

## Chapter 4

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# Face Neurons

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### The discovery of face neurons

C4.S1

In 1976 we recorded from single neurons in the awake behaving non-human primate to investigate reward systems in the brain. We had shown that neurons in the hypothalamus and orbitofrontal cortex were activated from brain sites where electrical stimulation produced reward, and wished to know whether neurons in these areas were activated by natural rewards (Rolls, 1976; Rolls et al., 1980). We discovered that single neurons in the lateral hypothalamus responded not only to the taste of food, but enormously interestingly, to the sight of food (Rolls et al., 1976). We showed that the neurons were involved in food reward, for they only responded to the sight and taste of food when hunger was present (Burton et al., 1976). Indeed, it was uncanny at the time that we could predict the behavior of the monkey on a single trial, whether he would eat the food, by the responses of these neurons that responded to the sight of food, a topic quantified later with information theoretic approaches (Rolls, 2008b; Rolls et al., 2009). These investigations triggered a whole area of research which showed how taste, olfactory, visual, and somatosensory reward was decoded and represented in the orbitofrontal cortex (which connects to the hypothalamus), and led to a theory of emotion, of how and why the brain implements emotion, of some emotional disorders produced by brain damage, of the reward systems involved in appetite control, and of the brain mechanisms of decision-making (Rolls, 2005; Rolls and Deco, 2010; Rolls and Grabenhorst, 2008).

We wished to test where the reward value of visual stimuli discovered in these hypothalamic recordings was decoded and represented. We wanted to test whether reward was represented in the highest visual cortical processing area, the inferior temporal visual cortex, or whether this was added in a later structure such as the orbitofrontal cortex that connects the inferior temporal visual cortex to the hypothalamus. We discovered that the reward value of visual stimuli is not represented in the inferior temporal visual cortex, as shown by the facts that the neurons did not reverse their responses when the reward association of the stimuli was reversed, and that the neurons' responses to a visual stimulus, even the sight of food, did not decrease after feeding to satiety (Rolls et al., 1977). The same rule that cortical object representations are computed before reward value then becomes a property of the representations at a later cortical stage has now been shown to apply in the taste and olfactory systems (Rolls, 2005; Rolls and Grabenhorst, 2008). During these recordings, we found neurons that responded to complex stimuli such as faces, and reported in the paper that "neurons were found which could apparently only be excited by more complicated stimuli" (than simple geometrical stimuli) (Rolls et al., 1977), and cited earlier observations of Charles Gross and colleagues (Gross et al., 1972) on the effectiveness of complex stimuli for some of these neurons in anesthetized macaques. (They reported that "For at least three TE units, complex colored patterns (e.g. photographs of faces, trees) were more effective than the standard stimuli, but the crucial features of these stimuli were never determined" (Gross et al., 1972).) In 1977, we (Rolls et al., 1977) needed more evidence before we were ready to describe face-selective neurons, with visual

neurophysiology so dominated by the inspiring discoveries of Hubel and Wiesel on neurons responding to bars and edges in the primary visual cortex (Hubel and Wiesel, 1968).

By 1979 we (Sanghera et al. (1979), with an abstract in 1977 (Sanghera et al. (1977)) were sufficiently convinced to report in the journal *Experimental Neurology* the presence of face-selective neurons in the amygdala and inferior temporal visual cortex, as follows:

It should also perhaps be noted that nine of the amygdaloid neurons with visual responses were found to respond primarily to faces or photographs of faces, and two more to respond to all stimuli except these. It is possible that innate or learned factors contributed to the responses of these neurons, as well as to the responses of a comparable group of neurons from which we have recorded in the anterior inferotemporal cortex.

A neuron with good responses to faces is illustrated in figure 1 of that paper (Sanghera et al., 1979), even if that neuron was chosen to illustrate different tuning than that of a face-selective neuron. Further reports on these amygdala face-selective neurons, and on comparable face-selective neurons in the temporal lobe cortex within the superior temporal sulcus, soon appeared (Rolls, 1981a,b, 1984). For example, Rolls (1981a,b) reported that in the cortex in the superior temporal sulcus eighteen neurons

responded selectively to faces . . . Masking out, or presenting isolated, parts of faces showed that some cells responded on the basis of different features. Some required eyes, some hair, some the mouth, and others showed parallel responses to each of a number of features. Some cells responded more strongly when such component features of faces were combined. Presenting a face in profile failed to elicit a response from some cells. Transformations of the face such as isomorphic rotation or alterations of color, size, or distance did not greatly affect the magnitude of the neuronal responses.

At about the time that we were making these recordings in the amygdala and inferior temporal visual cortex, David Perrett and Simon Thorpe joined the lab, and both were very interested in the face-selective neurons in the inferior temporal visual cortex (and also reported as present in the orbitofrontal cortex; Thorpe et al., 1983). By 1979 we (Perrett et al. (1979), with a fuller report in 1982 (Perrett et al., 1982)) had published a report describing some of the properties of these neurons, including their face selectivity, their invariance (for size, color, distance, and isomorphic rotation), their frequent tuning to a particular view of a face such as profile or front view, the responsiveness of some neurons to face parts such as eyes, mouth, or hair and of other neurons only to combinations of all these features in the correct relative spatial positions, and the fact that they do not respond on the basis of arousal.

Our 1979 report was as follows:

While recording from visual cells in the temporal lobe, we have observed a small number of cells which responded strongly to faces. Analysis of the responses of 50 such neurons in the vicinity of the fundus of the superior temporal sulcus in three hemispheres of two alert rhesus monkeys showed the following. (1) All 50 neurons responded to faces (which were human or rhesus monkey, 3-D or projected, and shown to the monkey through a large-aperture shutter with visual fixation monitored), and were almost unresponsive to gratings, simple geometrical, and other complex 3-D stimuli. (2) The neuronal responses to the sight of a face were sustained and had latencies of  $110 \pm 20$  ms. (3) 32 neurons responded also to some arousing or aversive visual stimuli. (4) 18 neurons responded selectively to faces, and had the following properties. (5) These neurons were in general unresponsive to auditory or tactile stimulation which was aversive, or arousing as shown by the GSR, or to stimuli such as a hand which signified a human or monkey. (6) Masking out, or presenting isolated parts of faces showed that some cells responded on the basis of different features. Some required eyes, some hair, some the mouth, and others showed parallel responses to each of a number of features. (7) Some cells responded more when such component features were combined. (8) Presenting the face in profile failed to elicit a response

for some cells. (9) Transformations of the face such as isomorphic rotation, or alterations of color, size or distance, did not greatly affect the magnitude of the neuronal responses. This evidence suggests that in the temporal lobe of the primate there are neurons specialized to respond to the component visual features present in faces. (Perrett et al., 1979.)

In 1981, Bruce and colleagues, citing our 1979 report of face-selective neurons in the cortex in the superior temporal sulcus (Perrett et al., 1979), described seven neurons in the same region that confirmed our findings in that their 7 neurons “appeared to be selective for faces”; “responded to a variety of human and monkey faces (real faces, slides, and photographs) differing in size, color, and movement”; “covering the eyes on the photograph reduced but did not eliminate the response”; and “scrambling the photographs eliminated the response” (Bruce et al., 1981).

Soon after our initial reports of face-selective neurons in the amygdala, inferior temporal visual cortex (Perrett et al., 1979, 1982; Rolls, 1984; Sanghera et al., 1977, 1979) and orbitofrontal cortex (Thorpe et al., 1983), others (Desimone, 1991; Desimone et al., 1984; Gross et al., 1985; Perrett et al., 1985a) as well as ourselves (Baylis et al., 1985; Leonard et al., 1985; Perrett and Rolls, 1983; Rolls, 1981b, 1984, 1991, 1992, 2000a, 2007b, 2008a,b) provided further descriptions and analyses of face-selective neurons, and these and many more recent discoveries are described in the remainder of this chapter.

These face-selective neurons have been helpful in many of the discoveries about the cortical mechanisms that implement face and object recognition at the neuronal and computational levels (Rolls, 2007a, 2008b, 2009; Rolls and Stringer, 2006b), and the further processing of faces beyond the visual cortical areas. Some of these discoveries are described in the following sections.

## The specialization of neuronal responses found in different temporal lobe cortex visual areas

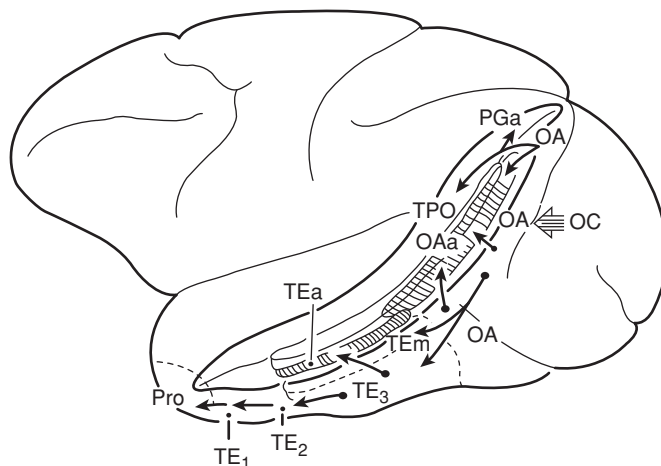
C4.S2

Considerable specialization of function is found in the architectonically defined areas of temporal visual cortex (Baylis et al., 1987; Rolls, 2008a) (Figure 4.1). 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% to 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 et al., 1990). Due to the fact that face-selective neurons, though found in high proportion in some subregions (Tsao et al., 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 interrupt outputs of these visual areas, would produce readily apparent face-processing deficits.

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 et al., 1989a).

The face-selective temporal cortex neurons we have studied are found mainly between 7 mm and 3 mm posterior to the sphenoid reference, which in a 3 to 4 kg macaque corresponds to approximately 11 to 15 mm anterior to the interaural plane (Baylis et al., 1987). The “middle face patch” of Tsao et al. (2006) identified with functional magnetic resonance imaging (fMRI) in the

C4.F1 **Fig. 4.1** Lateral view of the macaque brain 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 and Pandya (1978), with permission.



macaque was at A6, which is probably part of the posterior inferior temporal cortex; see Freiwald and Tsao (Chapter 36, this volume). Tsao et al. (2006) also described “anterior face patches” at A15 to A22 (see also Rajimehr et al., 2009). A15 might correspond to where we have analyzed face-selective neurons (it might translate to 3 mm posterior to our sphenoid reference).

Correspondingly, in human fMRI studies, evidence for specialization of function is described (Grill-Spector and Malach, 2004; Haxby et al., 2002; O’Toole et al., 2005; Spiridon et al., 2006; Spiridon and 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 et al., 1999; Robertson et al., 1998; Rolls, 1999c; Rolls and Kesner, 2006; Rolls et al., 1997a, 1998, 2005; Rolls and Xiang, 2006). See chapters by Kanwisher and Barton (Chapter 7) and Haxby and Gobbini (Chapter 6) in this volume for further discussion of human neuroimaging research.

The single neuron studies in macaques described in this chapter provide evidence on a number of questions difficult to resolve with fMRI. The neuronal recording studies show that individual neurons can be highly tuned in that they convey information about face identity, *or* about face expression, *or* about head movement, *or* about objects, *or* about 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 cytoarchitectonically 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 cytoarchitectonically 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 to several mm with tuning to one aspect of stimuli are common (e.g. face identity, or 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, 2008b; Rolls and Deco, 2002). Indeed, consistent with self-organizing map principles (Rolls, 2008b), there is a high concentration of face-selective neurons within a patch identified by fMRI (Tsao et al., 2006). Consistent with our 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 and Chaudhuri, 2005). 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 neo-cortex, and the resulting minimization of wiring length between neurons that are interconnected for computational reasons (Rolls, 2008). There are likely to be differences in neuronal activity between the different patches, at least in the sense that in more posterior areas it is often difficult to obtain clear responses without careful control of visual fixation (consistent with smaller receptive fields), whereas it is a computationally useful property of the neurons we have investigated, which are in the more anterior parts of the temporal cortical visual areas, that they respond under natural conditions during normal visual viewing of an object without precise control of eye position, consistent with larger receptive fields of the more anterior neurons (Aggelopoulos and Rolls, 2005; Rolls et al., 2003a).

C4.S3

## 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 two to 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 et al., 1985, 1987; Rolls, 1984, 1992, 1997, 2000a; Rolls and 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 degrees 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 to 100 ms.

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 and Tovee, 1995b; Rolls et al., 1997b). 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 (Rolls, 2008b).

## The selectivity of these neurons for individual face features or for combinations of face features

The fact that many face-selective neurons respond only to a combination of face features in the correct spatial configuration (Perrett et al., 1982; Rolls, 1981a, 2008b; Rolls et al., 1994; Tanaka

et al., 1990) (with one example also provided by Bruce et al., 1981) are consistent with the hypotheses that they are formed by competitive self-organization which provides a computational mechanism for the spatial binding of features in neural networks (Elliffe et al., 2002; Rolls, 2008b; Rolls and Deco, 2002).

## Distributed encoding of face and object identity

Barlow (1972) speculated that a particular object (or face) is represented in the brain by the firing of one or a few gnostic (or “grandmother”) cells. We showed that this is not the case, and that although a face-selective cell may respond only to faces, its firing rate is graded to a set of faces with some faces producing large responses, and more and more producing lower and lower responses, with each neuron having a different profile of responses to each face with an approximately exponential firing rate probability distribution (Baylis et al., 1985; Rolls and Tovee, 1995b), with the average sparseness being 0.65 (Baddeley et al., 1997; Baylis et al., 1985; Franco et al., 2007; Rolls and Tovee, 1995b; Treves et al., 1999) (see Figure 4.2). The sparseness of the representation provided by a neuron can be defined as:

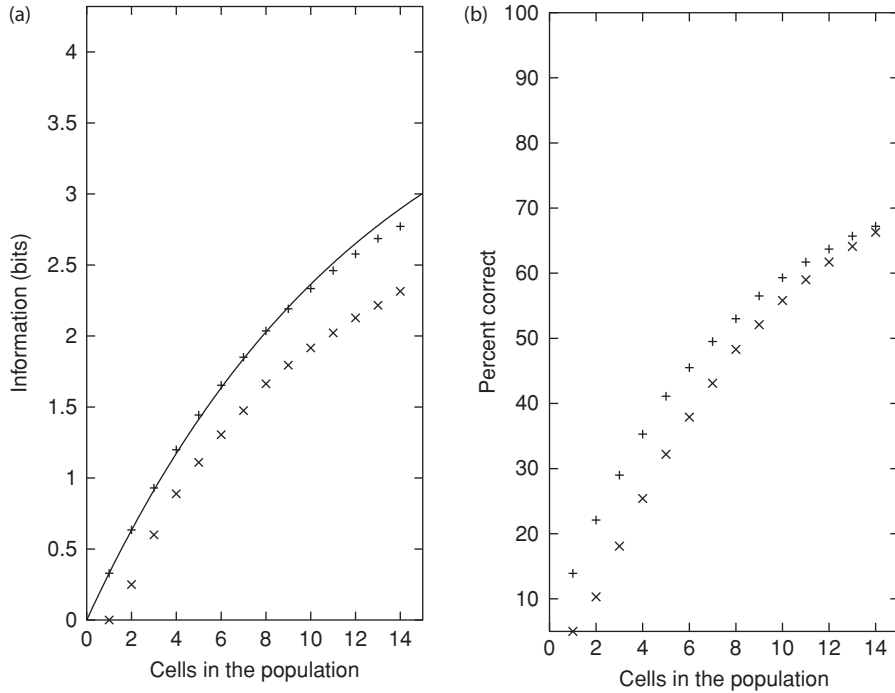
$$a = (3_{s=1,S} r_s / S)^2 / 3_{s=1,S} (r_s^2 / S)$$

where  $r_s$  is the mean firing rate of the neuron to stimulus  $s$  in the set of  $S$  stimuli.

Complementary evidence comes from applying information theory to analyze 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 4 stimuli was shown, 3 bits to specify which of 8 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, 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 4.3. 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, a dot product, to work (see below). Second, it is clear (Figure 4.3) 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 et al., 1996; Rolls and Treves, 1998; Rolls et al., 1997b), confirmed with simultaneous recordings from different neurons (Panzeri et al., 1999a; Rolls et al., 2004, 2006b). 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.

Some have postulated that there might be information available if neurons became temporally synchronized to some but not other stimuli in a set (Engel et al., 1992; Singer, 1999). With rigorous information theoretic techniques (Rolls, 2008b), we showed that for static faces and objects most of the information is available in the firing rates of the neurons (the number of spikes in a





**Fig. 4.3** (a) The values for the average information available in the responses of different numbers of inferior temporal cortex neurons on each trial, about which of a set of 20 face stimuli has been shown. The decoding method was Dot Product (DP, x) or Bayesian 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 per cent correct for the corresponding data to those shown in Figure 4.3a. After Rolls, et al. (1997), with permission.

short time period), and that there is little additional information (less than 5% of the total) in the relative time of firing of simultaneously recorded neurons (Franco et al., 2004; Panzeri et al., 1999a; Rolls et al., 2003b, 2004). This has been shown to apply to natural vision 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 et al., 2005).

#### C4.S6 Advantages of the sparse distributed representation of faces and objects for brain processing

The advantages of the distributed encoding found include the following explained in more detail elsewhere (Rolls, 2005, 2007b, 2008b; Rolls and Deco, 2002; Rolls and Treves, 1998), with a full



analysis of how information theory has helped in the understanding of neural representations in the brain provided by Rolls (2008b).

## Exponentially high coding capacity

C4.S6.1

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 4.3.

## Ease with which the code can be read by receiving neurons

C4.S6.2

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 et al., 1997b). 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 to the more efficient (Bayesian) 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

C4.S6.3

Because the information is decoded from a large population of neurons by inner product multiplication with the synaptic weight vector, there is less dependence on the random (almost Poisson) firing times for a given mean rate of single neurons, and thus there is resistance to noise inherent in the activity of single neurons (Rolls and Deco, 2010).

## Generalization

C4.S6.4

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 expressed as the firing rate on the set of input neurons with its synaptic weight vector (see further Rolls, 2008b; Rolls and Deco, 2002; Rolls and Treves, 1998).

## Completion

C4.S6.5

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.

## Graceful degradation or fault tolerance

C4.S6.6

Again, because the information is decoded from a large population of neurons by inner product multiplication with the synaptic weight vector, there is less dependence on the firing of any one neuron or on any particular subset of neurons, so that if some neurons are damaged, the performance of the system only gradually degrades, and is in this sense fault tolerant.

#### C4.S6.7 **Speed of readout of the information**

The information available in a distributed representation can be decoded by an analyzer 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 et al., 1999b; Rolls et al., 1997b, 2006b; Treves, 1993; Treves et al., 1996, 1997). 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, 2008b; Rolls and 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.

#### C4.S7 **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 and 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 gray 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 eight 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 eight cycles per face are included (Rolls et al., 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 can not be predicted from a linear combination of their responses to the narrow band stimuli (Rolls et al., 1987). This lack of linearity of these neurons, and their responsiveness to a wide range of spatial frequencies, indicate 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 anesthesia (see Gross et al., 1985), but also in the awake behaving primate (Tovee et al., 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

(Rolls and Tovee, 1995a)? 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 while large (typically 70 degrees 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 et al., 2003a) (cf. DiCarlo and Maunsell, 2003; Op De Beeck and 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 and Deco, 2002). These findings are an important step towards understanding how the visual system functions in a natural environment (Aggelopoulos and Rolls, 2005; Gallant et al., 1998; Rolls, 2008b; Rolls and Deco, 2002; Stringer and Rolls, 2008; Stringer et al., 2007).

## A view-invariant representation of faces and objects

C4.S8

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 et al., 1989b), although in most cases (16/18 neurons) the response was not perfectly view-independent. Mixed together in the same cortical regions there are neurons with view-dependent responses (Hasselmo et al., 1989b). 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 et al., 1985a). 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. View-independent representations are important for face and object recognition. View-independent object neurons are also found in the inferior temporal cortex (Booth and Rolls, 1998), as well as view-dependent neurons (Logothetis and Pauls, 1995).

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 et al., 1989b). For example, neurons responded to ventral flexion of the head irrespective of whether the head was upright or inverted. In this procedure, retinally encoded or viewer-centered 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 discovery 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 and Baylis, 1986).

## Learning of new representations in the temporal cortical visual areas

C4.S9

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 analyzed 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 (one to two) presentations of the set (Rolls, 1995; Rolls et al., 1989b). This evidence is consistent with the categorization being performed by self-organizing competitive neuronal networks, as described elsewhere (Rolls, 1989, 2008b; Rolls and Deco, 2002; Rolls and Treves, 1998; Rolls et al., 1989a).

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 gray-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 et al., 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 ss) 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 faces and 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, 2008b, 2009; Rolls and Deco, 2002; Rolls and Stringer, 2006b).

## C4.S10 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 to 50 ms, and in the anterior inferior temporal cortical areas approximately 80 to 100 ms, each stage may need to perform processing for only 15 to 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 and 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 of a set of faces 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 and 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 et al., 2006b).

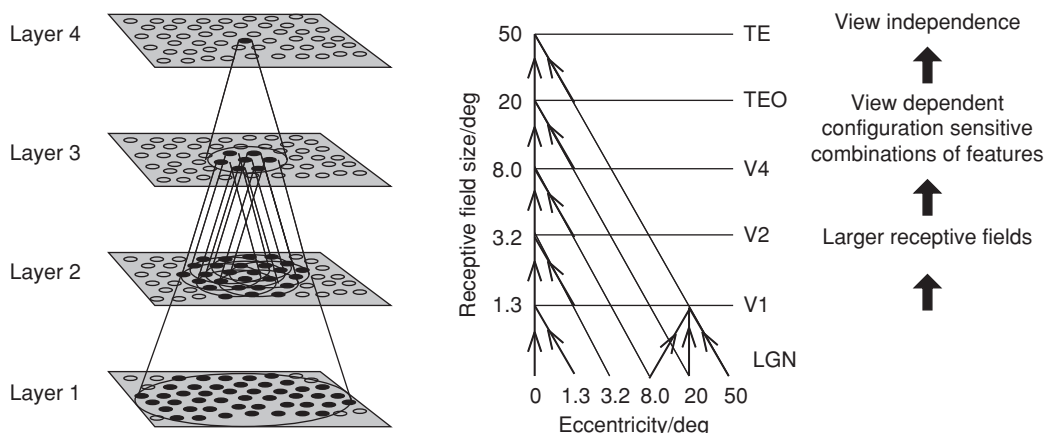
The next approach has been to use a visual backward masking paradigm. In this paradigm there is a brief presentation of a test stimulus which is rapidly followed (within 1 to 100 ms) by the presentation of a second stimulus (the mask), which impairs or masks the perception of the test stimulus. It has been shown (Rolls and Tovee, 1994) that when there is no mask, inferior temporal cortex neurons respond to a 16-ms presentation of the test stimulus for 200 to 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, which we propose is important in learning invariant representations (Rolls, 2008b). If the pattern mask followed the onset of the test face stimulus by 20 ms (a stimulus onset asynchrony of 20 ms), face-selective neurons in the inferior temporal cortex of macaques responded for a period of 20 to 30 ms before their firing was interrupted by the mask (Rolls and Tovee, 1994; Rolls et al., 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 to 30 ms (although it is true that for conscious perception, the firing needs to occur for 40 to 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 et al., 2001; Rolls, 2008b; Rolls and Treves, 1998; Treves, 1993; Treves et al., 1996).

## Computational mechanisms in the visual cortex for face and object recognition

C4.S11

One of the enormous computational problems solved by the brain is forming a representation of a face or object that is selective, and invariant with respect to position, view, scale, and even partly rotation, and that can be read by neurons performing dot-product decoding using multiple neurons for recognition, association, and action. The neurophysiological findings described above, and wider considerations on the possible computational properties of the cerebral cortex, have led to a theory of how invariant representations of objects are formed using hierarchical self-organizing competitive networks with the temporal and spatial continuity as an object transforms providing the basis for neurons learning to respond to the different transforms of objects (Figure 4.4). Due to space limitations, the theory is described elsewhere (Elliffe et al., 2002; Perry et al., 2006, 2010; Rolls, 1992, 2007a, 2008b, 2009; Rolls and Deco, 2002; Rolls and Milward, 2000; Rolls and Stringer, 2001, 2006b; Stringer et al., 2006; Stringer and Rolls, 2000, 2002; Wallis and Rolls, 1997). The theory proposes that neurons in these visual areas use a modified Hebb synaptic modification rule with a short-term memory trace to capture whatever can be captured at each stage that is invariant about faces or objects as they change in retinal view, position, size, and rotation. The statistics of the visual input are used to help build invariant representations. The model can use temporal continuity in an associative synaptic learning rule with a short-term memory trace, and/or it can use spatial continuity in spatial continuous transformation learning. The model of visual processing in the ventral cortical stream can build representations of objects that are invariant with respect to translation, view, size, and lighting. The model has been extended to incorporate top-down feedback connections to model the control of attention by biased competition in, for example, spatial and object search tasks (Deco and Rolls, 2004). Recent developments include a theory of how several faces or objects and their spatial positions can be represented simultaneously in a scene using asymmetries in the receptive fields revealed in crowded scenes



**C4.F4 Fig. 4.4** 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. A description of the operation of this model of cortical invariant face and object recognition is provided in chapter 4 of *Memory, Attention, and Decision-Making* (Rolls, 2008b), available online at <http://www.oxcns.org/papers/MemoryAttentionAndDecisionMakingContentsAndSampleChapter4.pdf>.

(Aggelopoulos and Rolls, 2005; Rolls et al., 2008b), how spatial information about the position of objects in the inferior temporal cortex can be used to build spatial scene representations in the hippocampal system (Rolls et al., 2008b), how invariant representations of individual faces or objects can be learned even when multiple faces or objects are present during learning (Stringer and Rolls, 2008; Stringer et al., 2007), and how a similar computational mechanism could lead to object global motion encoding in the dorsal visual system (e.g. looming, rotation, and object-based movement) (Rolls and Stringer, 2006a). This approach is more biologically plausible than some complementary approaches that assume a MAX function to help compute invariant representations (Riesenhuber and Poggio, 1999; Serre et al., 2007) or which implement slow learning (captured by our synaptic trace learning rule) using non-local backpropagation algorithms (Wiskott and Sejnowski, 2002), but which nevertheless in terms of the concepts support the computational hypotheses incorporated in the biologically plausible approach we have developed, and modeled with VisNet.

## **C4.S12 Attentional effects, models of attention, and their implications for neuropsychology**

In complex natural scenes, the receptive fields of inferior temporal cortex neurons shrink to a few degrees in diameter close to the fovea, and this helps to solve the binding problem in visual perception, for then IT neurons encode the object that is close to the fovea, and which is being fixated, providing the coordinates for actions directed to the object or face (Rolls et al., 2003a). Under these conditions, attention to a particular face or object increases the receptive field size for

that face or object (Rolls et al., 2003a) by a top-down biased competition process analyzed in an extended model of VisNet in which there are top-down effects implemented by cortico-cortical backprojections (Deco and Rolls, 2004).

Top-down biased competition models of attention (Desimone and Duncan, 1995) are now becoming sufficiently developed that they can provide an account of interactions between the dorsal and ventral visual systems (Deco and Rolls, 2004, 2005a; Rolls and Deco, 2002), of how non-linearities important in attention are implemented at the neuronal and biophysical level (Deco and Rolls, 2005b), of how fMRI signals may reflect the synaptic and neuronal mechanisms involved in attention (Deco et al., 2004), and of the psychophysics (Rolls and Deco, 2002) and neuropsychiatry (Loh et al., 2007; Rolls and Deco, 2010; Rolls et al., 2008a) 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 et al., 2002; Deco and Zihl, 2001; Rolls, 2008b; Rolls and Deco, 2002). It was possible to account for example for the neglect of the left half of each object (or face) 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 and Rolls, 2002).

## Different neural systems are specialized for face expression decoding and for face recognition

C4.S13

It has been shown that some neurons respond to face identity, and others to face expression (Hasselmo et al., 1989a). 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 TEm. Information about facial expression is of potential use in social interactions (Rolls, 1984, 1986a,b, 1990, 1999a, 2005). Damage to this population may contribute to the deficits in social and emotional behavior which are part of the Kluver–Bucy syndrome produced by temporal lobe damage in monkeys (see Leonard et al., 1985; Rolls, 1981b, 1984, 1986a,b, 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 et al., 1989a) and by Perrett et al. (1985b). Moreover, the neuronal responses to head motion are in head-based coordinates, that is they show invariance (Hasselmo et al., 1989a), and this has been modeled in a version of VisNet that includes visual motion flow inputs and computes invariant representations of global flow (Rolls and 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 et al., 1989a). 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 et al., 1989b), and eye gaze (Perrett et al., 1985b), 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 et al., 1989a) and with view-independent responses (Hasselmo et al., 1989b) 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.

#### C4.S14 **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 and 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 et al., 1990).

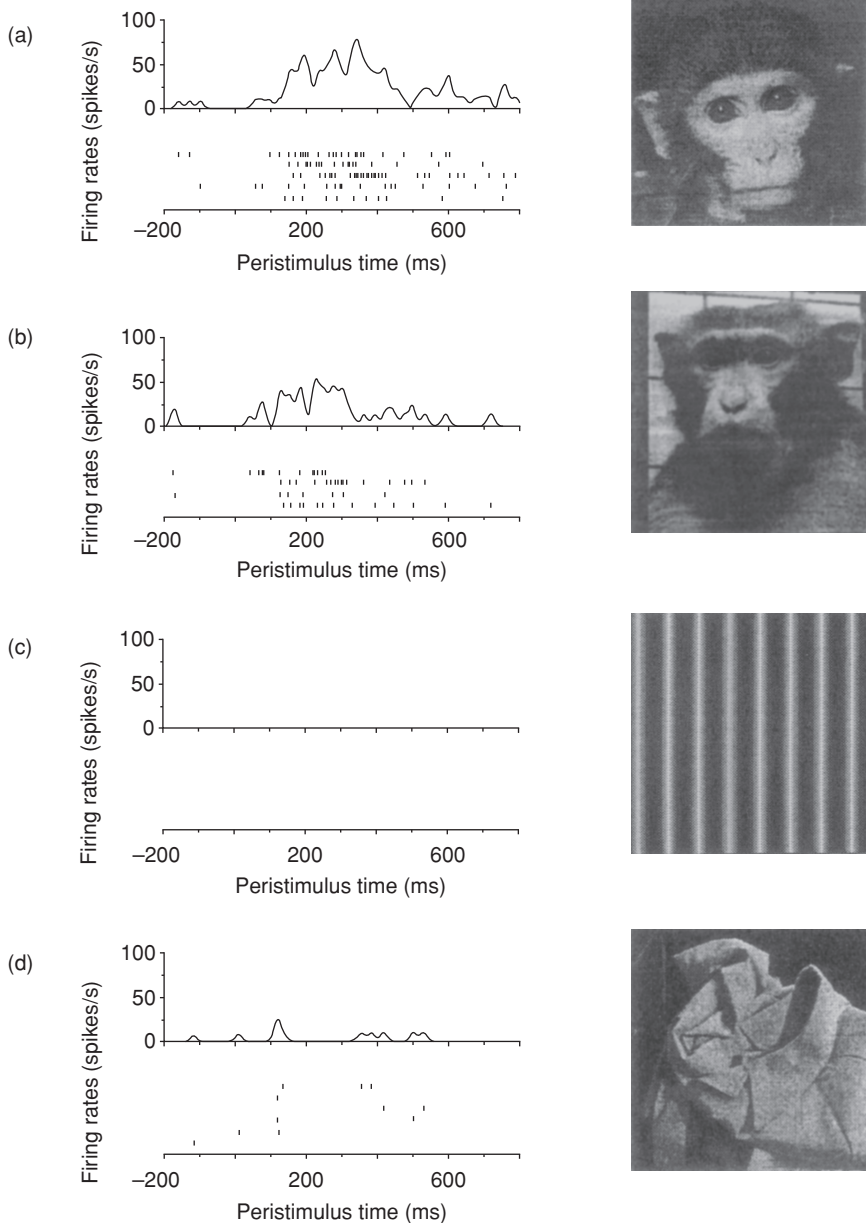
#### C4.S15 **A representation of faces in the orbitofrontal cortex**

Rolls et al. (2006a) have found a number of face-responsive neurons in the orbitofrontal cortex, and they are also present in adjacent prefrontal cortical areas (Wilson et al., 1993). The orbitofrontal cortex face-responsive neurons, first observed by Thorpe and colleagues (1983), then by Rolls et al. (2006a), 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 4.5); 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 and Baylis, 1986). Some of the orbitofrontal cortex face-selective neurons are responsive to face gesture or movement, and others to face expression (Rolls et al., 2006a). 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 et al., 1989a), 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 behavioral choice is represented in the human orbitofrontal cortex (for background, see Rolls, 2005). Kringelbach and Rolls (2003) 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 (2003) found that activation of a lateral 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. The study reveals that the human orbitofrontal cortex is very sensitive to social feedback from face expression when it must be used to change behavior (Kringelbach and 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. 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





**Fig. 4.5** 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, et al. (2006a), with permission. C4.F5

inappropriate behavior (Hornak et al., 1996, 2003; Rolls, 1999b). 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 (see further Rolls, 2008a).

## C4.S16 **Summary and conclusions**

Neurophysiological evidence is described showing that some neurons in the macaque inferior temporal visual cortex and cortex in the superior temporal sulcus have responses that are invariant with respect to the position, size, and in some cases view of faces, and that these neurons show rapid processing and rapid learning. Which face (or object) is present is encoded using a distributed representation in which each neuron conveys independent information in its firing rate, with little information evident in the relative time of firing of different neurons. This ensemble encoding has the advantages of maximizing the information in the representation useful for discrimination between stimuli using a simple weighted sum of the neuronal firing by the receiving neurons, and with the properties of generalization and graceful degradation. These invariant representations are ideally suited to provide the inputs to brain regions such as the orbitofrontal cortex and amygdala, where face-selective neurons are also found, that learn the reinforcement associations of an individual's face. This enables the learning in the orbitofrontal cortex and amygdala, and the appropriate social and emotional responses, to generalize to other views of the same face (Rolls, 2005, 2008b). These representations are also ideally suited for face recognition, and as an input to systems that implement episodic memory (Rolls, 2008b, 2010; Rolls and Kesner, 2006). In complex natural scenes the neuronal responses remain face-selective, but the receptive fields become reduced in size and asymmetric around the fovea, enabling several objects and their relative spatial positions to be simultaneously represented close to the fovea. Multiple instances of the same face or object can be represented simultaneously in this way. A different population of neurons in the cortex in the superior temporal sulcus responses encodes face gesture (movement) and face expression, and many of these neurons have view-dependent responses.

The responses of these neurons thus reflect solution of some of the major problems of visual perception. Analysis of their responses has helped in the development of a computational theory and model of how invariant representations of faces and objects may be produced in a hierarchically organized set of visual cortical areas with convergent connectivity and synaptic plasticity that reflects the statistics of the temporal and spatial continuity of objects in natural scenes (Rolls, 2008b, 2009).

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Some of the publications referred to here are available at <http://www.oxcns.org>.

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