm sem) of the population of 29 neurons to the unmasked and masked images, expressed as d' as in Figure 5.

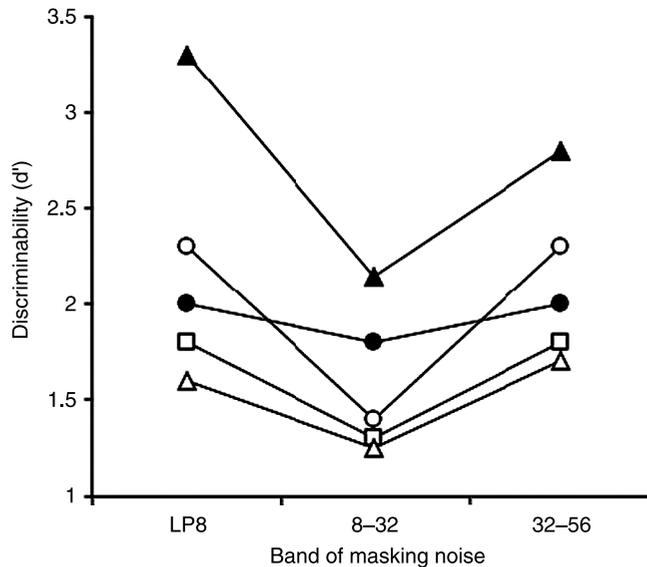


Figure 7. Critical band masking. The discriminability (d') of the masked and unmasked images for five human observers with a stimulus presentation time of 100 ms. The task was to discriminate which of four faces had been shown for each mask condition (no mask, noise added in the band 8–32 cycles per image, and noise added in the band 32–56 cycles per image).

temporal lobe are closely related to face recognition in humans. The finding that it was easier to disrupt the responses of single neurons with the mask than of human visual perception is an indication that the responses of many single neurons are involved in the type of perceptual judgements that were made in this investigation.

The critical band extended out to at least $3w$ neurophysiologically, in that the face image contained spatial frequencies up to 8 c/f, and masking was found with noise in the range 24–40 c/f ($3\text{--}5w$). This is an indication that the spatial frequency channels at this level of the visual system must be very wide, as suggested by Rolls *et al.* (1985). The implication in turn of this is that it is unlikely that the basis for the capability of the primate ventral visual system in face and object recognition depends on computations performed in the spatial frequency domain that depend on finely tuned spatial frequency channels. The implication instead is that face recognition as implemented by the neurons in the temporal lobe depend on computations that can make good use of information from a broad range of spatial frequencies, so that even quite distant ($3w$) noise can interfere with the computation.

12. Possible computational mechanisms in the visual cortex for face and object recognition

The neurophysiological findings described above and wider considerations on the possible computational properties of the cerebral cortex (Rolls, 1989a, 1989b, 1992; Rolls & Treves, 1998) lead to the following outline working hypotheses on object (including face) recognition by visual cortical mechanisms (Rolls, 2008; Rolls & Deco, 2002).

Cortical visual processing for object recognition is considered to be organized as a set of hierarchically connected cortical regions consisting at least of V1, V2, V4, posterior inferior temporal cortex (TEO), inferior temporal cortex (e.g. TE3, TEa, and TEm), and anterior temporal cortical areas (e.g. TE2 and TE1). There is convergence from each small part of a region to the succeeding region (or layer in the hierarchy) in such a way that the receptive field sizes of neurons (e.g. 1° near the fovea in V1) become larger by a factor of approximately 2.5 with each succeeding stage (see Figure 8a). Such zones of convergence would overlap continuously with each other (see Figure 8a). This connectivity would be part of the architecture by which translation invariant representations are computed. Each layer is considered to act partly as a set of local self-organizing competitive neuronal networks with overlapping inputs.

Translation, size, view, lighting, and spatial frequency invariance could be computed in such a system by utilizing competitive learning operating across short time scales to detect regularities in inputs when real objects are transforming in the physical world (Rolls, 1992, 2000a; Rolls & Deco, 2002; Wallis & Rolls, 1997). The hypothesis is that because objects have continuous properties in space and time in the world, an object at one place on the retina might activate feature analysers at the next stage of cortical processing, and when the object was translated to a nearby position, because this would occur in a short period (e.g. 0.5 s), the membrane of the postsynaptic neuron would still be in its ‘Hebb-modifiable’ state (caused, for example, by calcium entry as a result of the voltage-dependent activation of NMDA receptors, or by continuing firing of the neuron implemented by recurrent collateral connections forming a short-term memory), and the presynaptic afferents activated with the object in its new position would thus become strengthened on the still-activated postsynaptic neuron. It is suggested that the short temporal window (e.g. 0.5 s) of Hebb-modifiability helps neurons to learn the statistics of objects moving in the physical world, and at the same time to form different representations of different feature combinations or objects, as these are physically discontinuous and present less regular correlations to the visual

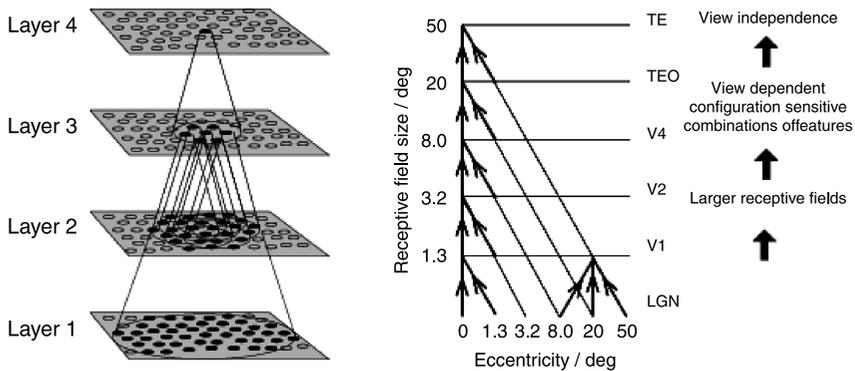


Figure 8. Right. Schematic diagram showing convergence achieved by the forward projections in the visual system, and the types of representation that may be built by competitive networks operating at each stage of the system from the primary visual cortex (V1) to the inferior temporal visual cortex (area TE) (see text). LGN, lateral geniculate nucleus. Area TEO forms the posterior inferior temporal cortex. The receptive fields in the inferior temporal visual cortex (e.g. in the TE areas) cross the vertical midline (not shown). Left. Hierarchical network structure of VisNet.

system. Other invariances, for example, size, spatial frequency, rotation, and view invariance, could be learned by similar mechanisms to those just described.

To test and clarify the hypotheses just described about how the visual system may operate to learn invariant object recognition, we have performed simulations which implement many of the ideas just described, and which are consistent with and based on much of the neurophysiology summarized above. The network simulated (VisNet, Figure 8) can perform object, including face, recognition in a biologically plausible way, and after training shows, for example, translation and view invariance, with the architecture and results reviewed elsewhere (Rolls, 2008; Rolls & Deco, 2002; Rolls & Milward, 2000; Rolls & Stringer, 2006b; Wallis & Rolls, 1997). The approach has also been extended to show that spatial continuity as objects gradually transform during training can be used with a purely associative learning rule to help build invariant representations (Perry, Rolls, & Stringer, 2006, 2008; Rolls & Stringer, 2006b; Stringer, Perry, Rolls, & Proske, 2006).

These results show that the proposed learning mechanism and neural architecture can produce cells with responses selective for stimulus identity with considerable position or view invariance, and can operate in cluttered scenes (Rolls, 2008; Rolls & Deco, 2002; Rolls & Stringer, 2006b). This ability to form invariant representations is an important property of the temporal cortical visual areas, for if a reinforcement association leading to an emotional or social response is learned to one view of a face, that learning will automatically generalize to other views of the face. This is a fundamental aspect of the way in which the brain is organized in order to allow this type of capability for emotional and social behaviour (Rolls, 1999a; 2005).

13. Models of attention, and their implications for neuropsychology, including object-based neglect

Top-down biased competition models of attention (Desimone & Duncan, 1995) are now becoming sufficiently developed that they can provide an account of interactions

between the dorsal and ventral visual systems (Deco & Rolls, 2004, 2005a; Rolls & Deco, 2002), of how non-linearities important in attention are implemented at the neuronal and biophysical level (Deco & Rolls, 2005b), of how fMRI signals may reflect the synaptic and neuronal mechanisms involved in attention (Deco, Rolls, & Horwitz, 2004), and of the psychophysics (Rolls & Deco, 2002) and neuropsychiatry (Loh, Rolls, & Deco, 2007a) of attention. These concepts are also being applied to the neuropsychology of attention, including object-based visual neglect understood in terms of a gradient of damage increasing to the right of the parietal cortex; the difficulty of disengaging attention; extinction and visual search; the effect on neglect of top-down knowledge; alterations in the search of hierarchical patterns after brain damage; and alterations in conjunction search after brain damage (Deco, Heinke, Zihl, & Humphreys, 2002; Deco & Zihl, 2001; Rolls, 2008; Rolls & Deco, 2002). It was possible to account, for example, for the neglect of the left half of each object arranged in a row of objects by local lateral inhibition interacting with damage increasing in a graded way to the right of the parietal cortex (Deco & Rolls, 2002).

14. Different neural systems are specialized for face expression decoding and for face recognition

It has been shown that some neurons respond to face identity and others to face expression (Hasselmo, Rolls, & Baylis, 1989). The neurons responsive to expression were found primarily in the cortex in the superior temporal sulcus, while the neurons responsive to identity (described in the preceding sections) were found in the inferior temporal gyrus including areas TEa and TE_m. Information about facial expression is of potential use in social interactions (Rolls, 1984, 1986a, 1986b, 1990, 1999a, 2005). Damage to this population may contribute to the deficits in social and emotional behaviour which are part of the Kluver-Bucy syndrome produced by temporal lobe damage in monkeys (see Leonard *et al.*, 1985; Rolls, 1981, 1984, 1986a, 1986b, 1990, 1999a, 2005).

A further way in which some of these neurons in the cortex in the superior temporal sulcus may be involved in social interactions is that some of them respond to gestures, e.g. to a face undergoing ventral flexion, as described above (Hasselmo, Rolls, & Baylis, 1989) and by Perrett *et al.* (1985). Moreover, the neuronal responses to head motion are in head-based coordinates, that is they show invariance (Hasselmo, Rolls, & Baylis, 1989), and this has been modelled in a version of VisNet that includes visual motion flow inputs and computes invariant representations of global flow (Rolls & Stringer, 2006a). The interpretation of these neurons as being useful for social interactions is that in some cases these neurons respond not only to ventral head flexion, but also to the eyes lowering and the eyelids closing (Hasselmo, Rolls, & Baylis, 1989). These two movements (head lowering and eyelid lowering) often occur together when a monkey is breaking social contact with another. It is also important when decoding facial expression to retain some information about the head direction of the face stimulus being seen relative to the observer, for this is very important in determining whether a threat is being made in your direction. The presence of view-dependent, head and body gesture (Hasselmo, Rolls, Baylis *et al.*, 1989), and eye-gaze (Perrett, Smith, Mistlin *et al.*, 1985) representations in some of these cortical regions where face expression is represented is consistent with this requirement. In contrast, the TE areas (more ventral, mainly in the macaque inferior temporal gyrus), in which neurons tuned to face identity

(Hasselmo, Rolls, & Baylis, 1989) and with view-independent responses (Hasselmo, Rolls, Baylis *et al.*, 1989) are more likely to be found, may be more related to a view invariant representation of identity. Of course, for appropriate social and emotional responses, both types of subsystem would be important, for it is necessary to know both the direction of a social gesture, and the identity of the individual, in order to make the correct social or emotional response.

15. A representation of faces in the amygdala

Outputs from the temporal cortical visual areas reach the amygdala and the orbitofrontal cortex, and evidence is accumulating that these brain areas are involved in social and emotional responses to faces (Rolls, 1990, 1999a, 2000b, 2005; Rolls & Deco, 2002). For example, lesions of the amygdala in monkeys disrupt social and emotional responses to faces, and we have identified a population of neurons with face-selective responses in the primate amygdala (Leonard *et al.*, 1985), some of which may respond to facial and body gesture (Brothers, Ring, & Kling, 1990). The amygdala representation of faces is discussed further in section 16.

16. A representation of faces in the orbitofrontal cortex

Rolls *et al.* have found a number of face-responsive neurons in the orbitofrontal cortex, and they are also present in adjacent prefrontal cortical areas (Wilson, O'Scalaidhe, & Goldman-Rakic, 1993). The orbitofrontal cortex face-responsive neurons, first observed by Thorpe, Rolls, & Maddison (1983), and then by Rolls *et al.*, (2006) tend to respond with longer latencies than temporal lobe neurons (140–200 ms typically, compared with 80–100 ms); they also convey information about which face is being seen, by having different responses to different faces (see Figure 9); and are typically rather harder to activate strongly than temporal cortical face-selective neurons, in that many of them respond much better to real faces than to two-dimensional images of faces on a video monitor (Rolls & Baylis, 1986). Some of the orbitofrontal cortex face-selective neurons are responsive to face gesture or movement, and others to face expression (Rolls, Critchley *et al.*, 2006). The findings are consistent with the likelihood that these neurons are activated via the inputs from the temporal cortical visual areas in which face-selective neurons are found. The significance of the neurons is likely to be related to the fact that faces convey information that is important in social reinforcement, both by conveying face expression (cf. Hasselmo, Rolls, & Baylis, 1989), which can indicate reinforcement, and by encoding information about which individual is present, also important in evaluating and utilizing reinforcing inputs in social situations. Consistent with a role in reinforcement for face-selective neurons in the orbitofrontal cortex, activations in the orbitofrontal cortex are related to the attractiveness of a face (O'Doherty *et al.*, 2003).

We have also been able to obtain evidence that non-reward used as a signal to reverse behavioural choice is represented in the human orbitofrontal cortex (for background see Rolls, 2005). Kringelbach and Rolls used the faces of two different people, and if one face was selected then that face smiled and if the other was selected, the face showed an angry expression. After good performance was acquired, there were repeated reversals of the visual discrimination task. Kringelbach and Rolls found that activation of a lateral

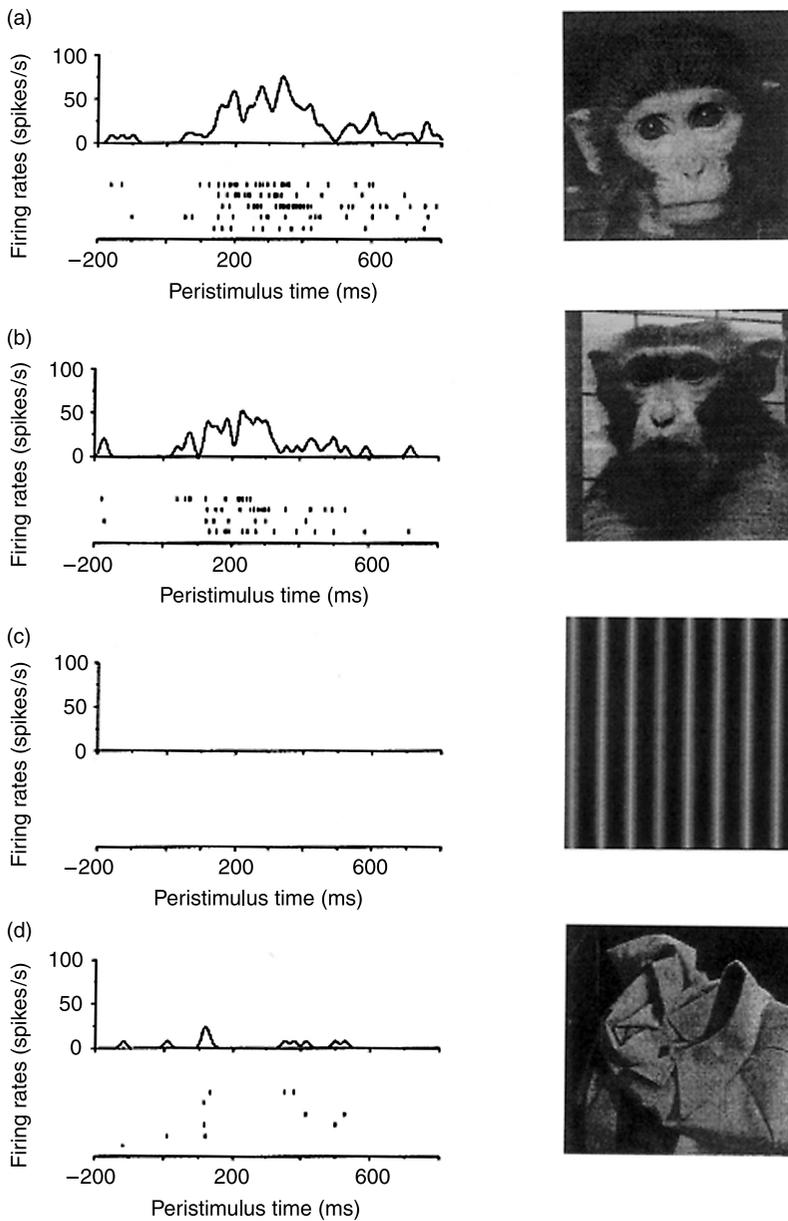


Figure 9. Orbitofrontal cortex face-selective neuron as found in macaques. Peristimulus rastergrams and time histograms are shown. Each trial is a row in the rastergram. Several trials for each stimulus are shown. The ordinate is in spikes/s. The neuron responded best to face (a), also responded, though less to face (b), had different responses to other faces (not shown), and did not respond to non-face stimuli (e.g. (c) and (d)). The stimulus appeared at time 0 on a video monitor. (After Rolls, Critchley, Browning, & Inoue, 2006).

part of the orbitofrontal cortex in the fMRI study was produced on the error trials, that is when the human chose a face, and did not obtain the expected reward (see Figures 10 and 11). Control tasks showed that the response was related to the error, and the mismatch between what was expected and what was obtained, in that just showing an angry face expression did not selectively activate this part of the lateral orbitofrontal cortex. An interesting aspect of this study that makes it relevant to human social behaviour is that the conditioned stimuli were faces of particular individuals, and the unconditioned stimuli were face expressions. Moreover, the study reveals that the human orbitofrontal cortex is very sensitive to social feedback when it must be used to change behaviour (Kringelbach & Rolls, 2003; 2004; Rolls, 2005).

To investigate the possible significance of face-related inputs to the orbitofrontal cortex visual neurons described above, we also tested the responses to faces of patients with orbitofrontal cortex damage. We included tests of face (and also voice) expression decoding, because these are ways in which the reinforcing quality of individuals is often indicated. Impairments in the identification of facial and vocal emotional expression were demonstrated in a group of patients with ventral frontal lobe damage who had socially inappropriate behaviour (Hornak, Rolls, & Wade, 1996; Rolls, 1999b). The expression identification impairments could occur independently of perceptual impairments in facial recognition, voice discrimination, or environmental sound recognition. The face and voice expression problems did not necessarily occur together

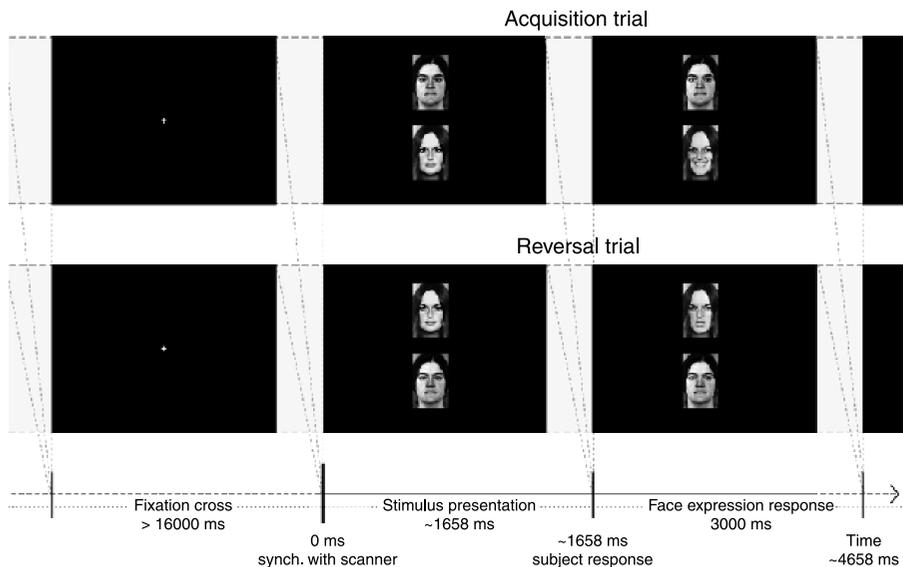


Figure 10. Social reversal task: The trial starts synchronized with the scanner and two people with neutral face expressions are presented to the subject. The subject has to select one of the people by pressing the corresponding button, and the person will then either smile or show an angry face expression for 3,000 ms depending on the current mood of the person. The task for the subject is to keep track of the mood of each person and choose the 'happy' person as much as possible (upper row). Over time (after between 4 and 8 correct trials), this will change so that the 'happy' person becomes 'angry' and *vice versa*, and the subject has to learn to adapt her choices accordingly (bottom row). Randomly intermixed trials with either two men or two women were used to control for possible gender and identification effects, and a fixation cross was presented between trials for at least 16,000 ms. (After Kringelbach & Rolls, 2003).

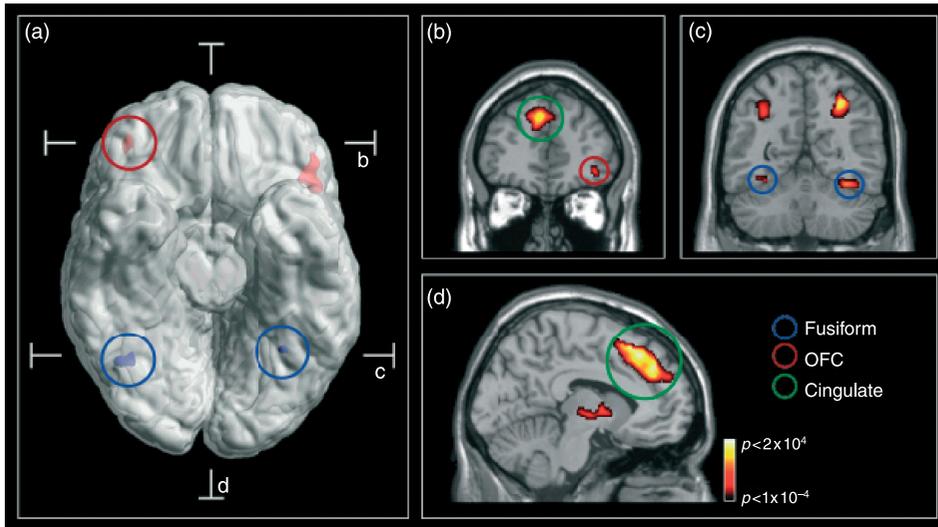


Figure 11. Social reversal: Composite figure showing that changing behaviour based on face expression is correlated with increased brain activity in the human orbitofrontal cortex. (a) The figure is based on two different group statistical contrasts from the neuroimaging data which are superimposed on a ventral view of the human brain with the cerebellum removed, and with indication of the location of the two coronal slices (b,c) and the transverse slice (d). The red activations in the orbitofrontal cortex (denoted OFC, maximal activation: $Z = 4.94$; $x, y, z = 42, 42, 8$; and $Z = 5.51$) shown on the rendered brain arise from a comparison of reversal events with stable acquisition events, while the blue activations in the fusiform gyrus (denoted Fusiform, maximal activation: $Z > 8$; $36, -60, -20$ and $Z = 7.80$; $-30, -56, -16$) arise from the main effects of face expression. (b) The coronal slice through the frontal part of the brain shows the cluster in the right orbitofrontal cortex across all nine subjects when comparing reversal events with stable acquisition events. Significant activity was also seen in an extended area of the anterior cingulate/paracingulate cortex (denoted Cingulate, maximal activation: $Z = 6.88$; $-8, 22, 52$; green circle). (c) The coronal slice through the posterior part of the brain shows the brain response to the main effects of face expression with significant activation in the fusiform gyrus and the cortex in the intraparietal sulcus (maximal activation: $Z > 8$; $32, -60, 46$; and $Z > 8$; $-32, -60, 44$). (d) The transverse slice shows the extent of the activation in the anterior cingulate/paracingulate cortex when comparing reversal events with stable acquisition events. Group statistical results are superimposed on a ventral view of the human brain with the cerebellum removed, and on coronal and transverse slices of the same template brain (activations are thresholded at $p = .0001$ for purposes of illustration to show their extent). (After Kringelbach & Rolls, 2003).

in the same patients, providing an indication of separate processing. Poor performance on both expression tests was correlated with the degree of alteration of emotional experience reported by the patients. There was also a strong positive correlation between the degree of altered emotional experience and the severity of the behavioural problems (e.g. disinhibition) found in these patients. A comparison group of patients with brain damage outside the ventral frontal lobe region, without these behavioural problems, was unimpaired on the face expression identification test, was significantly less impaired at vocal expression identification, and reported little subjective emotional change (Hornak *et al.*, 1996; Rolls, 1999b).

To obtain clear evidence that the changes in face and voice expression identification, emotional behaviour, and subjective emotional state were related to orbitofrontal cortex damage itself, and not to damage to surrounding areas which is present in many closed head injury patients, we performed further assessments in patients with circumscribed lesions made surgically in the course of treatment (Hornak *et al.*, 2003). This study also enabled us to determine whether there was functional specialization within the orbitofrontal cortex, and whether damage to nearby and connected areas (such as the anterior cingulate cortex) in which some of the patients had lesions could produce similar effects. We found that some patients with bilateral lesions of the orbitofrontal cortex had deficits in voice and face expression identification, and the group had impairments in social behaviour and significant changes in their subjective emotional state (Hornak *et al.*, 2003). (The same group of patients had deficits on a probabilistic monetary reward reversal task, indicating that they have difficulty not only in representing reinforcers such as face expression, but also in using reinforcers (such as monetary reward) to influence behaviour (Hornak *et al.*, 2004)). Some patients with unilateral damage restricted to the orbitofrontal cortex also had deficits in voice expression identification, and the group did not have significant changes in social behaviour, or in their subjective emotional state. Patients with unilateral lesions of the antero-ventral part of the anterior cingulate cortex and/or medial prefrontal cortex area BA9 were in some cases impaired on voice and face expression identification, had some change in social behaviour, and had significant changes in their subjective emotional state. Patients with dorsolateral prefrontal cortex lesions or with medial lesions outside the anterior cingulate cortex and medial prefrontal BA9 areas were unimpaired on any of these measures of emotion. In all cases in which voice expression identification was impaired, there were no deficits in control tests of the discrimination of unfamiliar voices and the recognition of environmental sounds.

These results (Hornak *et al.*, 2003) thus confirm that the damage restricted to the orbitofrontal cortex can produce impairments in face and voice expression identification, which may be primary reinforcers. The system is sensitive, in that even patients with unilateral orbitofrontal cortex lesions may be impaired. The impairment is not a generic impairment of the ability to recognize any emotions in others, in that frequently voice but not face expression identification was impaired, and *vice versa*. This implies some functional specialization for visual versus auditory emotion-related processing in the human orbitofrontal cortex. The results also show that the changes in social behaviour can be produced by damage restricted to the orbitofrontal cortex. The patients were particularly likely to be impaired on emotion recognition (they were less likely to notice when others were sad, happy, or disgusted); on emotional empathy (they were less likely to comfort those who are sad, afraid, or to feel happy for others who are happy); on interpersonal relationships (not caring what others think and not being close to his/her family); and were less likely to cooperate with others; were impatient and impulsive; and had difficulty in making and keeping close relationships. The results also show that changes in subjective emotional state (including frequently sadness, anger, and happiness) can be produced by damage restricted to the orbitofrontal cortex (Hornak *et al.*, 2003). In addition, the patients with bilateral orbitofrontal cortex lesions were impaired on the probabilistic reversal learning task (Hornak *et al.*, 2004). The findings overall thus make clear the types of deficit found in humans with orbitofrontal cortex damage, and can be directly related to underlying fundamental processes in which

the orbitofrontal cortex is involved (see Rolls, 2005), including decoding and representing primary reinforcers (including face expression), being sensitive to changes in reinforcers, and rapidly readjusting behaviour to stimuli when the reinforcers available change.

The results (Hornak *et al.*, 2003) also extend these investigations to the anterior cingulate cortex (including some of medial prefrontal cortex area BA9) by showing that lesions in these regions can produce voice and/or face expression identification deficits, and marked changes in subjective emotional state.

It is of interest that the range of face expressions for which identification is impaired by orbitofrontal cortex damage (Hornak *et al.*, 2003, 1996; Rolls, 1999b) is more extensive than the impairment in identifying primarily fear face expressions produced by amygdala damage in humans (Adolphs, Baron-Cohen, & Tranel, 2002; Adolphs *et al.*, 2005; Calder *et al.*, 1996) (for review see Rolls, 2005). In addition, the deficits in emotional and social behaviour described above that are produced by orbitofrontal cortex damage in humans seem to be more pronounced than changes in emotional behaviour produced by amygdala damage in humans, although deficits in autonomic conditioning can be demonstrated (Phelps, 2004). This suggests that in humans and other primates the orbitofrontal cortex may become more important than the amygdala in emotion, and possible reasons for this including the more powerful architecture for rapid learning and reversal that may be facilitated by the functional architecture of the neocortex with its highly developed recurrent collateral connections which may help to support short-term memory attractor states are considered by Rolls (2005).

17. Conclusions and future directions

Neurophysiological investigations of the inferior temporal cortex are revealing at least part of the way in which neuronal firing encodes information about faces and objects and are showing that one representation implements several types of invariance. The representation found has clear utility for the receiving networks. These neurophysiological findings are stimulating the development of computational self-organizing neuronal network models which suggest that part of the process involves the operation of a modified Hebb learning rule with a short-term memory trace to help the system learn invariances from the statistical properties of the inputs it receives. Neurons in the inferior temporal cortex which encode the identity of faces and have considerable invariance and a sparse distributed representation are ideal as an input to stimulus-reinforcer association learning mechanisms in the orbitofrontal cortex and amygdala which enable appropriate emotional and social responses to be made to different individuals. The neurons in the cortex in the superior temporal sulcus which respond to face expression, or for other neurons to eye-gaze, or for others to head movement, encode reinforcement-related information that is important in making the correct emotional and social responses to a face. Neurons of both these main types are also found in the orbitofrontal cortex (Rolls, Critchley *et al.*, 2006) and are important in human social and emotional behaviour, which are changed after damage to the orbitofrontal cortex. A more comprehensive description of the reinforcement-related signals and processing in brain regions such as the orbitofrontal cortex that are important in emotional and social behaviour, and how these depend on inputs from the temporal cortex visual areas, is provided elsewhere (Rolls, 2005).

Among key questions raised by this research are the following:

How does the brain learn invariant representations of individual objects in complex natural scenes? Part of the solution may be the reduced receptive field sizes of inferior temporal cortex neurons in complex scenes which helps to reduce interference from other stimuli (Rolls, Aggelopoulos *et al.*, 2003). Part of the solution may be top-down attentional facilitation, which if directed at a spatial location would increase the activity of neurons at that location which would, given the statistics of the world, be likely to contain the features of one or at most a few objects (Deco & Rolls, 2004; Rolls, 2008; Rolls & Deco, 2002, 2006). Part of the solution may be the interesting discovery that in competitive networks, which may provide the basis for the computations in feedforward hierarchical networks involved in face and object recognition, representations can be learned about individual objects if they are paired during learning with different objects on each occasion (Stringer & Rolls, in press).

How are multiple objects represented in a scene, even in a single glance? Part of the solution may be the asymmetry of the receptive fields of inferior temporal cortex neurons, which across neurons enable several objects close to the fovea, and their position relative to the fovea, to be encoded (Aggelopoulos & Rolls, 2005). But it is an interesting issue about how this information may be loaded into a visuospatial scratchpad short-term memory (Rolls, 2008).

What are the relative contributions of temporal continuity and spatial continuity in the learning of invariant representations of faces and objects? Both can be used and each has advantages (Perry *et al.*, 2006, 2008; Rolls, 2008; Rolls & Stringer, 2006b; Stringer *et al.*, 2006; Stringer & Rolls, 2006). Part of the answer may come from understanding how variations in the images presented to the retina in real time and position interact with the time constants of the neuronal processing systems they engage in the cortex, which include the moderately long-time constants of NMDA receptors (of order 100 ms), and the longer integration of information afforded by attractor short-term memory circuits implemented by recurrent collateral connections in the neocortex, which in the inferior temporal cortex enable firing to be maintained for 100 ms or more after stimulus offset (Rolls, 2008). One way to approach this is with integrate and fire simulations of learning in a VisNet-like architecture (Rolls, 2008) with stimuli presented at a time scale corresponding to that in the real world.

Another key issue is the high capacity of the face and object recognition systems. Although current models such as VisNet capture many of the computational mechanisms by which the brain may learn invariant representations (Rolls, 2008; Rolls & Deco, 2002; Rolls & Stringer, 2006b; Wallis & Rolls, 1997), the actual network simulated is quite small (1,024 neurons per layer and 4 layers), and it is not clear how the system will scale up. This will be an important issue for future research.

Another interesting issue is how decisions are made in visual perception, as well as in terms of behavioural choice. An approach to decision-making is the probabilistic settling of an attractor short-term memory network when it is biased with two or more inputs, each representing in this case the strength of the evidence for a particular decision (Deco & Rolls, 2006; Wang, 2002). It will be interesting to extend this approach to decision making in perception, in situations such as pattern rivalry, the probabilistic flipping of a Necker cube, and, more generally, the many situations in vision in which there are ambiguities in the nature of the interpretation of the visual scene (Rolls, 2008).

Finally, although many neuropsychological phenomena are starting to be understood at the level of operation of the neural machinery in the brain, including, for example, many types of attentional and neglect disorder including object-based neglect (Deco &

Rolls, 2002; Rolls & Deco, 2002), we may be mainly at the beginning of such explorations, with, for example, the rich area of the dynamics of the operation of the system, and the reasons for its non-linearities and instabilities, just starting to be explored (Deco & Rolls, 2004, 2005a; 2005b, 2005c; Deco, Rolls, & Horwitz, 2004; Loh *et al.*, 2007a; Loh, Rolls, & Deco, 2007b; Rolls, 2008; Rolls & Deco, 2002; Rolls & Deco, 2006).

Acknowledgements

The author has worked on some of the investigations described here with N. Aggelopoulos, P. Azzopardi, G. C. Baylis, H. Critchley, G. Deco, P. Földiák, L. Franco, M. E. Hasselmo, J. Hornak, M. Kadohisa, C. M. Leonard, T. J. Milward, D. I. Perrett, S. M. Stringer, M. J. Tovee, A. Treves, T. W. Vidyasagar and G. Wallis, and their collaboration is sincerely acknowledged. The experiments on critical band masking were performed by E. T. Rolls, G. C. Baylis, and T. R. Vidyasagar. Different parts of the research described were supported by the Medical Research Council, PG8513790; by The Wellcome Trust; by a Human Frontier Science Program grant; by an EC Human Capital and Mobility grant; by the MRC Oxford Interdisciplinary Research Centre in Cognitive Neuroscience; and by the Oxford McDonnell Centre in Cognitive Neuroscience. Procedures were carried out at Oxford University in accordance with the NIH Guide for the Care and Use of Laboratory Animals, and were licensed under the UK Animals (Scientific Procedures) Act, 1986.

References

- Abbott, L. F., Rolls, E. T., & Tovee, M. J. (1996). Representational capacity of face coding in monkeys. *Cerebral Cortex*, *6*, 498–505.
- Adolphs, R., Baron-Cohen, S., & Tranel, D. (2002). Impaired recognition of social emotions following amygdala damage. *Journal of Cognitive Neuroscience*, *14*, 1264–1274.
- Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, *433*(7021), 68–72.
- Aggelopoulos, N. C., Franco, L., & Rolls, E. T. (2005). Object perception in natural scenes: Encoding by inferior temporal cortex simultaneously recorded neurons. *Journal of Neurophysiology*, *93*, 1342–1357.
- Aggelopoulos, N. C., & Rolls, E. T. (2005). Natural scene perception: Inferior temporal cortex neurons encode the positions of different objects in the scene. *European Journal of Neuroscience*, *22*, 2903–2916.
- Baddeley, R. J., Abbott, L. F., Booth, M. J. A., Sengpiel, F., Freeman, T., Wakeman, E. A., *et al.* (1997). Responses of neurons in primary and inferior temporal visual cortices to natural scenes. *Proceedings of the Royal Society of London B*, *264*, 1775–1783.
- Baizer, J. S., Ungerleider, L. G., & Desimone, R. (1991). Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *Journal of Neuroscience*, *11*, 168–190.
- Ballard, D. H. (1993). Subsymbolic modelling of hand-eye coordination. In D. E. Broadbent (Ed.), *The simulation of human intelligence* (pp. 71–102). Oxford: Blackwell.
- Barlow, H. B. (1972). Single units and sensation: A neuron doctrine for perceptual psychology? *Perception*, *1*(4), 371–394.
- Baylis, G. C., Rolls, E. T., & Leonard, C. M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. *Brain Research*, *342*, 91–102.
- Baylis, G. C., Rolls, E. T., & Leonard, C. M. (1987). Functional subdivisions of the temporal lobe neocortex. *Journal of Neuroscience*, *7*, 330–342.
- Booth, M. C. A., & Rolls, E. T. (1998). View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. *Cerebral Cortex*, *8*, 510–523.

- Brothers, L., Ring, B., & Kling, A. (1990). Response of neurons in the macaque amygdala to complex social stimuli. *Behavioural Brain Research*, *41*(3), 199-213.
- Bruce, C., Desimone, R., & Gross, C. G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *Journal of Neurophysiology*, *46*(2), 369-384.
- Calder, A. J., Young, A. W., Rowland, D., Perrett, D. I., Hodges, J. R., & Etcoff, N. L. (1996). Facial emotion recognition after bilateral amygdala damage: Differentially severe impairment of fear. *Cognitive Neuropsychology*, *13*, 699-745.
- Deco, G., Heinke, D., Zihl, J., & Humphreys, G. (2002). A computational neuroscience account of visual neglect. *Neurocomputing*, *44-46*, 811-816.
- Deco, G., & Rolls, E. T. (2002). Object-based visual neglect: A computational hypothesis. *European Journal of Neuroscience*, *16*, 1994-2000.
- Deco, G., & Rolls, E. T. (2004). A neurodynamical cortical model of visual attention and invariant object recognition. *Vision Research*, *44*, 621-644.
- Deco, G., & Rolls, E. T. (2005a). Attention, short-term memory, and action selection: A unifying theory. *Progress in Neurobiology*, *76*, 236-256.
- Deco, G., & Rolls, E. T. (2005b). Neurodynamics of biased competition and co-operation for attention: A model with spiking neurons. *Journal of Neurophysiology*, *94*, 295-313.
- Deco, G., & Rolls, E. T. (2005c). Sequential memory: A putative neural and synaptic dynamical mechanism. *Journal of Cognitive Neuroscience*, *17*, 294-307.
- Deco, G., & Rolls, E. T. (2006). Decision-making and Weber's Law: A neurophysiological model. *European Journal of Neuroscience*, *24*, 901-916.
- Deco, G., Rolls, E. T., & Horwitz, B. (2004). 'What' and 'where' in visual working memory: A computational neurodynamical perspective for integrating fMRI and single-neuron data. *Journal of Cognitive Neuroscience*, *16*, 683-701.
- Deco, G., & Zihl, J. (2001). Top-down selective visual attention: A neurodynamical approach. *Visual Cognition*, *8*, 119-140.
- Desimone, R. (1991). Face-selective cells in the temporal cortex of monkeys. *Journal of Cognitive Neuroscience*, *3*, 1-8.
- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, *4*, 2051-2062.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193-222.
- Desimone, R., & Gross, C. G. (1979). Visual areas in the temporal cortex of the macaque. *Brain Research*, *178*, 363-380.
- DiCarlo, J. J., & Maunsell, J. H. (2003). Anterior inferotemporal neurons of monkeys engaged in object recognition can be highly sensitive to object retinal position. *Journal of Neurophysiology*, *89*, 3264-3278.
- Dolan, R. J., Fink, G. R., Rolls, E. T., Booth, M., Holmes, A., Frackowiak, R. S. J., *et al.* (1997). How the brain learns to see objects and faces in an impoverished context. *Nature*, *389*, 596-599.
- Elliffe, M. C. M., Rolls, E. T., & Stringer, S. M. (2002). Invariant recognition of feature combinations in the visual system. *Biological Cybernetics*, *86*, 59-71.
- Engel, A. K., Konig, P., Kreiter, A. K., Schillen, T. B., & Singer, W. (1992). Temporal coding in the visual system: New vistas on integration in the nervous system. *Trends in Neurosciences*, *15*, 218-226.
- Franco, L., Rolls, E. T., Aggelopoulos, N. C., & Jerez, J. M. (2007). Neuronal selectivity, population sparseness, and ergodicity in the inferior temporal visual cortex. *Biological Cybernetics*, *96*, 547-560.
- Franco, L., Rolls, E. T., Aggelopoulos, N. C., & Treves, A. (2004). The use of decoding to analyze the contribution to the information of the correlations between the firing of simultaneously recorded neurons. *Experimental Brain Research*, *155*, 370-384.
- Gallant, J. L., Connor, C. E., & Van Essen, D. C. (1998). Neural activity in areas V1, V2 and V4 during free viewing of natural scenes compared to controlled viewing. *NeuroReport*, *9*, 85-89.

- Gawne, T. J., & Richmond, B. J. (1993). How independent are the messages carried by adjacent inferior temporal cortical neurons? *Journal of Neuroscience*, *13*, 2758-2771.
- Georges-François, P., Rolls, E. T., & Robertson, R. G. (1999). Spatial view cells in the primate hippocampus: Allocentric view not head direction or eye position or place. *Cerebral Cortex*, *9*, 197-212.
- Grill-Spector, K., & Malach, R. (2004). The human visual cortex. *Annual Review of Neuroscience*, *27*, 649-677.
- Grill-Spector, K., Sayres, R., & Ress, D. (2006). High-resolution imaging reveals highly selective nonface clusters in the fusiform face area. *Nature Neuroscience*, *9*(9), 1177-1185.
- Gross, C. G., Desimone, R., Albright, T. D., & Schwartz, E. L. (1985). Inferior temporal cortex and pattern recognition. *Experimental Brain Research*, *11*, 179-201.
- Hacker, M. J., & Ratcliff, R. (1979). A revised table of d' for M-alternative forced choice. *Perception and Psychophysics*, *26*, 168-170.
- Harmon, L. D., & Julesz, B. (1973). Masking in visual recognition: Effects of two-dimensional filtered noise. *Science*, *180*, 1194-1197.
- Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research*, *32*, 203-218.
- Hasselmo, M. E., Rolls, E. T., Baylis, G. C., & Nalwa, V. (1989). Object-centred encoding by face-selective neurons in the cortex in the superior temporal sulcus of the the monkey. *Experimental Brain Research*, *75*, 417-429.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, *51*, 59-67.
- Hornak, J., Bramham, J., Rolls, E. T., Morris, R. G., O'Doherty, J., Bullock, P. R., *et al.* (2003). Changes in emotion after circumscribed surgical lesions of the orbitofrontal and cingulate cortices. *Brain*, *126*, 1691-1712.
- Hornak, J., O'Doherty, J., Bramham, J., Rolls, E. T., Morris, R. G., Bullock, P. R., *et al.* (2004). Reward-related reversal learning after surgical excisions in orbitofrontal and dorsolateral prefrontal cortex in humans. *Journal of Cognitive Neuroscience*, *16*, 463-478.
- Hornak, J., Rolls, E. T., & Wade, D. (1996). Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. *Neuropsychologia*, *34*, 247-261.
- Kringelbach, M. L., & Rolls, E. T. (2003). Neural correlates of rapid reversal learning in a simple model of human social interaction. *NeuroImage*, *20*, 1371-1383.
- Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: Evidence from neuroimaging and neuropsychology. *Progress in Neurobiology*, *72*, 341-372.
- Leonard, C. M., Rolls, E. T., Wilson, F. A. W., & Baylis, G. C. (1985). Neurons in the amygdala of the monkey with responses selective for faces. *Behavioural Brain Research*, *15*, 159-176.
- Loh, M., Rolls, E. T., & Deco, G. (2007a). A dynamical systems hypothesis of schizophrenia. *PLoS Computational Biology*, *3*(11), e228. doi:210.1371journal.pcbi.0030228.
- Loh, M., Rolls, E. T., & Deco, G. (2007b). Statistical fluctuations in attractor networks related to schizophrenia. *Pharmacopsychiatry*, *40*, 578-584.
- Munsell, J. H., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Reviews in Neuroscience*, *10*, 363-401.
- O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41*, 147-155.
- Op De Beeck, H., & Vogels, R. (2000). Spatial sensitivity of macaque inferior temporal neurons. *Journal of Comparative Neurology*, *426*, 505-518.
- O'Toole, A. J., Jiang, F., Abdi, H., & Haxby, J. V. (2005). Partially distributed representations of objects and faces in ventral temporal cortex. *Journal of Cognitive Neuroscience*, *17*, 580-590.

- Panzeri, S., Biella, G., Rolls, E. T., Skaggs, W. E., & Treves, A. (1996). Speed, noise, information and the graded nature of neuronal responses. *Network*, 7, 365–370.
- Panzeri, S., Rolls, E. T., Battaglia, F., & Lavis, R. (2001). Speed of feedforward and recurrent processing in multilayer networks of integrate-and-fire neurons. *Network: Computation in Neural Systems*, 12, 423–440.
- Panzeri, S., Schultz, S. R., Treves, A., & Rolls, E. T. (1999). Correlations and the encoding of information in the nervous system. *Proceedings of the Royal Society of London B*, 266, 1001–1012.
- Panzeri, S., Treves, A., Schultz, S., & Rolls, E. T. (1999). On decoding the responses of a population of neurons from short time epochs. *Neural Computation*, 11, 1553–1577.
- Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 335(1273), 23–30.
- Perrett, D. I., Rolls, E. T., & Caan, W. (1979). Temporal lobe cells of the monkey with visual responses selective for faces. *Neuroscience Letters*, S3, S358.
- Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurons responsive to faces in the monkey temporal cortex. *Experimental Brain Research*, 47(3), 329–342.
- Perrett, D. I., Smith, P. A. J., Mistlin, A. J., Chitty, A. J., Head, A. S., Potter, D. D., *et al.* (1985). Visual analysis of body movements by neurons in the temporal cortex of the macaque monkey: A preliminary report. *Behavioural Brain Research*, 16, 153–170.
- Perrett, D. I., Smith, P. A., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., *et al.* (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London B*, 223, 293–317.
- Perry, G., Rolls, E. T., & Stringer, S. M. (2006). Spatial vs temporal continuity in view invariant visual object recognition learning. *Vision Research*, 46, 3994–4006.
- Perry, G., Rolls, E. T., & Stringer, S. M. (2008). *Continuous transformation learning of translation invariant representations*. Manuscript in preparation.
- Phelps, E. A. (2004). Human emotion and memory: Interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology*, 14, 198–202.
- Robertson, R. G., Rolls, E. T., & Georges-François, P. (1998). Spatial view cells in the primate hippocampus: Effects of removal of view details. *Journal of Neurophysiology*, 79, 1145–1156.
- Rolls, E. T. (1981). Responses of amygdaloid neurons in the primate. In Y. Ben-Ari (Ed.), *The amygdaloid complex* (pp. 383–393). Amsterdam: Elsevier.
- Rolls, E. T. (1984). Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. *Human Neurobiology*, 3, 209–222.
- Rolls, E. T. (1986a). Neural systems involved in emotion in primates. In R. Plutchik & H. Kellerman (Eds.), *Emotion: Theory, research, and experience*. Vol. 3. *Biological foundations of emotion* (pp. 125–143). New York: Academic Press.
- Rolls, E. T. (1986b). A theory of emotion, and its application to understanding the neural basis of emotion. In Y. Oomura (Ed.), *Emotions: Neural and chemical control* (pp. 325–344). Basel: Karger.
- Rolls, E. T. (1989a). Functions of neuronal networks in the hippocampus and neocortex in memory. In J. H. Byrne & W. O. Berry (Eds.), *Neural models of plasticity: Experimental and theoretical approaches* (pp. 240–265). San Diego, CA: Academic Press.
- Rolls, E. T. (1989b). The representation and storage of information in neuronal networks in the primate cerebral cortex and hippocampus. In R. Durbin, C. Miall, & G. Mitchison (Eds.), *The computing neuron* (pp. 125–159). Wokingham, UK: Addison-Wesley.
- Rolls, E. T. (1990). A theory of emotion, and its application to understanding the neural basis of emotion. *Cognition and Emotion*, 4, 161–190.
- Rolls, E. T. (1991). Neural organisation of higher visual functions. *Current Opinion in Neurobiology*, 1, 274–278.

- Rolls, E. T. (1992). Neurophysiological mechanisms underlying face processing within and beyond the temporal cortical visual areas. *Philosophical Transactions of the Royal Society of London B*, 335, 11–21.
- Rolls, E. T. (1997). A neurophysiological and computational approach to the functions of the temporal lobe cortical visual areas in invariant object recognition. In M. Jenkin & L. Harris (Eds.), *Computational and psychophysical mechanisms of visual coding* (pp. 184–220). Cambridge: Cambridge University Press.
- Rolls, E. T. (1999a). *The brain and emotion*. Oxford: Oxford University Press.
- Rolls, E. T. (1999b). The functions of the orbitofrontal cortex. *Neurocase*, 5, 301–312.
- Rolls, E. T. (1999c). Spatial view cells and the representation of place in the primate hippocampus. *Hippocampus*, 9, 467–480.
- Rolls, E. T. (2000a). Functions of the primate temporal lobe cortical visual areas in invariant visual object and face recognition. *Neuron*, 27, 205–218.
- Rolls, E. T. (2000b). Neurophysiology and functions of the primate amygdala, and the neural basis of emotion. In J. P. Aggleton (Ed.), *The amygdala: A functional analysis* (2nd ed., pp. 447–478). Oxford: Oxford University Press.
- Rolls, E. T. (2003). Consciousness absent and present: A neurophysiological exploration. *Progress in Brain Research*, 144, 95–106.
- Rolls, E. T. (2005). *Emotion explained*. Oxford: Oxford University Press.
- Rolls, E. T. (2007). The representation of information about faces in the temporal and frontal lobes. *Neuropsychologia*, 45, 125–143.
- Rolls, E. T. (2008). *Memory, attention, and decision-making: A unifying computational neuroscience approach*. Oxford: Oxford University Press.
- Rolls, E. T., Aggelopoulos, N. C., Franco, L., & Treves, A. (2004). Information encoding in the inferior temporal cortex: Contributions of the firing rates and correlations between the firing of neurons. *Biological Cybernetics*, 90, 19–32.
- Rolls, E. T., Aggelopoulos, N. C., & Zheng, F. (2003). The receptive fields of inferior temporal cortex neurons in natural scenes. *Journal of Neuroscience*, 23, 339–348.
- Rolls, E. T., & Baylis, G. C. (1986). Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the monkey. *Experimental Brain Research*, 65(1), 38–48.
- Rolls, E. T., Baylis, G. C., & Hasselmo, M. E. (1987). The responses of neurons in the cortex in the superior temporal sulcus of the monkey to band-pass spatial frequency filtered faces. *Vision Research*, 27, 311–326.
- Rolls, E. T., Baylis, G. C., Hasselmo, M., & Nalwa, V. (1989a). The representation of information in the temporal lobe visual cortical areas of macaque monkeys. In J. J. Kulikowski, C. M. Dickinson, & I. J. Murray (Eds.), *Seeing contour and colour*. Oxford: Pergamon.
- Rolls, E. T., Baylis, G. C., Hasselmo, M. E., & Nalwa, V. (1989b). The effect of learning on the face selective responses of neurons in the cortex in the superior temporal sulcus of the monkey. *Experimental Brain Research*, 76, 153–164.
- Rolls, E. T., Baylis, G. C., & Leonard, C. M. (1985). Role of low and high spatial frequencies in the face-selective responses of neurons in the cortex in the superior temporal sulcus in the monkey. *Vision Research*, 25(8), 1021–1035.
- Rolls, E. T., Critchley, H. D., Browning, A. S., & Inoue, K. (2006). Face-selective and auditory neurons in the primate orbitofrontal cortex. *Experimental Brain Research*, 170, 74–87.
- Rolls, E. T., Critchley, H. D., & Treves, A. (1996). The representation of olfactory information in the primate orbitofrontal cortex. *Journal of Neurophysiology*, 75, 1982–1996.
- Rolls, E. T., & Deco, G. (2002). *Computational neuroscience of vision*. Oxford: Oxford University Press.
- Rolls, E. T., & Deco, G. (2006). Attention in natural scenes: Neurophysiological and computational bases. *Neural Networks*, 19, 1383–1394.

- Rolls, E. T., Franco, L., Aggelopoulos, N. C., & Perez, J. M. (2006). Information in the first spike, the order of spikes, and the number of spikes provided by neurons in the inferior temporal visual cortex. *Vision Research*, *46*, 4193–4205.
- Rolls, E. T., Franco, L., Aggelopoulos, N. C., & Reece, S. (2003). An information theoretic approach to the contributions of the firing rates and correlations between the firing of neurons. *Journal of Neurophysiology*, *89*, 2810–2822.
- Rolls, E. T., & Kesner, R. P. (2006). A computational theory of hippocampal function, and empirical tests of the theory. *Progress in Neurobiology*, *79*, 1–48.
- Rolls, E. T., & Milward, T. (2000). A model of invariant object recognition in the visual system: Learning rules, activation functions, lateral inhibition, and information-based performance measures. *Neural Computation*, *12*, 2547–2572.
- Rolls, E. T., Robertson, R. G., & Georges-François, P. (1997). Spatial view cells in the primate hippocampus. *European Journal of Neuroscience*, *9*, 1789–1794.
- Rolls, E. T., & Stringer, S. M. (2006a). Invariant global motion recognition in the dorsal visual system: A unifying theory. *Neural Computation*, *19*, 139–169.
- Rolls, E. T., & Stringer, S. M. (2006b). Invariant visual object recognition: A model, with lighting invariance. *Journal of Physiology - Paris*, *100*, 43–62.
- Rolls, E. T., & Tovee, M. J. (1994). Processing speed in the cerebral cortex and the neurophysiology of visual masking. *Proceedings of the Royal Society of London B*, *257*, 9–15.
- Rolls, E. T., & Tovee, M. J. (1995). Sparseness of the neuronal representation of stimuli in the primate temporal visual cortex. *Journal of Neurophysiology*, *73*, 713–726.
- Rolls, E. T., Tovee, M. J., & Panzeri, S. (1999). The neurophysiology of backward visual masking: Information analysis. *Journal of Cognitive Neuroscience*, *11*, 335–346.
- Rolls, E. T., Tovee, M. J., Purcell, D. G., Stewart, A. L., & Azzopardi, P. (1994). The responses of neurons in the temporal cortex of primates, and face identification and detection. *Experimental Brain Research*, *101*(3), 473–484.
- Rolls, E. T., & Treves, A. (1998). *Neural networks and brain function*. Oxford: Oxford University Press.
- Rolls, E. T., Treves, A., Robertson, R. G., Georges-François, P., & Panzeri, S. (1998). Information about spatial view in an ensemble of primate hippocampal cells. *Journal of Neurophysiology*, *79*, 1797–1813.
- Rolls, E. T., Treves, A., & Tovee, M. J. (1997). The representational capacity of the distributed encoding of information provided by populations of neurons in the primate temporal visual cortex. *Experimental Brain Research*, *114*, 177–185.
- Rolls, E. T., & Xiang, J.-Z. (2006). Spatial view cells in the primate hippocampus, and memory recall. *Reviews in the Neurosciences*, *17*, 175–200.
- Rolls, E. T., Xiang, J.-Z., & Franco, L. (2005). Object, space and object-space representations in the primate hippocampus. *Journal of Neurophysiology*, *94*, 833–844.
- Scharf, B. (1961). Complex sounds and critical bands. *Psychological Bulletin*, *58*, 205–217.
- Seltzer, B., & Pandya, D. N. (1978). Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. *Brain Research*, *149*, 1–24.
- Spiridon, M., Fischl, B., & Kanwisher, N. (2006). Location and spatial profile of category-specific regions in human extrastriate cortex. *Human Brain Mapping*, *27*, 77–89.
- Spiridon, M., & Kanwisher, N. (2002). How distributed is visual category information in human occipito-temporal cortex? An fMRI study. *Neuron*, *35*, 1157–1165.
- Stringer, S. M., Perry, G., Rolls, E. T., & Proske, J. H. (2006). Learning invariant object recognition in the visual system with continuous transformations. *Biological Cybernetics*, *94*, 128–142.
- Stringer, S. M., & Rolls, E. T. (2006). Self-organizing path integration using a linked continuous attractor and competitive network: Path integration of head direction. *Network: Computation in Neural Systems*, *17*, 419–445.
- Stringer, S. M., & Rolls, E. T. (in press). Learning transform invariant object recognition in the visual system with multiple stimuli present during training. *Neural Networks*.

- Tanaka, K., Saito, C., Fukada, Y., & Moriya, M. (1990). Integration of form, texture, and color information in the inferotemporal cortex of the macaque. In E. Iwai & M. Mishkin (Eds.), *Vision, memory and the temporal lobe* (pp. 101–109). New York: Elsevier.
- Thorpe, S. J., & Imbert, M. (1989). Biological constraints on connectionist models. In R. Pfeifer, Z. Schreter, & F. Fogelman-Soulie (Eds.), *Connectionism in perspective* (pp. 63–92). Amsterdam: Elsevier.
- Thorpe, S. J., Rolls, E. T., & Maddison, S. (1983). Neuronal activity in the orbitofrontal cortex of the behaving monkey. *Experimental Brain Research*, *49*, 93–115.
- Tovee, M. J., & Rolls, E. T. (1995). Information encoding in short firing rate epochs by single neurons in the primate temporal visual cortex. *Visual Cognition*, *2*(1), 35–58.
- Tovee, M. J., Rolls, E. T., & Azzopardi, P. (1994). Translation invariance in the responses to faces of single neurons in the temporal visual cortical areas of the alert macaque. *Journal of Neurophysiology*, *72*(3), 1049–1060.
- Tovee, M. J., Rolls, E. T., & Ramachandran, V. S. (1996). Rapid visual learning in neurones of the primate temporal visual cortex. *NeuroReport*, *7*, 2757–2760.
- Tovee, M. J., Rolls, E. T., Treves, A., & Bellis, R. P. (1993). Information encoding and the responses of single neurons in the primate temporal visual cortex. *Journal of Neurophysiology*, *70*(2), 640–654.
- Treves, A. (1993). Mean-field analysis of neuronal spike dynamics. *Network*, *4*, 259–284.
- Treves, A., Panzeri, S., Rolls, E. T., Booth, M., & Wakeman, E. A. (1999). Firing rate distributions and efficiency of information transmission of inferior temporal cortex neurons to natural visual stimuli. *Neural Computation*, *11*, 611–641.
- Treves, A., Rolls, E. T., & Simmen, M. (1997). Time for retrieval in recurrent associative memories. *Physica D*, *107*, 392–400.
- Treves, A., Rolls, E. T., & Tovee, M. J. (1996). On the time required for recurrent processing in the brain. In V. Torre & F. Conti (Eds.), *Neurobiology: Ionic channels, neurons, and the brain* (pp. 325–353). New York: Plenum.
- Tsao, D. Y., Freiwald, W. A., Tootell, R. B., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, *311*, 617–618.
- Wallis, G., & Rolls, E. T. (1997). Invariant face and object recognition in the visual system. *Progress in Neurobiology*, *51*, 167–194.
- Wang, X. J. (2002). Probabilistic decision making by slow reverberation in cortical circuits. *Neuron*, *36*, 955–968.
- Williams, G. V., Rolls, E. T., Leonard, C. M., & Stern, C. (1993). Neuronal responses in the ventral striatum of the behaving macaque. *Behavioural Brain Research*, *55*, 243–252.
- Wilson, F. A. W., O'Scalaidhe, S. P. O., & Goldman-Rakic, P. S. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science*, *260*, 1955–1958.
- Zangenehpour, S., & Chaudhuri, A. (2005). Patchy organization and asymmetric distribution of the neural correlates of face processing in monkey inferotemporal cortex. *Current Biology*, *15*(11), 993–1005.

Received 20 March 2007; revised version received 17 October 2007