UNDERSTANDING THE RECOGNITION OF FACIAL IDENTITY AND FACIAL EXPRESSION

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Abstract | Faces convey a wealth of social signals. A dominant view in face-perception research has been that the recognition of facial identity and facial expression involves separable visual pathways at the functional and neural levels, and data from experimental, neuropsychological, functional imaging and cell-recording studies are commonly interpreted within this framework. However, the existing evidence supports this model less strongly than is often assumed. Alongside this two-pathway framework, other possible models of facial identity and expression recognition, including one that has emerged from principal component analysis techniques, should be considered.

FUNCTIONAL ACCOUNT
A theoretical framework that is based on the information-processing characteristics of a set of cognitive subsystems rather than their underlying neural mechanisms

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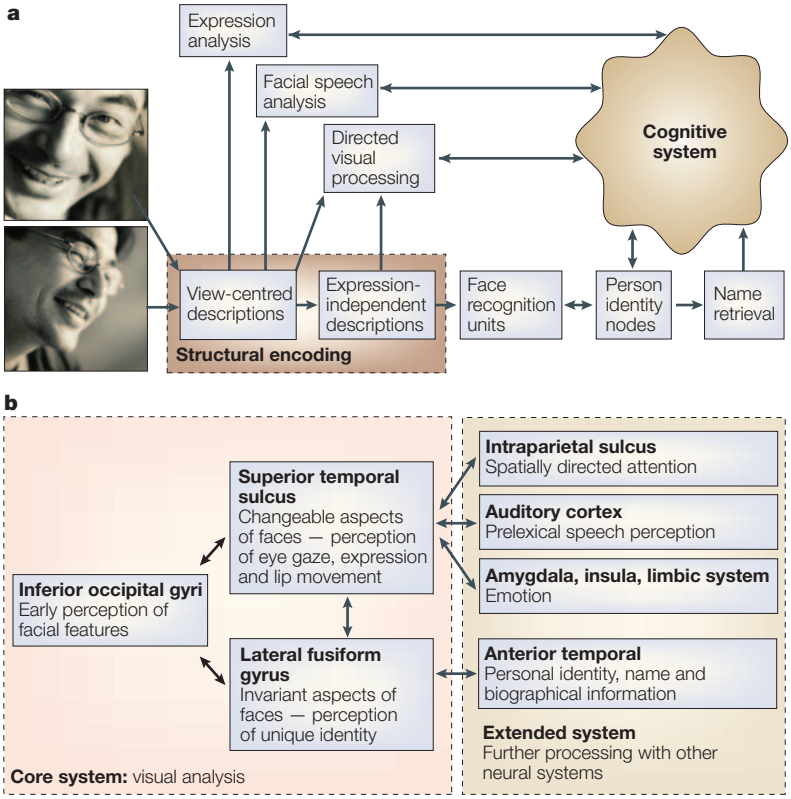
Nearly 20 years ago, Bruce and Young[1] presented a model of face recognition that posited separate functional routes for the recognition of facial identity and facial expression (BOX 1). This framework has remained the dominant account of face perception; few papers have challenged it and none has offered a widely accepted alternative. Here we discuss the relevant evidence, and show why a different conception from that offered by Bruce and Young[1] should be considered.

As a FUNCTIONAL ACCOUNT, the Bruce and Young[1] model did not incorporate a neural topography of its separate components. However, the recent neurological account of face perception proposed by Haxby and colleagues[2] (BOX 1) is compatible with the general conception offered by Bruce and Young. The core system of Haxby and colleagues' model[2] contains two functionally and neurologically distinct pathways for the visual analysis of faces (BOX 1): one codes changeable facial properties (such as expression, lipspeech and eye gaze) and involves the inferior occipital gyri and superior temporal sulcus (STS), whereas the other codes invariant facial properties (such as identity) and involves the inferior occipital gyri and lateral fusiform gyrus. The models proposed by Haxby and colleagues[2], and Bruce and Young[1], share the idea of distinct pathways for the visual analysis of facial identity and expression, but differ in terms of whether the perceptual coding of expression is carried out by a dedicated system for expressions[1] or by a system that codes expression alongside other changeable facial characteristics[2].

At the heart of both models is the idea that facial identity and expression are recognized by functionally and — by implication for Bruce and Young[1], and explicitly for Haxby and colleagues[2] — neurologically independent systems. This idea is supported by many psychological studies. For example, the familiarity of a face does not affect the ability of a healthy participant to identify its expression and *vice versa*[3–6]. Brain injury in humans can produce selective impairments in the recognition of facial identity or facial expression[7–11], in nonhuman primates, different cell populations respond to facial identity and expression[12], and functional imaging studies show that the perception of facial identity and facial expression have different neural correlates[13–15]. Therefore, the central idea of some form of dissociation between these two facial cues is not at issue. Rather, we focus on how this dissociation should be interpreted. In particular, we ask whether the concept of distinct parallel visual routes that process

Box 1 | **Cognitive models of face perception**



Bruce and Young's[1] functional model of face processing (panel a) contains separate parallel routes for recognizing facial identity, facial expression and lipspeech. The route labelled 'directed visual processing' is involved in the direction of attention to a particular face or facial feature. It is generally considered that the idea of separate routes for the recognition of facial identity and expression is supported by studies in cognitive psychology[4,5], cognitive neuropsychology[7–10], single-cell recording in nonhuman primates[12] and functional imaging[13,14]. Panel a modified, with permission, from REF. 1 **© (1986) British Psychological Society.**

The Bruce and Young[1] framework is compatible with the distributed human neural system for face perception proposed by Haxby and colleagues[2] (panel b). This identifies the neural structures that are involved in recognizing two types of facial information: changeable (dynamic) characteristics, such as expression, gaze and lipspeech; and invariant (relatively nonchangeable) characteristics, such as identity. Panel b reproduced, with permission, from REF. 2 **© (2000) Elsevier Science.**

This model is divided into a core system for the visual analysis of faces, which comprises three occipital/temporal regions, and an extended system that includes neural systems that are involved in other cognitive functions. Visuoperceptual representations of changeable characteristics are associated with the superior temporal sulcus (STS), whereas invariant characteristics are coded by the lateral fusiform gyrus (including the fusiform face area or FFA). The extended systems act together with the core system to facilitate the recognition of different facial cues.

This review is structured around four questions that we regard as central to interpreting dissociations between facial identity and expression. The first asks at what level of analysis the facial identity route bifurcates from the facial expression route. The remaining three questions relate specifically to the recognition of facial expressions: are all expressions processed by a single system, do the mechanisms for recognizing expression incorporate a multimodal level of analysis, and does the facial expression system deal with anything other than expression?

Where do the two routes separate?

Although each face is a single object, it conveys many socially important characteristics (such as identity, age, sex, expression, lipspeech and gaze), at least some of which (for example, identity and expression) show considerable functional independence. Face processing therefore requires a different conceptual framework from object recognition, and any plausible model requires a 'front-end' system that can both extract and separate different facial cues.

Both Bruce and Young[1] and Haxby and colleagues[2] propose that functional (and neural) separation of the facial identity and expression routes occurs immediately after the front-end component, which is involved in the initial structural and visual analysis of faces, with each route incorporating distinct visuoperceptual representations of the relevant facial characteristic. So, what evidence is there that facial identity and facial expression are coded in distinct visual representational systems?

In cognitive neuropsychology, support for this framework requires the identification of patients with impairments in the visual recognition of facial identity or facial expression alone. Cases of PROSOPAGNOSIA without impaired facial expression recognition would support the independence of identity processing; however, remarkably few prosopagnosics show well-preserved facial expression recognition. In fact, the idea that prosopagnosics can recognize facial expression is usually supported only by anecdote; on formal testing, most such patients show impairments of facial expression recognition. These difficulties are usually less severe than the problems with recognizing facial identity, although this might reflect the many procedural differences between standard tests of facial identity and expression. Instead, much of the evidence for impaired facial identity with intact facial expression recognition comes from studies in which the cause of the identity impairments has not been established[7,8,16,17]. Such data can provide evidence of a dissociation between the recognition of identity and expression, but they do not prove that this dissociation has a visuoperceptual origin.

So, a crucial issue that is often overlooked is that impaired recognition of facial identity, but not facial expression, can occur in neuropsychological conditions other than selective damage (or disrupted access) to the perceptual representation of human faces (prosopagnosia), and these causes of the dissociation do not necessarily support separate visuoperceptual codes for facial identity and expression. The alternative facial identity and facial expression offers the best fit to current findings. This view is endorsed by both models of face perception[1,2] and has dominated previous research. We review the evidence and conclude that, although there is some separation between the coding of facial identity and expression, the dominant view of independent visual pathways is not strongly supported; the present data are consistent with other potential frameworks that deserve to be more fully explored.

PROSOPAGNOSIA
A visual agnosia that is largely restricted to face recognition, but leaves intact recognition of personal identity from other identifying cues, such as voices and names. Prosopagnosia is observed after bilateral and, less frequently, unilateral lesions of the inferior occipitotemporal cortex.

causes include the following: impaired learning (and, therefore, recognition) of faces that are encountered after, but not before, neurological damage (prosopamnesia)[10,18,19]; impaired access to knowledge of familiar people[20–22], which affects recognition of identity from not only faces but also names, voices and so on; and other cognitive impairments, including amnesia or general semantic deficits, which some earlier studies did not eliminate[7,16].

The observation that impaired matching of unfamiliar faces can occur in the absence of impaired recognition of familiar faces and *vice versa*[8,23] adds a further complication. Therefore, impaired unfamiliar face matching with preserved facial expression recognition (or matching) cannot be considered to be equivalent to impaired recognition of familiar faces with preserved expression recognition[8].

If we restrict ourselves to studies that have used documented testing procedures and have excluded most of these alternative explanations, it is notable that only two reports offer evidence of prosopagnosia with preserved facial expression recognition[9,10], and there are some questions even with these. For example, Tranel and colleagues[10] described a prosopagnosic (subject 1) who scored 17 out of 24 (healthy controls scored 20.6) when asked to categorize facial expressions[24] as one of six options (happiness, sadness, anger, fear, disgust or surprise). However, the authors assigned two labels as correct for 5 of the 24 stimuli, because the controls were divided in their responses. Given that participants showing impaired facial expression recognition might select the next most likely option (for example, confusing disgust with anger)[25,26], this unusual method of scoring might have overestimated the ability of subject 1 to recognize expression. This report included two further cases showing impaired facial identity with intact expression recognition, but neither was prosopagnosic — one patient had general amnesia and the other had prosopamnesia[10].

A second frequently cited case is that of Mr W[9]. Most facial expression tests in this study used a 'two-alternative choice' format (such as happy versus sad). Healthy participants tend to have little difficulty with this form of task and near-ceiling performance makes the results difficult to interpret. The most demanding facial expression task used with Mr W consisted of finding four further examples of a target expression among an array of 16 faces that each displayed one of four expressions[9]. The control data in this study were from individuals with damage to either the left or the right hemisphere. The performance of Mr W fell between these two groups, but no statistical comparisons were reported. In light of work showing that both right and left hemisphere damage (including nonspecific damage[27]) can impair facial expression recognition[8,27,28], the absence of healthy control data makes it difficult to conclude that Mr W's facial expression recognition was fully preserved.

Although one or both of these patients with prosopagnosia might have preserved facial expression recognition, this was not conclusively demonstrated[9,10]. The data could equally reflect a 'trend dissociation'[29] in which both facial identity and expression are disrupted to greater and lesser extents, respectively. This would be consistent with most other reported cases of prosopagnosia. The most direct interpretation of this overall pattern involves the impairment of a system that codes visual representations of both identity and expression, with the identity deficit being exacerbated because facial identity recognition tasks are generally more difficult (BOX 2).

So, if we are to accept that facial identity and facial expression are coded by distinct visuoperceptual representational systems, it will be necessary to identify and verify further cases of preserved facial expression recognition in prosopagnosia. An example of the experimental rigour that is required can be found in a recent report of a developmental prosopagnosic who showed a marked discrepancy between her impaired facial identity and intact facial expression perception across several experiments[30]. However, there are reasons why investigations of developmental disorders should not be considered as directly equivalent to studies of ACQUIRED NEUROPSYCHOLOGICAL DISORDERS[31,32]. The main argument is that developmental cases violate a fundamental assumption of the dissociation logic — namely, that the brain injury affected a normally organized system. For this reason, evidence from cases of acquired neuropsychological disorders is vital.

In summary, the idea that the system for processing facial identity bifurcates from the facial expression route before the stage that codes visuoperceptual representations of facial identity and expression is less well supported by patient-based research than is widely assumed. It is therefore worth considering an alternative framework in which the perceptual representations of both facial identity and expression are coded by a single representational system.

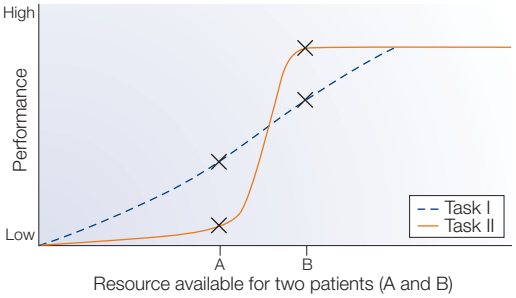
A PCA framework for face perception. An understanding of how different characteristics can be extracted from a single facial image is central to achieving an accurate conceptual framework for all aspects of face perception. However, the underlying computations of this system have received comparatively little attention. It is therefore of interest that insight has emerged from image-based analysis techniques, such as PRINCIPAL COMPONENT ANALYSIS (PCA) and similar statistical procedures (BOX 3).

PCA-based systems can reliably extract and categorize facial cues to identity[33–36], sex[37,38], race[39] and expression[40–42], and simulate several face-perception phenomena, including distinctiveness effects[34,35,39], caricature effects[43,44], the other-race effect[39] and the composite effect[41]. More recent work has shown that a PCA of facial expressions posed by different identities[24] generated distinct sets of principal components (PCs) coding expression and identity[42], and others that coded both of these facial cues (see also REF. 41) (BOX 3); expression and sex, but not identity and sex, showed a similar degree of separation. Moreover, this partial independence of the PCs was sufficient

ACQUIRED NEUROPSYCHOLOGICAL DISORDERS
Cognitive impairments that follow neurological damage to previously healthy individuals who have no known genetic or developmental disorders.

PRINCIPAL COMPONENT ANALYSIS
(PCA). A statistical technique that been applied to the analysis of faces. Facial images, which are originally described in terms of a large number of variables (for example, the greyscale values of individual pixels), are recoded in relation to a smaller set of basis vectors (principal components) by identifying correlations between sets of pixels across the entire set of facial images.

Box 2 | **Level of difficulty**



A neuropsychological dissociation is defined as impaired performance on one task (task I) and (relatively) spared performance on another (task II) after brain injury. One interpretation is that tasks I and II exploit different cognitive subsystems. Alternatively, this pattern could reflect damage to a single subsystem if spared performance on task II requires less of the system's resources than spared performance on task I (that is, if task II is easier). This is a genuine problem for face research. Facial expression tasks tend to use alternative-choice labelling or matching procedures that involve a small set of expressions, whereas typical facial identity tasks require the participant to provide identifying information for a series of various celebrities' faces.

It is generally assumed that a double dissociation, which is defined as two complementary dissociations, is sufficient to eliminate the possibility of a resource (level of difficulty) artefact. However, it is important to be cautious of double dissociations that involve a so-called 'trend dissociation', where a patient is impaired on both tasks, but shows significantly better performance on one task[29] (patient A in the figure). The graph shows the possible resource levels of two patients, A and B. Here, patient A does better on task I than task II, whereas the pattern is reversed for patient B. As illustrated, a double dissociation could arise because the performance–resource curve of one task is steeper than the other, which means that one cognitive subsystem could be responsible for both tasks. Consequently, Shallice[29] suggested that a double dissociation has its maximal interpretive value when patient A performs better than patient B on task I and *vice versa* for task II. However, even if the criterion proposed by Shallice is satisfied, a double dissociation between facial identity and expression can be correctly interpreted as evidence for separate neural systems underlying the visual representation of facial identity and expression only if each respective dissociation is specific to the facial domain. As discussed, there is little evidence for a face-specific double dissociation between facial identity and expression. Figure reproduced, with permission, from REF. 29 **© (1988) Cambridge University Press.**

to model the independent perception of facial identity and expression[6,41,42] (BOX 3). In addition, the partial overlap in the PCs for facial identity and expression offers a potential account of previously puzzling and unusual incidences in which facial identity and expression produced interference effects[45].

Therefore, independent coding of facial identity and facial expression can be achieved by a single multidimensional system in which the independence is partial (statistical) rather than absolute. Moreover, because PCA is an unsupervised algorithm with no prior knowledge of the physical structure of these facial cues, it is the different visual properties of facial identity and expression that create this separate coding. Therefore, the dissociation between identity and expression that is seen in healthy participants might be driven, at least in part, by the different visual cues that are optimal for conveying each type of information. In this sense, image-based techniques offer a new approach to understanding facial identity and expression perception, because they show that the dissociation is present in the statistical properties of facial images.

Note that we are not claiming that there is necessarily anything special about PCA *per se*. Further research might show that similar algorithms work equally well. However, at present, we use the term 'PCA framework' to refer to this image-based approach.

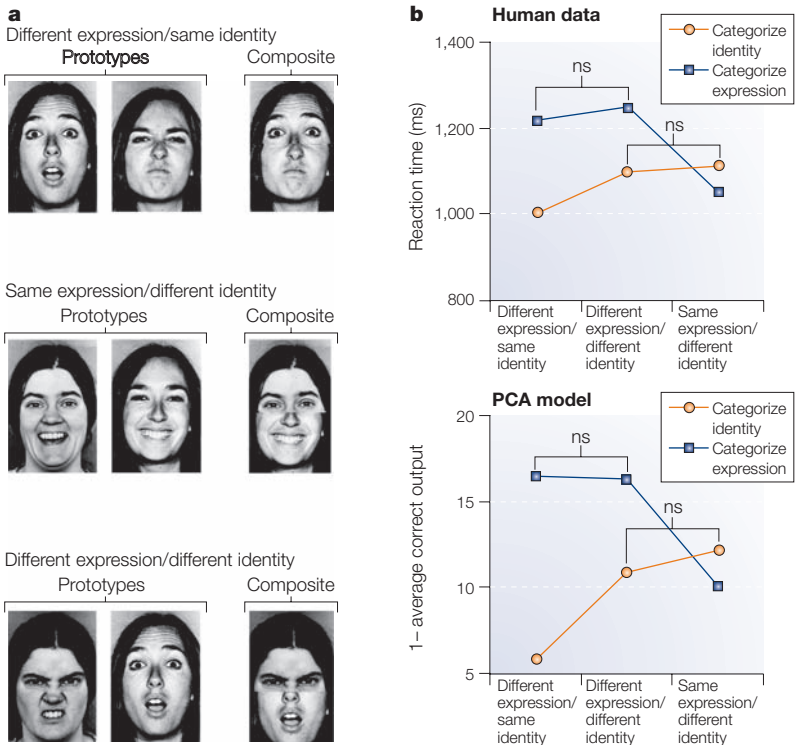
We have introduced the PCA framework at this stage to provide an alternative conception of face perception that can be evaluated along with those of Bruce and Young[1], and Haxby and colleagues[2], in relation to the further research we discuss. So, there are two plausible levels at which the facial identity route might bifurcate from the facial expression route: immediately after the structural encoding stage (Bruce and Young[1], and Haxby and colleagues[2]) or after a common representational system that codes both facial identity and expression (PCA framework).

Neurophysiology and functional imaging. The idea that facial identity and facial expression are processed by different neural systems is supported by data from patient studies, functional imaging and cell recording in monkeys. However, although functional imaging and cell-recording techniques allow more precise localization of brain regions that are sensitive to facial identity and expression, an important limiting factor is that they identify neural correlates of experimental procedures and the underlying functional contributions are difficult to derive from correlations. Therefore, the implications of these data for issues such as the point at which the facial identity route bifurcates from the facial expression route are not straightforward.

Relatively few functional imaging and cell-recording studies have investigated the processing of facial identity and expression in a single experiment[12–15,46,47], and their results have been inconsistent. Of interest is the extent to which these studies concur with the wider distinction made by Haxby and colleagues[2] between the involvement of inferotemporal areas (including the fusiform face area or FFA) in coding facial identity and that of the STS in coding changeable facial cues (such as expression, lipspeech and gaze).

Box 3 | **Modelling face perception with principal component analysis**

Principal component analysis (PCA) is a form of linearized compact coding that seeks to explain the relationships among many variables in terms of a smaller set of principal components (PCs). As applied to faces, the pixel intensities of a standardized set of images are submitted to a PCA. Correlations among pixels are identified, and their coefficients (PCs) are extracted[33]. The PCs can be thought of as dimensions that code facial information and can be used to code further faces. The particular advantage of techniques such as PCA is that they can reveal the statistical regularities that are inherent in the input with minimal assumptions.



Advocates of PCA-based models of face perception do not claim that the details of PCA are implemented in the human brain. Rather, PCA is viewed as a statistical analogue and not a literal account[34].

A PCA of facial expressions posed by different identities generates separate sets of PCs that are important for coding facial identity, facial expression, or both facial identity and facial expression[41,42]. This partial separation can model the independent coding of configural cues for facial identity and expression in healthy subjects[6,41], as illustrated by the composite effect[41,42].

Panel a shows composite faces that were prepared by combining the top and bottom halves of two faces with different expressions posed by the same identity, the same expression posed by different identities, or different expressions posed by different identities. Reaction times for reporting the expression in one face half were slowed when the two halves showed different expressions (that is, different expression/same identity and different expression/different identity) relative to when the same expressions (posed by different identities) were used (that is, same expression/different identity); however, no further cost was found when the two halves contained different expressions and identities compared with when they contained different expressions and same identities (top graph in panel b). A corresponding effect was found when subjects were asked to report the identity of one face half. The bottom graph in panel b shows a simulation of this facial identity–expression dissociation using a PCA-based model[41]. (ns, not significant; all other comparisons among the 'categorize identity' or 'categorize expression' levels were statistically reliable.) Panels a and b modified, with permission, from REF. 6 **© (2000) American Psychological Association. Panel b also modified from** REF. 41**.**

Functional imaging investigations into the recognition of both facial identity and expression have consistently identified occipitotemporal regions as being activated by identity[13–15,46]. However, the results have been less consistent as regards the brain areas that are involved in expression, and only two studies[15,46] found that the STS was involved. One of these investigations used an adaptation procedure whereby repetition of the identity or expression of a face was manipulated[15]. The FFA and posterior STS were more sensitive to repetition of facial identity, whereas a more anterior section of the STS was more sensitive to repetition of expression. This study provides evidence that representations of facial identity and expression are coded separately; however, as further research shows that facial and vocal expressions engage a similar area of the superior temporal cortex[48], it is possible that this region is not specific to facial signals of emotion *per se* (see below).

The second study showed STS activation for facial expression, but equivalent activity in the FFA for facial identity and expression[46]. However, the poor temporal resolution of functional MRI (fMRI) makes it difficult to determine whether feedback from areas such as the amygdala, which can modulate extrastriate responses[49], contributes to the FFA response to facial expression. Therefore, it is of interest

that a recent magnetoencephalography study found that the amplitude of a relatively early signal (onset ~144 ms) in the fusiform gyrus was modulated by different facial expressions in the following rank order: happiness > disgust > neutral[50].

The remaining functional imaging evidence that the FFA is involved in coding facial identity, and the STS is involved in coding expression, comes from studies that did not include both identity and expression conditions[48,51–54]. So, it would be helpful to conduct further investigations of the neural correlates of facial identity and expression in a single experiment, and to use varying experimental tasks to identify the conditions under which the STS/FFA distinction is optimized.

Clearer evidence of the distinction between facial identity (inferotemporal) and facial expression (STS) has come from an investigation of face-responsive cells in macaques[12]. However, in relation to the PCA framework, it is of interest that this dissociation was not complete and some cells were sensitive to both facial dimensions[12]; similarly, it should be remembered that the PCs found by PCA were tuned to identity, expression or both[42].

Other research indicates that the idea of a complete neurological dissociation might be too rigid. For example, one study found that the STS contains cells that are sensitive to facial identity and facial expression[55]. Some of the identity-responsive cells generalized across different views of faces, in contrast to inferotemporal face-sensitive cells, which tend to be view specific[56]. This led the authors to propose that the STS might pool the outputs of inferotemporal cells[56].

A further study found that face-responsive cells, which were recorded mainly in the anterior inferotemporal cortex but also in the STS, were sensitive to various stimulus dimensions — namely, their 'global category' (monkey face, human face or simple shape) and membership of each of four 'fine categories' (monkey identity, monkey expression, human identity or human expression)[47]. Global information was coded by the earlier part of a cell's response, which led the authors to postulate that this might enhance subsequent processing by switching the cell's processing mode.

A different perspective comes from Young and Yamane[57], who showed that the response profiles of face-selective cells in the anterior inferotemporal cortex (AIT) can be predicted by the physical (structural) properties of faces. Moreover, this information is distributed across a network of AIT cells in a POPULATION CODING format, as opposed to a highly localized or GRANDMOTHER CELL format (see also REFS 58,59). By contrast, the responses of STS neurons were not related to physical properties, but rather to how familiar the faces were or possibly to the social status of the bearer. Therefore, we should be cautious of assuming that these regions have analogous roles in coding representations of facial identity and expression. This is underlined by the fact that AIT and STS cells differ in several respects: the former are primarily visual, whereas regions of the STS are multimodal[60] and receive inputs from other polysensory brain regions that are involved in social/emotional processing[61]. As we discuss below, the polysensory properties of the STS might help to explain the greater association of this region with facial expression and other changeable facial cues.

Finally, the concept of population coding has similarities with the PCA framework in which face representations are distributed across a series of PCs. The analogy is further strengthened by the fact that most inferotemporal cells that respond to a particular face are tuned to a specific facial view[56]. Given the idea of a single PCA framework that codes facial identity and expression, it would be of interest to discover whether population coding can account for cell responses to the physical properties of both facial identity and expression, and whether cells that respond to each form part of the same, or different, neuronal populations.

In summary, both cell recording and functional imaging support the idea of separable mechanisms that are involved in facial identity and expression recognition, and provide evidence that the former is associated with inferotemporal regions and the latter with the STS. However, this distinction seems to reflect a bias rather than a categorical dissociation, so it would be helpful to explore under what circumstances this bias is optimized or minimized. These studies provide little evidence that an exclusive facial identity route bifurcates from an exclusive facial expression route after a structural encoding stage, such that the visual representations of each are coded separately. As it stands, evidence from neuropsychology, functional imaging and cell recordings fits more easily with the account implied by PCA in terms of relative segregation of facial identity and expression, rather than fully independent coding.

Is there one system for expressions?

As discussed above, a potential problem for interpreting neuropsychological cases in which facial identity recognition is impaired but expression recognition is relatively spared is that facial identity tasks are often harder than tests of expression recognition (BOX 2). It is generally assumed that any problems that arise from an asymmetry of task difficulty are minimized if the converse dissociation can be found (that is, impaired facial expression without impaired facial identity). However, in relation to whether the visuoperceptual representations of facial identity and expression are coded by analogous distinct systems, this logic only applies if the two dissociations affect functionally comparable mechanisms, leading to dissociable face-specific deficits — one affecting facial identity and the other affecting facial expression. There are good reasons, though, to believe that this might not be the case, and that selective impairments in the recognition of facial identity or facial expression are not simple mirror images of one another.

For example, impairments relating to facial identity affect the recognition of all familiar faces equivalently. By contrast, some facial expression impairments disproportionately affect one emotional category, such as fear[62–65], disgust[25,26,66] or anger[67,68]. Similarly, brain-imaging research has shown that some neural

POPULATION CODING
The idea that objects, such as faces, are coded as distributed patterns of activity across neuronal populations, so that cells show broadly graded responses to a single stimulus, as opposed to an 'all-or-none'-type response pattern.

GRANDMOTHER CELL
A hypothetical cell that responds specifically to a single face (such as one's grandmother). Although no such highly specialized cell has been found so far, the temporal cortex contains cells that respond preferentially to faces or hands, and some are maximally (although not exclusively) responsive to a particular persons' face. These cells are sometimes referred to as 'grandmother cells'.

regions are particularly involved in coding certain expressions (such as fear or disgust)[69–72], and comparative research has shown that the same systems are involved in behavioural responses that are associated with these emotions. Detailed discussions of emotion-specific neuropsychological deficits can be found elsewhere[65,73].

These emotion-specific impairments are often not restricted to the recognition of emotion from faces alone; vocal expressions are generally also affected[25,26,63–65,67,74]. Where exceptions to this pattern have been observed, the facial–vocal dissociation was expressed as a disproportionate deficit in recognizing fear from facial, but not prosodic, signals[75,76] and all but one of these cases[75] showed abnormal prosody recognition for emotions other than fear. Moreover, spared performance on emotion prosody tasks could reflect a supporting role of intact language systems.

The disproportionate role of certain brain regions in recognizing particular facial expressions shows that all expressions are not processed by a single system. Moreover, evidence is accumulating that these brain regions are not specialized for interpreting emotion from facial signals *per se*, but have a more general role in processing emotion from several sensory inputs. Indeed, recent research on disgust processing has shown that the insula might be involved in the perception of this emotion in others and its experience by the self[26,69,73,77–79]. In relation to the brain regions associated with emotion-specific impairments (amygdala, insula and ventral striatum), these deficits are best accounted for by damage to components of the extended system proposed by Haxby and colleagues.

Is multimodal analysis involved?

The co-occurrence of impairments in the recognition of facial and vocal expression is not restricted to cases that show disproportionate impairments for one emotion; in fact, the relationship is if anything more striking in patients who have general problems in recognizing facial expressions[25,80–82]. Moreover, other emotional impairments (affecting memory for emotional material, fear conditioning or subjective emotional experience) have also been identified in patients with specific and general facial expression impairments[11,83–89], whereas recognition of facial identity is generally preserved. Therefore, it seems likely that at least some facial expression impairments reflect damage to emotion systems rather than to face-specific mechanisms.

However, because not all patients have completed facial, vocal and general emotional tasks, and details of neurology are not always available, the overall picture is patchy. Impaired facial and vocal expression recognition could result from damage to a mechanism that is involved in processing both of these cues, such as bi- or multimodal representations of emotional signals, or from damage to a system for integrating emotional cues from different modalities. There is evidence that STS cells in macaques are sensitive to both visual and auditory components of animated biologically relevant stimuli, including facial signals[90].

There is little functional imaging evidence relating to multimodal emotional signals[91]. However, fMRI research has shown that the STS is important for processing other types of changeable facial cue in combination with cues from other modalities, such as lipspeech and speech[92,93] (see REFS 94,95 for STS sensitivity to unimodal lipspeech and vocal cues). These observations concur with research showing that regions of the STS constitute a point of multisensory convergence[60,61,96,97]. Therefore, the prominent role of the STS in coding facial expressions and other changeable facial signals might relate to the fact that, in everyday life, these signals are associated with more than one perceptual channel (that is, they have facial, vocal and dynamic components), which must be integrated to optimize communication. Consistent with this view, emotion and speech can be identified from facial, vocal or dynamic (point-light display) cues, combinations of which can interact[74,98–101]. Similarly, the contribution of the STS to the perception of social attention[56,102,103] might relate to the need to integrate gaze, head direction, body posture and associated dynamic information to accurately determine the focus of attention of another individual[104,105]. This is illustrated by human cognitive studies showing that the direction of attention that is signalled by gaze interacts with that signalled by head orientation[105], and by research in monkeys showing that many STS cells that respond to a particular gaze direction also respond to the same direction when it is signalled by head orientation or body posture[56]. Furthermore, there is evidence that interactions between the different dimensions that are associated with changeable cues occur both within and between cues associated with emotion, social attention, lipspeech and gesture[98,99,106,107]; for example, gaze can modulate perceived emotional state from facial expressions[107].

By contrast, identity is signalled primarily by the face[108,109] and there is little evidence that facial identity interacts with other facial cues[4] (although for an alternative view see REF. 45). An integration hypothesis might also explain the involvement of the STS in the perception of other biological cues, such as hand actions[110], body movement[111] and even HEIDER-SIMMEL-LIKE ANIMATIONS[112] (for a review, see REF. 113); all of these would benefit from the integration of different stimulus dimensions and, in particular, form and motion. In fact, there is evidence that integration of the form and motion of biological motion stimuli takes place in the STS[97,114].

However, most research into the neural correlates of changeable facial cues has been conducted with unimodal static photographs of faces and these are sufficient to engage STS mechanisms[2]. This observation can be explained by several factors. First, STS cells that respond to combinations of stimulus dimensions will also often respond to a single dimension alone[90,93,97]. Second, a proportion of the STS response to unimodal static faces might derive from the idea that these images imply other perceptual dimensions that are not explicitly represented by virtue of their strong association in everyday life; for example, lipspeech in the absence of auditory information engages the auditory

HEIDER-SIMMEL-LIKE ANIMATIONS
Short animations that depict the movements of geometric shapes in a manner that is normally perceived as suggestive of social interactions among 'human-like' characters. For example, one shape might be perceived as aggressive and intimidating towards another.

cortex and STS[94,115]. Third, cells that are sensitive to both unimodal (single dimension) and multimodal (dimension combinations) stimuli are found in the STS[56,90,93,97]. In relation to the latter, an interesting issue is whether STS cell networks that respond to unimodal or multimodal versions of these stimuli constitute stored unimodal and multimodal representations, or whether the unimodal cells reflect the first stage of an integration system in which unimodal projections from elsewhere (such as the inferotemporal cortex for visual form) undergo a preliminary analysis before being combined.

Does the expression system do anything else?

Our final question concerns whether the perceptual representations of facial expression are coded separately from other changeable facial cues (such as gaze and lipspeech)[1] or whether all changeable facial properties are coded by a single representational system, with separate routes only emerging in the extended system[2] (BOX 1). Alternatively, it is worth considering whether the visual form of all facial characteristics (identity, expression, lipspeech, gaze and so on) might be coded in a single multidimensional framework: that is, an extension of the PCA framework.

Few previous studies are relevant to this question. There are reports that brain injury can cause impaired facial expression recognition with preserved gaze perception[25] or lipspeech[116], and impaired lipspeech perception with preserved facial expression recognition[116]. However, as we have already discussed, dissociations can occur for different reasons and, when appropriate tests were used, these impairments were not found to be face specific[25,116]. This indicates that they are best accounted for by damage (or impaired access) to components of the extended system of Haxby and colleagues' model[2], whereby lipspeech impairments are associated with impaired access to language mechanisms, facial expression impairments with impaired access to emotion systems, and so on. Similarly, functional imaging research supports the involvement of language, emotion and attention systems in the perception of lipspeech, facial expression and gaze, respectively[2].

Studies using healthy volunteers are also potentially consistent with the idea that facial expressions are coded alongside other facial cues. Perception of emotion from faces can be modulated by the gaze direction of the model[107,117], which leads to changes in the amygdalar response to facial expression that can be detected with fMRI[118]. Another fMRI study found that both mouth and eye movements engaged a similar region of the posterior STS[102], which again implies that a common neural region is associated with changeable cues.

In summary, although there is some evidence for neuropsychological dissociations among the recognition of changeable cues, these dissociations do not seem to be face specific. At present, there is no clear evidence from neuropsychology that distinct representational systems are used for different changeable facial cues. That said, the paucity of relevant studies makes it difficult to draw firm conclusions at this time.

Discussion

We began by pointing out that the prevalent view in face perception research is that facial identity and facial expression are processed by separate functional routes — from their visual representations through to mechanisms for their interpretation[1,2]. As we explained, clear support for this theoretical position would arise from a double dissociation between facial identity and expression recognition that is restricted to the facial domain. One side of such a dissociation requires evidence for prosopagnosia without impaired facial expression recognition. However, contrary to common perception, the evidence for this pattern is limited. The opposite dissociation requires preserved recognition of facial identity with impaired recognition of emotion from the face, but not other emotional impairments. Evidence for this pattern is weaker still and it seems increasingly likely that selective disruption of facial expression recognition does not reflect damage (or impaired access) to visual representations of facial expression *per se*, but rather to more general emotion systems. In short, the idea that prosopagnosia compromises the recognition of facial identity but not facial expression, whereas 'prosopo-affective agnosias' compromise the recognition of facial expression but not facial identity, is an oversimplification. We have become sceptical about the view that facial expression recognition is simply the converse of facial identity recognition.

We also considered the contribution of cell recording and functional imaging to this debate. Although these techniques support the idea that there is a degree of neural separation between the mechanisms that are involved in the recognition of identity and expression from the face, they have contributed little to issues such as the level of analysis at which the facial identity route bifurcates from the facial expression route.

In effect, most of us working in this field have been trying to fit data to a strongly held *a priori* hypothesis of separate 'modules' for facial identity and expression analysis. This model comes from a long tradition that has emphasized the importance of facial expressions as communicative signals and placed less emphasis on the need to combine them with other sources of information. It has been bolstered by the intuitive appeal of the idea that facial expression recognition deficits would show an opposite pattern to prosopagnosia, as well as the belief that separate perceptual representations for facial identity and expression might be expected, because changes in expression would otherwise interfere with identifying the individual. This logical argument for the independent coding of facial identity and expression is supported by experimental data from healthy volunteers[3–6], but the term 'independent' in this context has gradually acquired a neurological connotation that lacks persuasive empirical support.

The PCA approach offers a different perspective, in that it shows that the independent perception of facial identity and expression[3–6] arises from an image-based analysis of faces with no explicit mechanism for

routing identity- or expression-relevant cues to different systems. This produces a single multidimensional framework in which facial identity and expression are coded by largely (although not completely) different sets of dimensions (PCs)[42]. Therefore, independent perception does not need to rely on totally separate visual codes for these facial cues. Image-based analysis techniques, such as PCA, also offer a ready solution to an important problem for implemented models of face perception — an operational front-end mechanism that can both extract and separate the visual codes of different facial characteristics from a single facial image. Moreover, the fact that this separation falls out of an objective (unsupervised) statistical analysis underlines the potential value of combining an analysis of the physical stimulus with an exploration of the functional and neural mechanisms that are involved in face perception.

Taking all these factors into account, the PCA framework should be given serious consideration. At this stage, too many pieces of the puzzle are missing to promote it as the definitive answer; not only from studies of brain-injured participants but also from nonhuman primate and functional imaging research. Nonetheless, it has a strong theoretical grounding, can mop up numerous observations (including previously unexplained ones) and serves a useful function in encouraging researchers to view face perception from an image-based perspective. We hope that it provides an alternative approach that will facilitate new research.

Unpacking the identity–expression distinction

At the heart of the model proposed by Haxby and colleagues[2] is a dissociation — supported by several empirical studies — between the involvement of the STS in coding facial expression, lipspeech and gaze, and the involvement of the inferotemporal cortex (including the FFA) in coding facial identity[2]. However, this distinction begs more fundamental questions; for example, why are facial characteristics divided in this manner, and why is the STS more interested in facial expression, lipspeech and gaze?

Haxby and colleagues[2] drew attention to the fact that facial expressions, gaze and lipspeech are dynamic and constantly changing (changeable cues), whereas facial identity is invariant. Therefore, projections from motion-sensitive regions — the human homologues of the middle temporal area (MT) or medial superior temporal area (MST) — to the STS might help to explain the role of the STS in the processing of changeable cues[119]. However, it might also be useful to consider other ways in which facial identity and changeable cues differ.

We have emphasized that the STS is sensitive not only to changeable facial characteristics, but also to other perceptual dimensions that are inherently linked with them (such as their associated vocalizations and dynamic information). Moreover, concurrent with research showing that the STS receives inputs from various sensory modalities[60], there is evidence that the STS underlies the integration of these different channels[56,90,92,97]. Consequently, we have proposed that the more prominent role of the STS in coding facial expressions and other changeable characteristics relative to facial identity might reflect the increased reliance of changeable cues on integrative mechanisms.

The integration hypothesis can also account for the involvement of the STS in the perception of other biological cues that require integration of form and motion[97]. However, there are other ways in which facial identity and changeable cues differ, which might prove important in interpreting the STS/inferotemporal distinction. One relates to the manner in which these cues are monitored during a social encounter. Although changeable cues require constant online monitoring during social interaction, the same is not true for facial identity — after registering a person's identity at the beginning of a social encounter there is little need to monitor it further. Indeed, consistent with the latter point, one study showed that a remarkable 60% of participants failed to realize that a stranger they began a conversation with had been switched with another person after a brief staged separation during the social encounter[120].

Another potentially relevant way in which changeable facial cues and facial identity differ is that only the former can be 'simulated' by perceivers. For example, viewing the facial expression or lipspeech of another person produces activation in corresponding facial muscles or facial motor brain regions[121,122], and facial expression tasks engage brain areas that underlie the experience of emotion[77], which has led some researchers to posit the idea of facial expression perception by simulation[78,79]. Similarly, seeing a face with leftward or rightward gaze induces an attentional shift towards the same direction in the observer[123–125] and engages brain systems that are involved in attention[2,102,103]. Conversely, there is no obvious sense in which we simulate another person's identity. Discovering how these different points relate to the neurological pathways that are associated with facial identity and expression might be important in understanding their psychological basis.

In conclusion

We have pointed out the value of an approach to face perception that emphasizes the different physical properties and information-processing demands (for example, reliance on integrative mechanisms) of different facial characteristics. This differs from the classic approach, which has tended to emphasize distinctions based mainly on informational content (identity versus expression). At the heart of our discussion is the issue of whether differences between neural mechanisms that are involved in the perception of facial identity and expression reflect a relatively straightforward bifurcation of visual pathways that are dedicated to different types of analysis, or a more complex arrangement in which the separation of identity and expression is relative rather than absolute. Linked to this issue is the question of whether the perception of facial expressions depends more on an intrinsically multimodal level of analysis (involving the STS) than facial identity.

Contrary to common opinion, we have argued that the idea of fully separate visual pathways for facial identity and expression is less well supported than is generally assumed, and that other options (including PCA) can provide credible approaches that should be explored. However, we recognize that there is some degree of neural separation between the mechanisms for recognition of identity and expression (and other changeable cues). Moreover, we are not denying that face perception is a complex task that involves the concerted action of different functional components. The inferotemporal/STS distinction is one component of this neural separation that has received considerable attention; however, an understanding of its psychological basis is lacking. The integration hypothesis offers one approach that might prove fruitful, but other distinctions should also be explored.

We do not know which of the various possibilities will prove correct and will not be disconcerted if the standard account is shown to be right. Our aim is simply to show that most researchers in this field have settled for an option that is not particularly well supported by the current data and that alternatives should therefore be seriously entertained. If our article stimulates the research that is required to resolve these issues, then it will have served a useful role.

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Competing interests statement
The authors declare no competing financial interests.

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