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Face processing in different brain areas and face recognition

Edmund T Rolls
Oxford Centre for Computational Neuroscience,
Oxford, UK
Department of Computer Science, University of
Warwick, Coventry, UK

Introduction

Face-selective neurons were discovered in the inferior temporal visual cortex by Perrett et al. (1982), in the amygdala by Sanghera, Rolls, and Roper-Hall (Sanghera et al. 1979; Rolls 2011) and Leonard et al. (1985), and in the orbitofrontal cortex by Rolls et al. (2006). These neurons respond 2–20 times more to the best face compared to the best nonface, and different brain regions provide the basis for face recognition and for emotional responses to faces. These neurons are described here.

## Neuronal Responses to Faces 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 in which some neurons that respond selectively to faces are found (Perrett et al. 1982; Rolls 2007, 2011, 2012, 2016a). 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 (Seltzer and Pandya 1978; Baylis et al. 1987) (see Fig. 1). Of these latter areas, TPO receives inputs from temporal, parietal, and occipital cortex; PGa and IPa from parietal and temporal cortex; and TS and TAa primarily from auditory areas.

Considerable specialization of function was found in recordings made from more than 2600 neurons in these architectonically defined areas (Baylis et al. 1987). Areas TPO, PGa, and IPa are multimodal, with neurons that respond to visual, auditory and/or somatosensory inputs (though not typically with corresponding bimodal auditory and visual responses (Sliwa et al. 2016)); 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; 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%. Moreover, neurons with responses related to facial expression, movement, and gesture are more likely

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Fig. 1 Lateral view of the macaque brain (*left*) and coronal section (*right*) showing the different architectonic areas (e.g., TEm, TPO) in and bordering the anterior part of the superior temporal sulcus (STS) of the macaque (see text; after Seltzer and Pandya 1978)
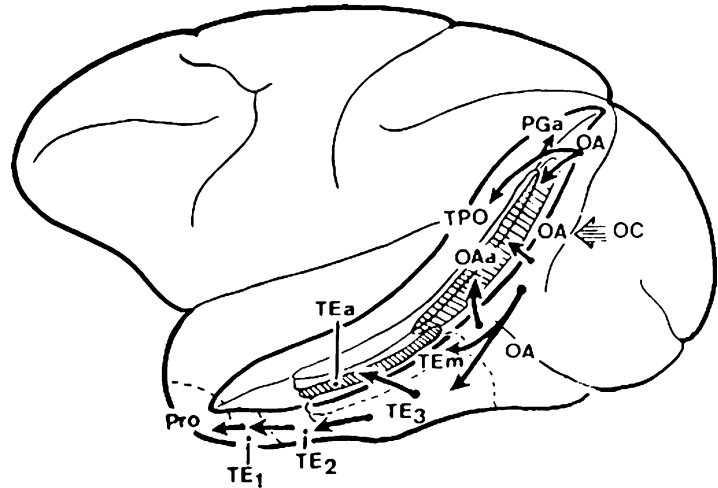
to be found in the cortex in the superior temporal sulcus, whereas neurons with activity related to facial identity are more likely to be found in the TE areas (Hasselmo et al. 1989; Rolls 2007). Indeed, we can think of the cortex in the superior temporal sulcus as being a more dorsal face processing stream than the stream in the inferior temporal visual cortex (Baylis et al. 1987; Rolls 2012).

Using fMRI in macaques, the segregation of face cells into 6 face patches has been described: 1 posterior (PL), 2 middle (ML, MF), and 3 anterior (AL, AF, AM) (Tsao et al. 2008a, 2014). Neurons in ML and MF are view-specific; neurons in AL are tuned to identity mirror-symmetrically across views, thus achieving partial view invariance; neurons in AM, the most anterior face patch, achieve almost full view invariance and provide a sparse representation of face identity. Neurons in ML/MF respond to both monkey and human faces, whereas in AM many cells are selective for either monkey or human faces.

Human subjects showed 4 face areas or patches (occipital, fusiform, anterior to fusiform, and superior temporal sulcus face areas (Tsao et al. 2008a). In human fMRI studies, evidence for specialization of function related to visual processing in areas similar to those in macaques has been described (Spiridon et al. 2006; Said et al. 2011; Vul et al. 2012; Weiner et al. 2017). The fusiform face area, which corresponds to part of the macaque inferior temporal cortex, is implicated

in the processing of face identity. The cortex in the superior temporal sulcus and just above it in the middle temporal gyrus, which corresponds to the macaque cortex in the superior temporal sulcus, is implicated in face expression and gesture (i.e., moving faces) (Critchley et al. 2000), and has reduced functional connectivity in autism (Cheng et al. 2015). An area that may correspond to the macaque inferior temporal cortex has a highly developed representation of objects (Rolls 2012, 2016a). A parahippocampal area is implicated processing spatial scenes and 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; Rolls et al. 2005, 2016a; Kesner and Rolls 2015). This parahippocampal spatial scene area may receive input from an occipito-temporal lateral place patch (Kornblith et al. 2013).

Some of the key discoveries about face-responsive neurons in the anterior parts of the temporal lobe, and in the amygdala and orbitofrontal cortex, are described next.

The Selectivity of One Population of Neurons for Faces

The neurons discovered 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 3-D objects (Perrett et al. 1982; Rolls 1984, 2007). 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) nonface stimuli is being seen (on average 0.07 bits) (Rolls et al. 1997a, b, 2007). These information theoretic procedures provide an objective and quantitative way to show what is "represented" by a particular population of neurons (Rolls and Treves 2011).

Neurons Selective 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, and some require all the features to be present in the correct spatial configuration (i.e., not jumbled) (Perrett et al. 1982; Rolls 2007).

Distributed Encoding of Face 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, 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 face is present is distributed. For example, in a study using 23 faces and 45 nonface natural images a distributed representation was found, with rather few stimuli producing high firing rates, and increasingly large numbers of stimuli producing lower and lower firing rates (Rolls and Tovee 1995) (see Fig. 2). Indeed, the firing rate probability distribution of many neurons is approximately exponential (Franco et al. 2007).

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, 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 increases approximately linearly with the number of neurons in the population (see Fig. 3), and thus the representational capacity increases exponentially with the number of neurons in the ensemble (Fig. 4) (Rolls et al. 1997a; Rolls and Treves 2011; Rolls 2016a). This is further evidence for distributed encoding, and for the power of the code used.

The code that is used in the inferior temporal visual cortex is primarily the number of spikes from each neuron (i.e., a rate code), for very little (not more than approximately 5% of the total information) was available from stimulus-dependent synchrony (Rolls and Treves 2011; Rolls 2016a). 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 (Rolls and Treves 2011; Rolls 2016a).

The advantages of the code that has been found include exponentially high coding capacity,

Face processing in different brain areas and face recognition, Fig. 2 Firing rate distribution of a single neuron in the temporal visual cortex to a set of 23 face (*F*) and 45 nonface images of natural scenes. The firing rate to each of the 68 stimuli is shown. *P* indicates a face profile stimulus, *B* a body part stimulus such as a hand (After Rolls and Tovee 1995)
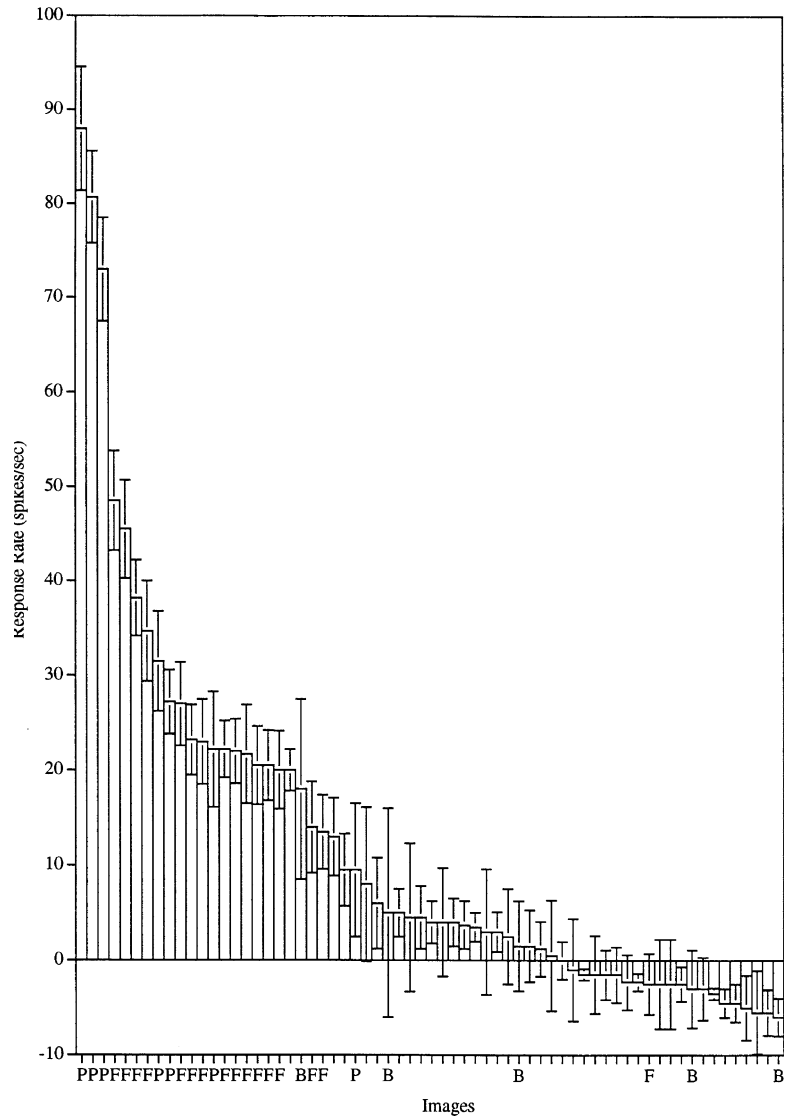
readability by a neuronally plausible (synaptically) weighted sum of the firing rates of different neurons, resistance to noise, generalization, completion, graceful degradation or fault tolerance, and speed of readout of the information, as described elsewhere (Rolls and Treves 2011; Rolls 2016a).

Invariant Representations

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 (e.g., the amygdala, orbitofrontal cortex, and hippocampus) learn about one view, position, etc. of the object, the organism generalizes correctly to other positions, views, etc. of the object. It has been shown that the majority of face-selective anterior inferior temporal cortex neurons have responses that are relatively invariant with respect to the size of the stimulus, and the exact position of the face on
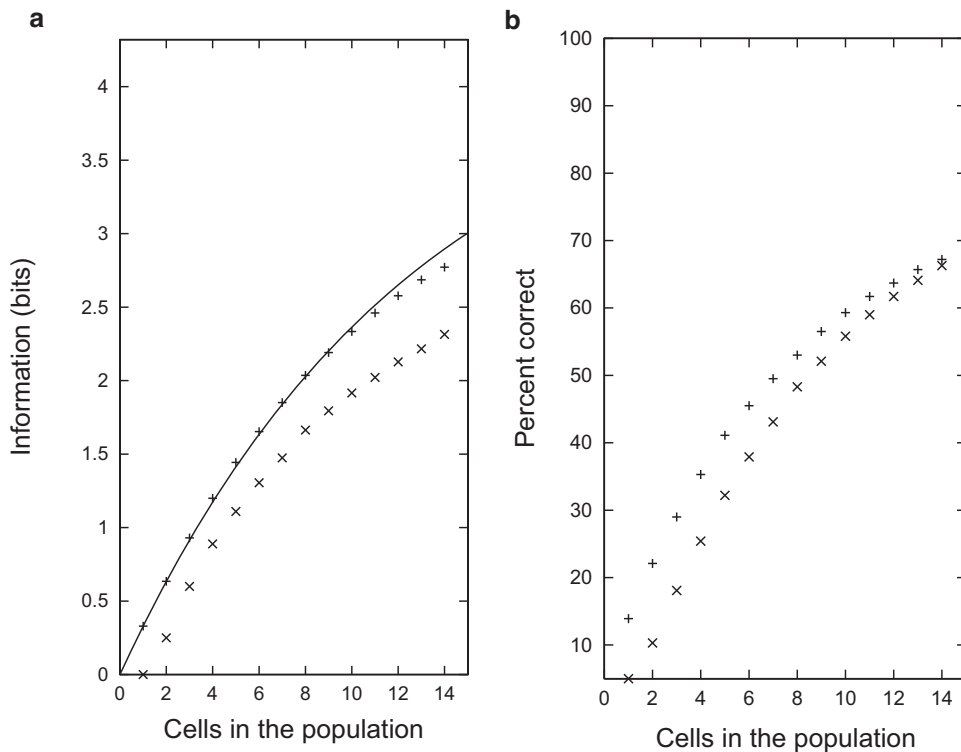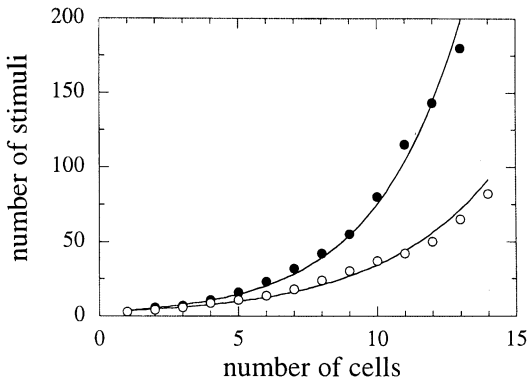
Face processing in different brain areas and face recognition, Fig. 3 (**a**) The values for the average information available in the responses of different numbers of these neurons on each trial, about which of a set of 20 face stimuli has been shown. The decoding method was dot product (DP, ×) or probability estimation (PE, +), and the effects obtained with cross validation procedures utilizing 50% of the trials as test trials are shown. The remainders of the trials in the cross-validation procedure were used as training trials. 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 percent correct for the corresponding data to those shown in Fig. 3 (After Rolls et al. 1997a)

the retina (translation invariance) (Rolls and Baylis 1986; Rolls 2007, 2016a). Interestingly, the receptive fields become smaller (and still include the fovea) when faces or objects are seen against a complex natural background, and this helps with the binding problem (Aggelopoulos et al. 2005). It 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 (Rolls 2007, 2016a). Some neurons have view invariant responses to faces (which would be useful for face recognition, and indeed these neurons tend to be tuned to face identity)

(Hasselmo et al. 1986; Rolls 2000). Other neurons have view-specific responses, and indeed are found in the cortex in the superior temporal sulcus where some neurons are tuned to face expression, and typically to face motion and face gesture (change of expression), all of which are important in social interactions (Hasselmo et al. 1989; Rolls 2007, 2016a). These discoveries have been confirmed (Said et al. 2011; Polosecki et al. 2013; Tsao 2014).

A computational model of how invariant representations for faces and objects are built in the ventral visual system can account for the responses of many of these neurons. The model, VisNet, utilizes competitive learning at each stage of the hierarchy of visual cortical areas in the

Face processing in different brain areas and face recognition, Fig. 4 The number of stimuli (in this case from a set of 20 faces) that are encoded in the responses of different numbers of neurons in the temporal lobe visual cortex, based on the results shown in Fig. 3. The decoding method was dot product (DP, *open circle*) or probability estimation (PE, *filled circle*) (After Rolls et al. 1997a)

ventral visual system with convergence from stage to stage to form feature combination neurons, and slow learning implemented by an associative synaptic learning rule with a short-term trace memory of previous activity to enable the learning of invariant representations (Wallis and Rolls 1997; Rolls 1992, 2012, 2016a) (Fig. 5). Consistent with this, macaque face cells respond to combinations of several metric properties of human faces (Chang and Tsao 2017). VisNet can locate and identify objects and people in complex scenes by adding an emulation of the dorsal visual system to foveate salient stimuli (Rolls and Webb 2014). VisNet can also learn deformation-specific representations of pose, which are likely to be useful for the emotional and intentional interpretation of faces and people (Webb and Rolls 2014).

A Representation of Faces in the Amygdala

Outputs from the temporal cortical visual areas reach the amygdala, and evidence is accumulating that these brain areas are involved in social and emotional responses to faces (Rolls 2014). For example, we have identified a population of

neurons with face-selective responses in the primate amygdala, some of which may respond to facial and body gesture (Leonard et al. 1985). In humans, amygdala damage can impair the recognition of fear face expressions, and extraversion influences whether activations will be found to happy faces (Rolls 2014).

A Representation of Faces in the Orbitofrontal Cortex

Rolls et al. (2006) have found a number of face-responsive neurons in the orbitofrontal cortex, and they are also present in adjacent prefrontal cortical areas (Rolls 2007, 2016a). The orbitofrontal cortex face-responsive neurons, first observed by Thorpe et al. (1983), tend to respond with longer latencies than temporal lobe neurons (140–200 ms typically, compared with 80–100 ms) and can convey information about which face is being seen, by having different responses to different faces. Some of the orbitofrontal cortex face-selective neurons are responsive to face gesture or movement and others to face expression (Rolls 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, which can indicate reinforcement, and by encoding information about which individual is present, also important in evaluating and utilizing reinforcing inputs in social situations (Rolls 2014). The existence of these neurons has been confirmed using fMRI (Tsao et al. 2008b).

We have also been able to obtain evidence that nonreward used as a signal to reverse behavioral choice is represented in the human orbitofrontal cortex (see Rolls 2014). 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
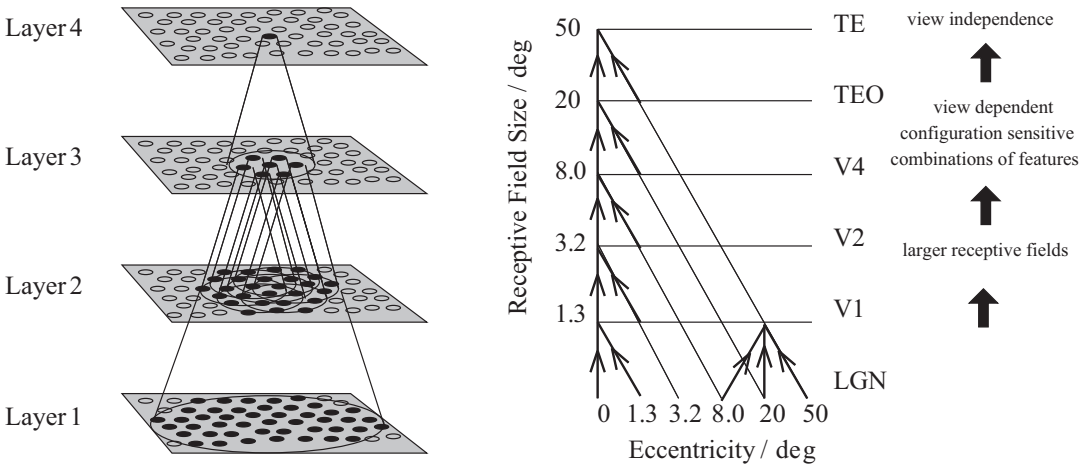
Face processing in different brain areas and face recognition, Fig. 5 *Right*. Schematic diagram showing convergence achieved by the forward projections in the visual system, and the types of representation that may be built by competitive networks operating at each stage of the system from the primary 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 (See Rolls 2012)

expression. After good performance was acquired, there were repeated reversals of the visual discrimination task. Kringelbach and Rolls 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 (see Figs. 6 and 7). The investigation reveals that the human orbitofrontal cortex is very sensitive to social feedback when it must be used to change behavior (Rolls 2014) and that provides some evidence for the theory that depression is related to overactivity in a lateral orbitofrontal cortex nonreward attractor network (Rolls 2016b).

To investigate the possible significance of the neurons in the orbitofrontal cortex with face-related inputs, 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 behavior (Rolls 2007, 2014). 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 in the same patients, providing an indication of separate processing.

To obtain clear evidence that the changes in face and voice expression identification, emotional behavior, 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). We found that some patients with bilateral lesions of the orbitofrontal cortex had deficits in voice and face expression identification (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
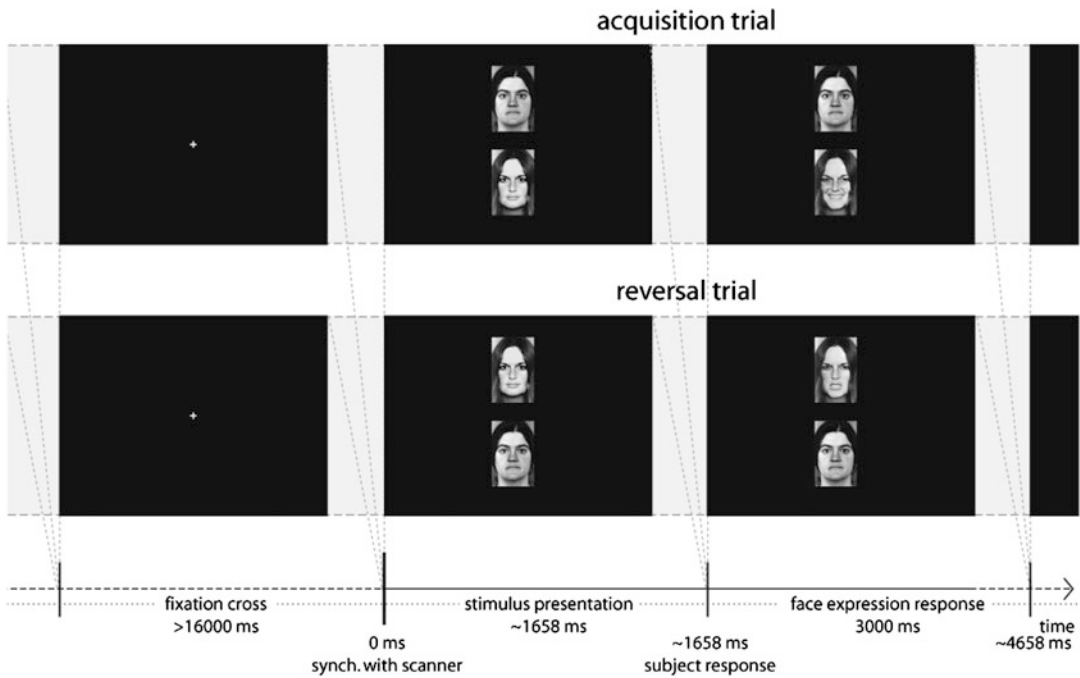
Face processing in different brain areas and face recognition, Fig. 6 Social reversal task: The trial starts synchronized with the scanner and two people with neutral face expressions are presented to the subject. The subject has to select one of the people by pressing the corresponding button, and the person will then either smile or show an angry face expression for 3000 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 and Rolls 2003)

but also in using reinforcers (such as monetary reward) to influence behavior.) Some patients with unilateral damage restricted to the orbitofrontal cortex also had deficits in voice expression identification. 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.

"Concept Cells" Recorded in Humans: Correspondence with Object-Place Memory-Related Neurons in Macaques

Some neurons in the human medial temporal lobe, in structures that include parahippocampal regions, respond to the faces of particular individuals, such as Jennifer Aniston (Quiroga 2012). These neurons are multimodal, in that they may respond to the voice of the person, and to the place associated with a person, and have been termed "concept cells" (Quiroga 2012). These neurons thus appear to correspond to the hippocampal/parahippocampal system memory-related neurons in macaques, which respond to an object or the place in which it is located, and which are part of an episodic memory system (Georges-François et al. 1999; Rolls et al. 2005; Kesner and Rolls 2015; Rolls 2016a). These neurons, like face neurons, use sparse distributed encoding, and are not grandmother cells (Quiroga et al. 2008).
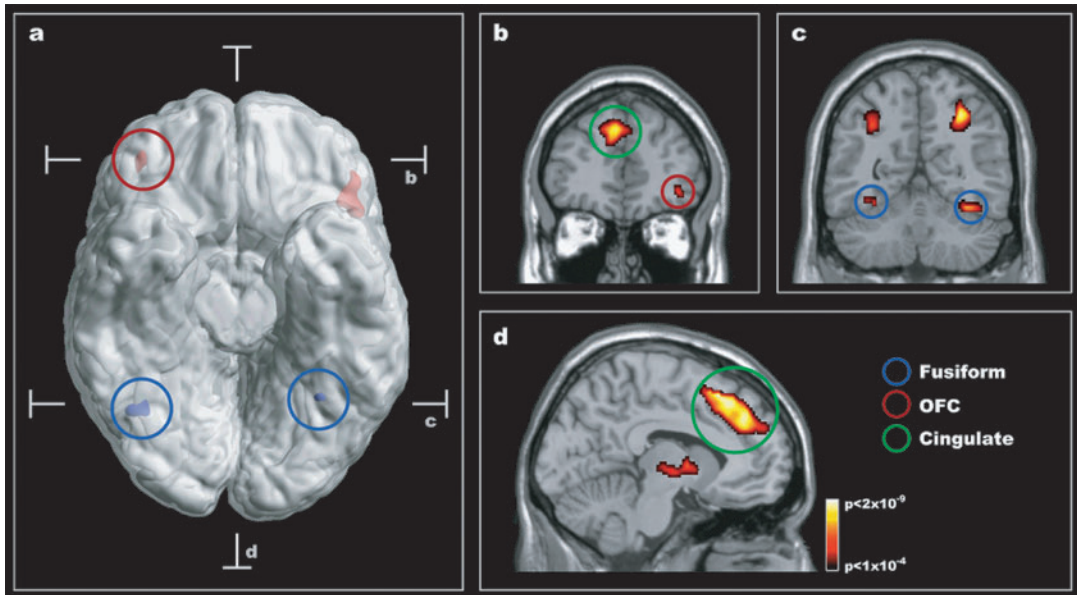
Face processing in different brain areas and face recognition, Fig. 7 Social reversal: Composite figure showing that changing behavior based on face expression is correlated with increased brain activity in the human orbitofrontal cortex. (**a**) The figure is based on two different group statistical 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: 42, 42, −8; and Z = 5.51; x, y, z = −46, 30, −8) 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 = 0.0001 for purposes of illustration to show their extent) (After Kringelbach and Rolls 2003)

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