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Research report

Reconstructing dynamic mental models of facial expressions in prosopagnosia reveals distinct representations for identity and expression

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ABSTRACT

The human face transmits a wealth of signals that readily provide crucial information for social interactions, such as facial identity and emotional expression. Yet, a fundamental question remains unresolved: does the face information for identity and emotional expression categorization tap into common or distinct representational systems? To address this question we tested PS, a pure case of acquired prosopagnosia with bilateral occipitotemporal lesions anatomically sparing the regions that are assumed to contribute to facial expression (de)coding (i.e., the amygdala, the insula and the posterior superior temporal sulcus – pSTS). We previously demonstrated that PS does not use information from the eye region to identify faces, but relies on the suboptimal mouth region. PS's abnormal information use for identity, coupled with her neural dissociation, provides a unique opportunity to probe the existence of a dichotomy in the face representational system. To reconstruct the mental models of the six basic facial expressions of emotion in PS and age-matched healthy observers, we used a novel reverse correlation technique tracking information use on dynamic faces. PS was comparable to controls, using *all* facial features to (de)code facial expressions with the exception of fear. PS's normal (de)coding of dynamic facial expressions suggests that the face system relies either on distinct representational systems for identity and expression, or dissociable cortical pathways to access them. Interestingly, PS showed a selective impairment for categorizing many *static* facial expressions, which could be accounted for by her lesion in the right inferior occipital gyrus. PS's advantage for *dynamic* facial expressions might instead relate to a functionally distinct and sufficient cortical pathway directly connecting the early visual cortex to the spared pSTS. Altogether, our data provide critical insights on the healthy and impaired face systems, question evidence of deficits obtained from patients by using static images of facial expressions, and offer novel routes for patient rehabilitation.

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1. Introduction

The human face transmits a wealth of visual signals relevant for the identification and the categorization of facial expressions of emotion. The brain, as a decoder, flexibly filters the incoming visual information transmitted by the face to rapidly achieve complex perceptual categorizations (Schyns, Petro, & Smith, 2009). For example, the uniqueness of facial features characterizing a given individual, and their overall organization in the face, constitute the core information for identification and also for dissociating familiar from unfamiliar faces. Other signals can also be extracted from faces, such as the cues disclosing age (e.g., George & Hole, 1995), gender (e.g., Brown & Perrett, 1993; Ekman & Friesen, 1976, 1978; Schyns, Bonnar, & Gosselin, 2002; Tranel, Damasio, & Damasio, 1988), race (e.g., Caldara & Abdi, 2006; Caldara, Rossion, Bovet, & Hauert, 2004; Vizioli, Foreman, Rousselet, & Caldara, 2010; Vizioli, Rousselet, & Caldara, 2010) and emotional state (e.g., Bruce & Young, 1986; Calder & Young, 2005; Ekman & Friesen, 1976, 1978; Smith, Cottrell, Gosselin, & Schyns, 2005). Overt emotional states can also be extracted from face signals; they are mostly conveyed by facial expressions of emotion. The basic signals (i.e., "happy," "surprise," "fear," "disgust," "anger," and "sad") are only weakly correlated with each other to minimize confusions for their decoding (Smith et al., 2005), and we recently reported cross-cultural tunings in the way the emotion signals are transmitted and decoded (Jack, Blais, Scheepers, Schyns, & Caldara, 2009; Jack, Caldara, & Schyns, 2012; Jack, Garrod, Yu, Caldara, & Schyns, 2012). Yet, a fundamental question remains unresolved: does the face information used to recover identity and emotional expressions tap into common or distinct representational systems?

According to influential cognitive (Bruce & Young, 1986) and neuroanatomical (Haxby, Hoffman, & Gobbini, 2000) models of face processing, two distinct functional and neural systems accomplish the recognition of facial identity and facial expression. The first system – performing facial identification (Haxby et al., 2000) – is proposed to mainly involve the inferior occipital gyri and lateral fusiform gyrus, whereas the second system – performing facial expression categorization – is proposed to involve the inferior occipital gyri, the posterior superior temporal sulcus (pSTS) and the amygdala (for a review see, Calder & Young, 2005; Pessoa, 2008). However, some authors have questioned the idea of independence between those systems, by mainly relying on results from computational modelling and neuroimaging evidence (Calder, 2011; Calder & Young, 2005). A single model based on a Principal Component Analysis (PCA) can achieve independent coding of facial identity and facial expression, suggesting the possible existence of a multidimensional system, with a more partial than absolute independence (Calder, Burton, Miller, Young, & Akamatsu, 2001). These simulations have thus challenged the view of an independence between the coding for identity and expression, at least suggesting that those models are less strongly supported than what is often assumed (Calder & Young, 2005). In line with this position, Palermo, O'Connor, Davis, Irons, and McKone (2013) have recently put forward the theory of a first common step in the processing of expression and identity, and the occurrence of a splitting at a later stage; a view that is in agreement with the functional involvement of the inferior occipital gyrus as the entry level for both tasks (Calder & Young, 2005; Haxby et al., 2000; Pitcher, 2014). However, even though a neural dissociation for the processing of identity and emotional expression is supported by electrophysiological studies in primates (e.g., Hasselmo, Rolls, & Baylis, 1989) functional neuroimaging in humans (e.g., Winston, Henson, Fine-Goulden, & Dolan, 2004) and brain-damaged patients (Haxby et al., 2000), recent evidence suggests that the neural computations occurring in the inferior occipital gyrus and the right pSTS are functionally distinct and have a causal involvement in processing facial expressions (Pitcher, Duchaine, & Walsh, 2014). To sum up, more evidence is necessary to clarify this debate and, as acknowledged by Calder and Young (2005), further studies with brain-damaged patients are necessary to probe the hypothesis of distinct visuoperceptual systems for facial identity and facial expression categorization.

Following brain lesions, some patients lose the ability to recognize facial identity, despite no other obvious impairments of the visual system and a preserved identification via other modalities (e.g., voice, gait and so forth). The specificity of this face recognition deficit is spectacular, rare and has elicited considerable attention within the neuropsychological literature since the first clinical observations (Quaglino, 1867; Wigan, 1844) and the introduction of the term *prosopagnosia* by Bodamer (1947). Acquired prosopagnosia typically follows brain damage to bilateral occipitotemporal areas (e.g., Damasio, Damasio, & Van Hoesen, 1982; Farah, 1990; Landis, Regard, Bliestle, & Kleihues, 1988; Sergent & Signoret, 1992). Anatomical descriptions of prosopagnosia endorse the necessary and sufficient role of the right hemisphere (Landis et al., 1988; Sergent & Signoret, 1992) in the occipitotemporal pathway of face processing (for a review see, Bouvier & Engel, 2004). The clinical and anatomical conditions of prosopagnosia have always received great interest in cognitive neuroscience, as they clarify the neurofunctional mechanisms of normal face processing. The different sub-functions of the cognitive architecture of face processing have been isolated by the occurrence of distinct double dissociations in brain-damaged patients, for instance: a functional segregation between the ability to recognize unfamiliar and familiar faces (e.g., Malone, Morris, Kay, & Levin, 1982) and between lip reading and face identification (Campbell, Landis, & Regard, 1986). Yet, the neuropsychological literature remains controversial on the spared ability of prosopagnosic patients to identify facial expressions despite their impairment to recognize facial identity, and on patients showing impaired facial expression recognition with preserved facial identity recognition (for a detailed review see, Calder, 2011). Some *acquired* prosopagnosic patients showed a marked impairment in the categorization of facial expressions (Bowers, Bauer, Coslett, & Heilman, 1985; De Gelder, Pourtois, Vroomen, & Bachoud-Levi, 2000; De Renzi & Di Pellegrino, 1998; Humphreys, Donnelly, & Riddoch, 1993). Other studies reported preserved recognition of emotion in *acquired* prosopagnosia (Bruyer et al., 1983; Cole & Perez-Cruet, 1964; Mattson, Levin, & Grafman, 2000; Sergent & Villemure, 1989; Shuttleworth, Syring, & Allen, 1982; Tranel et al., 1988; Young, Newcombe, de

Haan, Small, & Hay, 1993). In addition, as pointed out by Calder and Young (2005) and Calder (2011), the decoding of face identity, as well as facial expressions of emotion, activates a similar network of regions in the occipitotemporal cortex. Facial expression impairments in patients are often correlated with a deficit to decode emotions from other modalities, which suggests a *general*, multimodal deficit in those patients, rather than a *selective* impairment of facial expression representations. In addition, a better understanding of the patients' information use (i.e., representations) for both tasks is necessary to clearly understand the very nature of the deficits in the face processing system (Calder & Young, 2005; Calder et al., 2011). Consequently, the question of dissociation between the identity and expression systems with acquired cases of prosopagnosia remains unclear.

To address this issue, we tested PS – a pure case of acquired prosopagnosia. PS is a 64-year-old woman (born in 1950) who sustained a closed-head injury in 1992. PS shows normal object recognition (e.g., Busigny, Graf, Mayer, & Rossion, 2010; Rossion et al., 2003) and relies on atypical cues to determine the identity of a person, such as voice, clothes, or other salient non-face features (e.g., glasses, haircut, beard, posture). She has major lesions on the left mid-ventral and the right inferior occipital cortex. Minor lesions of the left posterior cerebellum and the right middle temporal gyrus were also detected (for a complete anatomical description see, Rossion, 2008; Sorger, Goebel, Schiltz, & Rossion, 2007), whereas the regions that are assumed to be critical for the decoding of emotional expressions (i.e., the amygdala, the insula and the pSTS) are anatomically spared. Note that even if the occipital temporal regions are not playing a central role for facial expression decoding, the right inferior occipital gyrus is damaged in PS and represents the entry level for expression and identity in posited neuroanatomical models (Haxby et al., 2000; Pitcher, 2014). Thus, it remains to be clarified whether these lesions in the patient have also an impact on the processing of facial expressions. Of interest, we previously used a response classification technique – *Bubbles* – to reveal the diagnostic information used by PS for face identification (Caldara et al., 2005). *Bubbles* is a response classification technique sampling the information in 3-D space (2D image × spatial frequencies) (Gosselin & Schyns, 2001), to present sparse versions of the faces as stimuli. Observers categorize the sparse stimuli, and *Bubbles* keeps track of the samples of information that lead to correct and incorrect identification responses. From this information, we can establish how each region of the input space contributed to face identification performance and depict the diagnostic information used to effectively decode the stimulus. In contrast to healthy observers, PS did not use information from the eye region to identify familiar faces, but instead the lower part of the face, including the mouth and the external contours. To sum up, PS's well-established bias to use information from the mouth to identify faces and her anatomical neural dissociation provide a unique opportunity to probe the existence of a dichotomy in the representations used for facial identity and expression categorization.

Here, we first assessed her categorization performance of the six facial expressions of emotion using the classical Ekman and Friesen (1976) FACS (Facial Action Coded System) *static* face database. The FACS provides an anatomical taxonomy of the human muscles activated during the transmission of facial expressions of emotion (Ekman & Friesen, 1978), by quantifying facial movements for every expression in terms of so-called Action Units (AUs – each of them relating to a particular muscle). We then modelled PS's 3D dynamic mental representations of the six classic facial expressions by using a *dynamic* FACS-based Generative Face Grammar (GFG, see Fig. 1, the methods section and Yu, Garrod, & Schyns, 2012) on the AUs combined with a reverse correlation technique (see the methods and also Jack, Caldara, et al., 2012). The use of dynamic facial expressions provides a more ecologically valid approach to study the perception and processing of facial expressions, as our natural environment is surrounded with dynamic, temporal and multimodal information (Johnston, Mayes, Hughes, & Young, 2013). Pertinently, it has also been recently demonstrated that there is a causal involvement of the right pSTS in the processing of *dynamic* facial information (Pitcher et al., 2014), a region anatomically spared in PS.

The main goal of our study was to test whether the representations for identity and facial expressions are distinct or common. Mapping out the facial features used by a prosopagnosic patient to perform facial expression categorization is necessary to achieve this goal. As PS shows a suboptimal use of facial information for identity (i.e., by using the mouth region and external contours), we put forward the hypothesis that if she adequately uses all facial features for expression categorization, this observation would support the hypothesis of distinct sets of representations for identity and emotion recognition.

2. Participants

2.1. *PS's case report*

PS is a 64-year-old case of acquired prosopagnosia with normal object recognition. Despite the multiple and extensive brain lesions in the occipitotemporal cortex, PS recovered well in the months following her accident and with the support of neuropsychological rehabilitation she restarted working as a kindergarten teacher. PS's low-level vision is well preserved with a good visual acuity in both eyes, except to a small right paracentral scotoma. She reads normally (although slowly) and has normal object perception and recognition, even for subordinate-level discriminations (Rossion et al., 2003). However, as a consequence of the lesions, she reports her face recognition is severely impaired, even for close relatives (husband, children, mother, father) and her own. PS can categorize a face as a face, discriminate faces from objects and from a complex scene background, even at brief presentations (Schiltz et al., 2006). Her ability to categorize gender is impaired, in both accuracy and sensitivity (Rossion et al., 2003). Her performance in categorizing facial expressions is not as good as those of controls. In a 3AFC expression categorization task where the stimuli were presented for a maximum of 10 sec, PS's reaction times were significantly slower than those of controls and her response accuracy was below range for the first block of expressions comprising joy, fear and anger. She was normal for the second block testing

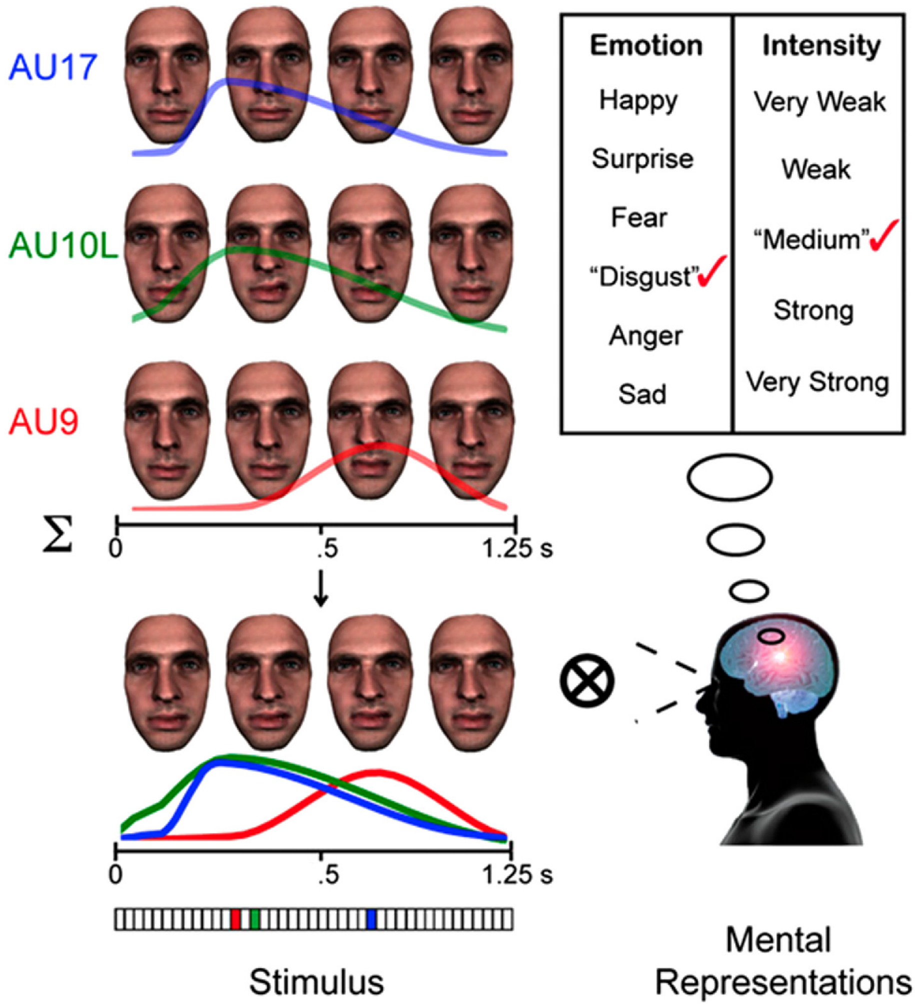

Fig. 1 – Stimulus generation – On each trial, the generative face grammar (GFG) randomly selected a subset of action units (AUs; AU17, AU10L, and AU9 are shown here with colour-coded labels) and values for six temporal parameters (see the colour-coded AU curves, which illustrate the amplitude and acceleration or deceleration of movement over time). The colour-coded vector at the bottom of the figure represents the 3 (of 41) randomly selected AUs that make up the stimulus on this illustrative experimental trial. We then applied the random facial animation to one of eight neutral-expression face identities using the procedure described in Yu et al. (2012). Mental representations – Observers categorized each random facial animation according to the six basic emotion categories (plus "don't know") and rated the emotional intensity on a five-point scale. Observers will interpret the random facial animation as a meaningful facial expression (here, "disgust," "medium intensity") when the facial movements correspond to the observer's mental representation of that facial expression.

disgust, sadness and surprise (Rossion et al., 2003). However her performance was collapsed across the expressions presented within a block and she was normal for the second block testing disgust, sadness and surprise (Rossion et al., 2003). Therefore, we had to assess PS's categorization accuracy of static facial expressions properly by using a 7AFC task (Experiment 1). PS is able to draw correctly a schematic face and perfectly points out all the single features and estimates age in the normal range. This latter result contrasts with her inability to recognize previously seen or familiar faces and to match unfamiliar faces, including changes of viewpoints (Rossion et al., 2003). As reported by Rossion et al. (2003) she is ranked as highly impaired on the Benton Face Matching Test (Benton & Van Allen, 1972) scoring 27/54 (percentile 1). She is also impaired on the Short Recognition Memory Test for Faces, a set of the Camden Memory Tests (Warrington, 1984) scoring 18/25 (percentile 3). When confronted with the pictures of 60 famous people (all known by the patient), she was able to classify 14 of them as familiar, and correctly classified all the unfamiliar ones (Rossion et al., 2003). Nevertheless, when asked to report the individual names of the faces classified as familiar, as well as their semantic information, she was correct for only four of them. Finally, PS has been tested extensively with simultaneous and delayed face and non-face (cars and novel objects) matching tasks in previous studies (Rossion et al., 2003). Although she is consistently impaired and slowed down for the face conditions, her performance with the non-face objects is in the normal range. Given the restriction of her deficit to the face category and that PS is alert, cooperative, and without any learning difficulties (Caldara et al., 2005) she represents an ideal case to isolate the nature of the facial information extracted by an impaired face system for the processing of facial expressions.

2.2. *Control participants*

The age-matched healthy observers who voluntarily took part in our experiments had normal or corrected to normal vision with no neurological or psychiatric history. The number of healthy observers and their age is reported in the method section of each experiment. For all our experiments, PS as well as the control participants signed a consent form describing the main goals of our experiments. The Ethical Committee of the Department of Psychology of the University of Fribourg approved all the studies reported here.

3. Experiments

3.1. *Preliminary experiment: categorization of the six classic facial expressions of emotion*

We first assessed categorization accuracy of static facial expressions using a standard set of posed facial expression stimuli – the Pictures of Facial Affect series (POFA) (Ekman & Friesen, 1976, 1978).

3.1.1. *Material and methods*

3.1.1.1. Control participants. Twelve age-matched healthy control subjects (8 female) participated in the experiment (mean age = 59.41; *SD* = 3.98).

3.1.1.2. Stimuli. We selected seven posed facial expression images from 22 identities (11 female) – one per emotion category (happy, surprise, fear, disgust, anger, sad, and neutral) – from the Pictures of Facial Affect (POFA) database (Ekman & Friesen, 1976, 1978). The pictures were in grayscale and not cropped.

3.1.1.3. Procedure. Observers categorized each stimulus according to emotion (happy, surprise, fear, disgust, anger, sad and neutral) in a 7AFC task using a computer keyboard in which we labelled the keys accordingly. Each image was presented for 2000 msec in random order in the centre of the observers' visual field with 30 repetitions of each expression, resulting in a total of 210 trials. Faces subtended a visual angle of 9.54° (vertical) and 8.11° (horizontal) on the screen.

3.1.2. *Results and discussion*

To determine whether PS's average accuracy is significantly different from that of the age-matched healthy participants, we used a modified independent samples t-test for single case studies (Crawford & Garthwaite, 2002). The statistical level of significance is $p < .05$. As shown in Table 1, PS's categorization of static, posed, FACS-coded facial expressions is significantly impaired for anger [$t(11) = -4.38$, $p < .05$], fear [$t(11) = -2.41$, $p < .05$], surprise [$t(11) = -2.69$, $p < .05$] and sad [$t(11) = -3.27$, $p < .05$] compared to the age-matched healthy controls.

Table 1 – Recognition accuracy of PS and age-matched controls on Ekman and Friesen's facial expression recognition test. PS showed impaired recognition of anger, fear, surprise and sad compared to healthy controls.

	PS		Age-matched controls	
	Score %	*Modified t-test*	Mean %	SD %
Ekman and Friesen (1978)				
Anger	36.33	−4.38*	71.95	8.46
Disgust	88.55	1.53	79.45	6.16
Happy	97.78	.55	96.11	3.12
Neutral	79.17	1.47	72.40	4.77
Fear	45.67	−2.41*	67.22	9.30
Surprise	48.89	−2.69*	70.00	8.16
Sad	47.22	−3.27*	70.00	7.24

*$p < .05$.

3.2. *Experiment 1 – reconstructing PS's dynamic mental models of facial expressions of emotion*

Using a novel method, we modelled the 3D dynamic mental representations of the six facial expressions plus neutral of PS and control participants, by using the FACS-based GFG computer graphics platform and a reverse correlation technique.

3.2.1. *Material and methods*

3.2.1.1. Control participants. Five healthy age-matched controls (3 women) participated in the experiment (mean age = 60.2; *SD* = 3.27).

3.2.1.2. Stimuli. Using the GFG (Jack, Garrod, et al., 2012; Yu et al., 2012) we synthesized a series of photorealistic facial animations by randomly selecting a subset of groups of muscles moving in synergy on the face – AUs (Ekman & Friesen, 1976, 1978). Practically, they were measured and modelled in 4D (3D face plus time), from the mapping of actors trained by Ekman to produce them. Existing as mathematical models in the GFG, we can animate each AU over time independently, using 6 temporal parameters (onset, acceleration, peak amplitude, peak latency, deceleration, offset) (see Fig. 1 and Movie C1 for an example stimulus).

Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.11.015.

Each animation is displayed on one of 8 unfamiliar 3D photorealistic white Caucasian face identities (4 female), which were acquired with a 3D photorealistic capture system (Dimensional Imaging). On any given trial, the GFG selects amongst the 41 core AUs a subsample of AUs using a binomial distribution ($n = 5$, $p = .6$, median = 3). The mental representation of each facial expression was then modelled for each observer by reverse correlating the random AUs and their temporal parameters with the observer's emotion responses. This technique has been validated in previous studies (Gill, Garrod, Jack, & Schyns, 2014; Jack, Caldara, et al., 2012; Jack, Garrod, et al., 2012).

3.2.1.3. Procedure. The experiment consisted in 12 sessions of 4 blocks that ran on a computer using a program written with Adobe Flash. Each block included 50 trials, consisting of 4D facial animations (3D + time) displaying a random subset of AUs movements. All the observers categorized a total of 2400 of such animations, comprising 30 frames (24 frames/second) of 1.25 sec duration. The facial animations subtended approximately 9.54° (vertically) and 6.68° (horizontally) of visual angle. On each trial, observers viewed the facial animation and categorized it according to the 6 classic emotions: happy, surprise, fear, disgust, anger and sad and a “don't know” response. Furthermore, observers rated the intensity of emotion perceived on a 5 point-rating scale (“Very weak”, to “Very strong”). We adapted the response to our senior population using the Geneva Emotion Wheel (GEW) introduced by Scherer (2005). We labelled the emotion categories in the outer boundaries of a circle, with the “don't know” response option in the centre. Additionally, we used 5 circles gradually increasing from the centre towards the respective emotional category placed on the border to allow participants to report the intensity of the perceived facial expression. Observers navigated with a mouse to select the basic emotion and its intensity. We did not provide feedback and did not place any time pressure on participants (including PS) to respond. All of the observers were familiar with using a computer and did not have difficulty with this interface. The whole experiment lasted for about 6 h, over a period of 6 weeks.

3.2.2. *Results*

3.2.2.1. Representation of the six basic emotions. For each participant, we modelled their mental representations of the six basic emotions, by reverse correlating the AUs randomly selected on each trial with the responses of the observers. For each observer, this resulted in a 41-dimensional (one dimension per AU) ON/OFF vector, with ON AUs being significantly correlated with an emotion category. The *p*-value of .05 was used to determine whether the correlation coefficient between each AU's presence or absence and the participant's emotional response was significantly larger than zero. For the final models only those AUs whose correlation coefficient was significantly larger than zero were displayed, but the regression coefficients for each AU were not affected by whether or not other AU were deemed significantly correlated or not. We then regressed for each ON AU, the six temporal parameters with the intensity responses of observers to model the activation dynamics (Jack, Caldara, et al., 2012; Jack, Garrod, et al., 2012; Yu et al., 2012). Figs. 2 and 3 report the results. Fig. 2 illustrates the static version of the dynamic stimuli, computed by collapsing the highest amplitude of each AU involved in the models of the “Very Strong” intensity judgement. Fig. 3 represents a static rendering of the facial parts that move (with amplitude of movement represented in millimetres).

Figs. 2 and 3 convey that the models of PS are within the range of those of controls. That is, for each individual expression, at least one control is very similar to that of PS (e.g., as Fig. 3 reveals PS's “happy” is similar to all controls, “surprise” to control 5, “fear” to 5 again, “disgust” to at least control 3, “anger” to control 4 and “sad” to control number 3). Movie 2 presents the 4D dynamic version of the mental models of PS and Movies 3, 4, 5, 6, 7 those of the 5 control subjects”. To test whether the patients' AUs preferences for each emotion fell within the normal range of the population we computed Pearson correlations between each of the patient's AUs ON/OFF vectors and the corresponding vectors for the control group (Table 2, column 1).

Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.11.015.

A permutation test confirmed that the 95% confidence interval of the expected correlation (between any control and the remaining controls, Table 2, column 2) for the null hypothesis (Patient = Controls) contained the correlation between the patient and controls for each of the six emotions. Table 2, column 3 contains the difference between the patient–controls correlations and the mean of the permutation test correlations expressed as Z-scores. PS fell in the normal range for AU preference. Fig. 3 represents a static rendering of the facial parts that move (with amplitude of movement represented in millimetres) for every expression and observer – the deviation maps.

3.2.3. *Discussion*

The reconstructed mental models of PS show that her representations of facial expressions are comparable to those of the age-matched controls. Of interest, PS uses information from the eye region to represent basic emotions as demonstrated by the analysis on the deviation maps. These results conflict with her inability to accurately categorize most of the static, posed facial expressions of the Ekman and Friesen (1978) face database (i.e., anger, fear, surprise and sad). How can we reconcile such a discrepancy?

3.3. *Experiment 2 – assessing categorization of facial expressions of emotion with PS's* static *and* dynamic *reconstructed mental models*

To clarify our previous observations, we carried out a verification task in which we presented PS and a new group of age-matched controls with *static* and *dynamic* mental models of the patient, and asked all observers to categorize the facial expressions of these stimuli.

3.3.1. *Material and methods*

3.3.1.1. Control participants. A new group of 10 age-matched controls (6 women) and PS participated in the experiment (mean age = 58.4; *SD* = 4.19).

3.3.1.2. Stimuli

3.3.1.2.1. Static reconstructed models. This experiment comprised static and dynamic versions of the same facial expressions. That is, for each dynamic 4D model (3D + time), we created a static version by collapsing time, keeping only the highest amplitude of each AU involved in the model (see Fig. 2 and Movies 2 & 3 for examples). We used PS's mental models of each of the basic emotions (happy, surprise, fear, disgust, anger and sad) at three levels of intensity (low, medium and high). The judgement of intensity was only kept to maintain attention and provide observers with a fine-grained scale, but its analysis is beyond the scope of the present work. This resulted in 18 facial expressions presented 6 times, for a given total of 108 images. The faces were subtending the same

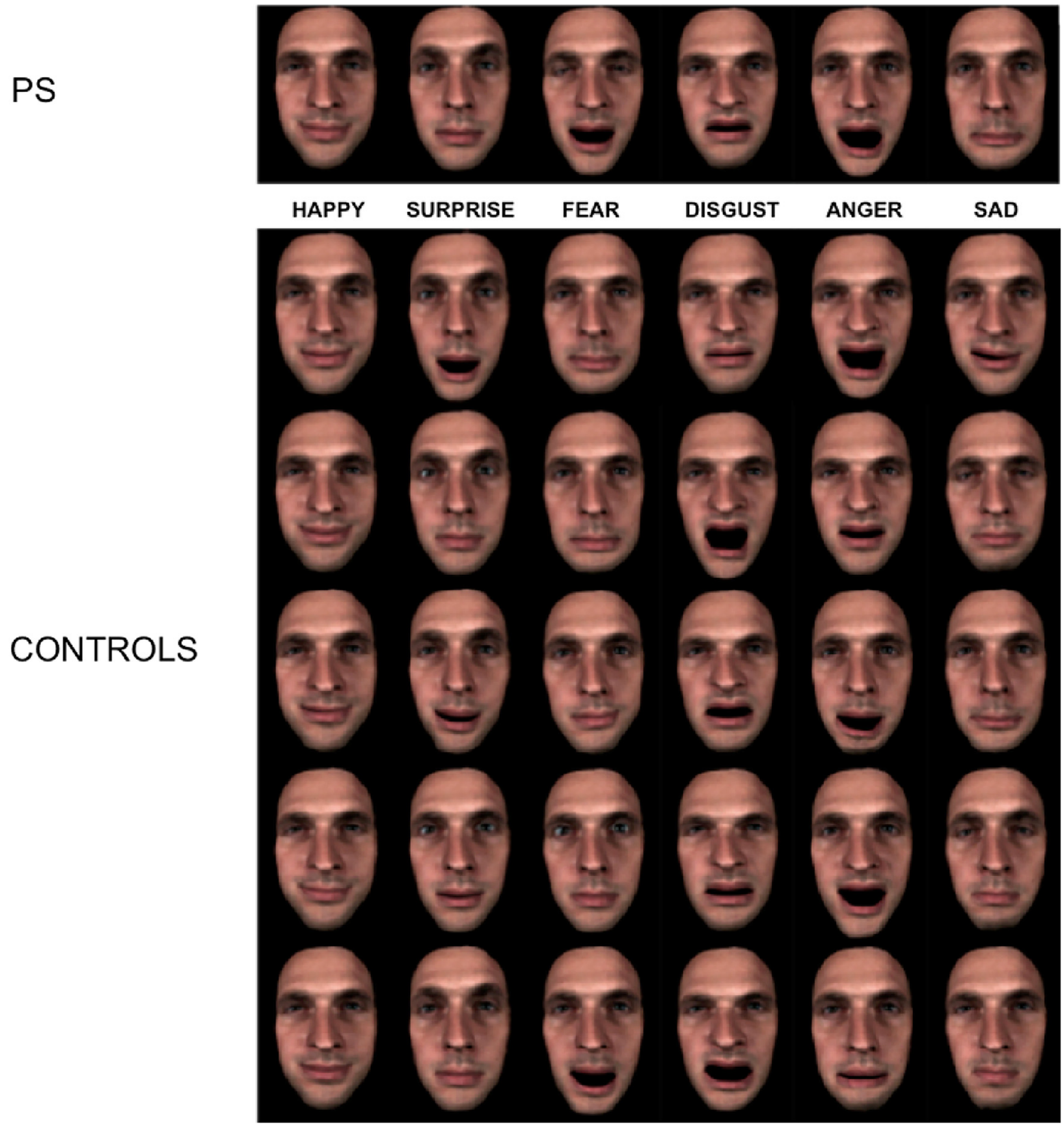

Fig. 2 – PS's and controls' reconstructed mental models of *happy, surprise, fear, disgust, anger* and *sad*. Positive correlation coefficients between active Action Units and emotional responses are represented as AU intensity. Active AUs for a given observer and emotion correspond to those whose correlation coefficient is significantly greater than zero ($p < .05$, one-tailed). Rows – observer (top row PS, bottom rows controls). Columns – emotion (happy, surprise, fear, disgust, anger, sad).

visual angles as in the previous experiment and were presented for 1250 msec.

3.3.1.2.2. Dynamic reconstructed models. Each dynamic facial expression consisted of 30 frames (24 frames/second) and lasted for 1250 msec. The facial animations and their static version were covering the same visual angle of the previous experiment.

3.3.1.3. Procedure

3.3.1.3.1. Static reconstructed models. The stimuli were presented in a random order, one at a time on the computer screen. PS and the controls were instructed to categorize each stimulus as accurately as possible by pressing one of six labelled keys on the computer keyboard (one per expression). No feedback was provided.

3.3.1.3.2. Dynamic reconstructed models. We used 12 animations for each emotion (4 per intensity) for a total of 72 trials. These animations were taken from the same identities used for the static presentation. After each presentation, observers categorized the dynamic facial expression according to the six classic emotions (i.e., happy, surprise, fear, disgust, anger and sad), as accurately as possible by pressing one of six labelled keyboard keys (one per expression). No feedback was provided.

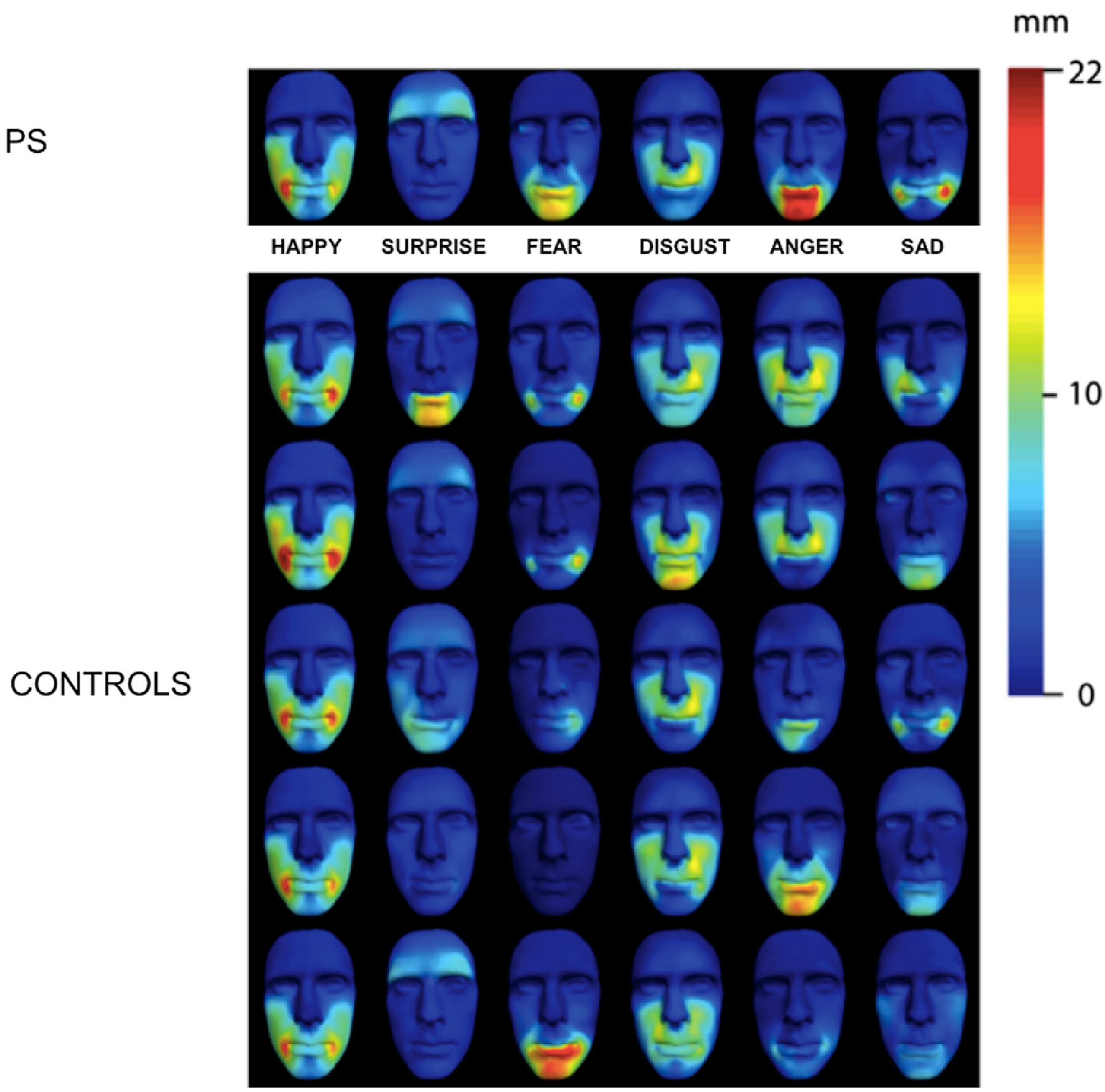

Fig. 3 – Deviation maps of PS's and controls' reconstructed mental models of happy, surprise, fear, disgust, anger, and sad. Colour scale represents peak magnitude of facial movement relative to neutral over the course of the expression at the corresponding position on the face. Facial movements are combinations of active AUs weighted by positive Pearson correlation coefficients (negative correlations are not shown) with emotional responses. Active AUs for a given observer and emotion correspond to those whose correlation coefficient is significantly greater than zero (*p* < .05, one-tailed). Rows – observer (top row PS, bottom rows controls). Columns – emotion (happy, surprise, fear, disgust, anger, sad).

3.3.2. *Results and discussion*

3.3.2.1. STATIC AND DYNAMIC RECONSTRUCTED MODELS. PS could not categorize the static version of many of her own mental models of facial expressions (see Fig. 4).

As shown in Table 3, PS was significantly impaired in the recognition of static images of her own mental models of anger [$t(9) = -2.04$, $p < .05$], disgust [$t(9) = -3.008$, $p < .05$] and surprise [$t(9) = -2.57$, $p < .05$]. In contrast, controls categorized the static models of PS successfully, with the exception of "fear."

In addition, PS categorized her own dynamic mental models (with the exception of fear) without difficulty. She was perfectly accurate for "anger, disgust, happiness, surprise and sad". A one-way repeated-measures analysis of variance (ANOVA) was performed to examine whether dynamic presentations facilitated performance for controls in the same way as for PS. There was no significant effect of display presentation (static *vs* dynamic) [$F_{(1,18)} = .74$, $p = .4$] and no significant interaction of emotion × display presentation [$F_{(1,18)} = .14$, $p = .98$].

3.4. *Experiment 3 – assessing categorization of facial expressions of average* static *and* dynamic *reconstructed mental models*

To verify whether PS's ability to categorize dynamic emotional expressions is restricted to the recognition of the expressions reconstructed from her mental model, we assessed her ability to categorize *average* static and dynamic reconstructed mental models. Given the limited number of mental models from

Table 2 – For each expression, Pearson correlations between PS's ON/OFF AU vectors and age-matched controls (column 1). Permutations of one control with other controls produced the expected correlations (column 2). Z-score difference between patient–controls correlations and the expected correlations (column 3). None of those differences was significant.

	PS versus Age-matched controls, Pearson correlations		
	PS versus Controls	Expected correlation	Z-scored difference
Static reconstructed model			
Anger	.3028	.2020	.9096
Disgust	.4131	.3585	.3630
Happy	.5027	.5679	−.8744
Fear	.0175	.0745	−.4265
Surprise	.4185	.3638	.5040
Sad	.1040	.1053	−.0096

Table 3 – Percentage accuracy score of PS and age-matched controls for PS's *static* and *dynamic* reconstructed mental models. The scores are given for the recognition of anger, disgust, happy, fear, surprise and sad. (Experiment 2).

	PS		Age-matched controls	
	Score %	*Modified t-test*	Mean %	SD %
Static reconstructed model				
Anger	16.67	−2.04*	80.03	32.19
Disgust	25.00	−3.008*	90.00	22.49
Happy	86.11	−1.04	96.67	10.54
Fear	8.33	−.05	10.00	31.62
Surprise	25.00	−2.57*	83.33	23.57
Sad	41.67	−.80	73.33	40.98
Dynamic reconstructed model				
Anger	100	.56	81.67	33.75
Disgust	100	.49	93.33	14.05
Happy	100	.33	96.67	10.54
Fear	17	–	0	0
Surprise	100	.76	74.97	34.52
Sad	100	.85	68.27	38.95

*$p < .05$.

healthy controls in the present experiment, we reconstructed an average mental model by using the data of 30 Westerner observers of our previous study (Jack, Garrod, et al., 2012). In line with experiment 2, this comprised the categorization of static and dynamic versions of the same facial expressions.

3.4.1. *Material and methods*

3.4.1.1. Control participants. PS and 12 age-matched control subjects (7 women) took part in this experiment (mean age = 59; SD = 3.71).

3.4.1.2. Stimuli

3.4.1.2.1. Average static and dynamic 4D mental models. We used an average of the mental models of 30 Westerners for each of the basic emotions (Jack, Garrod, et al., 2012), all presenting the highest level of intensity. We then rendered these models on 10 Caucasian actors (5 female). The faces were randomly expressing the six basic emotional expressions of fear, happy, anger, disgust, sad and surprise. As in the previous experiment, we created a static version of the average models by collapsing the time factor and keeping only the highest amplitude of each AU involved in the model (see Fig. 5). All observers were required to categorize both the static and dynamic facial expressions of the stimuli. We then randomly sampled 10 times all the mental models of each of the basic emotions (happy, surprise, fear, disgust, anger and

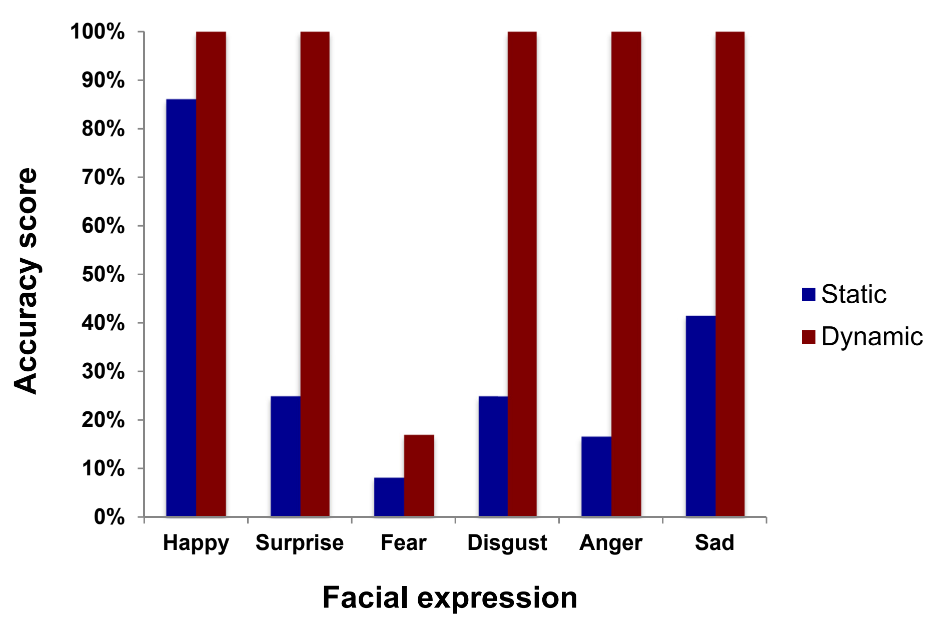

Fig. 4 – PS's percentage accuracy score for the recognition of happy, surprise, fear, disgust, anger and sad, from her *static* and *dynamic* reconstructed mental models. With the exception of fear, PS showed the maximum accuracy score of 100% for the recognition of all the dynamic emotions.

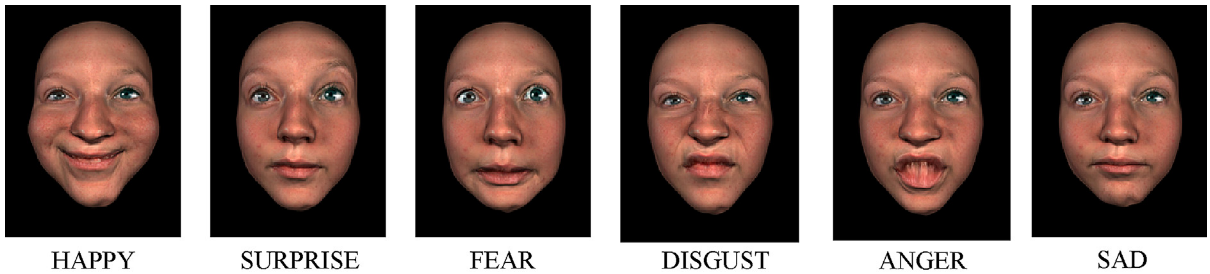

Fig. 5 – Average *static* reconstructed mental model for the expressions of happy, surprise, fear, disgust, anger and sad. The *static* version of the average models was created by collapsing the time factor and keeping only the highest amplitude of each AU involved in the model.

sad) on each face, which resulted in a total of 60 trials in both the static and dynamic conditions. The faces subtended the same visual angle as in the previous experiment and each stimulus was presented for 1250 msec in random order at the centre of the screen.

3.4.1.3. Procedure. We followed the same procedure as the one in experiment 2.

3.4.2. *Results and discussion*

PS was impaired in categorizing the static emotions of fear [$t(11) = -2.15, p < .05$], as well as sad [$t(11) = -2.70, p < .05$] from *average* mental models compared to the age-matched healthy control observers (see Table 4).

However, PS was accurate for categorizing all the *dynamic* emotions. Of interest, her performance for decoding fear from the dynamic average of healthy mental models was preserved.

For the controls, a repeated-measures ANOVA yielded a statistically significant main effect of the presentation (static *vs* dynamic) [$F_{(1, 22)} = 9.48$, $p < .05$], reflecting that the average performance with dynamic presentations was higher ($M = 83.61\%$, $SD = 9.55\%$) than with static ones ($M = 71.25\%$, $SD = 19.94\%$). A highly significant emotion × presentation interaction [$F_{(1, 22)} = 7.45$, $p < .001$], indicated that accuracy scores for dynamic presentations were higher for some emotions, but not for others. Post-hoc t-tests revealed that this effect was driven only by ‘surprise’, which was significantly higher with the dynamic presentation ($M = 89.17\%$, $SD = 13.79\%$) than with its static version ($M = 39.17\%$, $SD = 17.30\%$) [$t(11) = 7.54$, $p < .001$].

Table 4 – Percentage accuracy score of PS and age-matched controls for average *static* and *dynamic* reconstructed mental models. The scores are given for the recognition of anger, disgust, happy, fear, surprise and sad. (Experiment 3).

	PS		Age-matched controls	
	Score %	*Modified t-test*	Mean %	SD %
Static reconstructed models				
Anger	53.33	−.20	60.00	−.20
Disgust	76.67	−.23	80.83	−.23
Happy	90.00	−1.72	97.50	−1.72
Fear	33.33	−2.15*	71.67	−2.15
Surprise	40.00	−.05	39.17	.05
Sad	56.57	−2.70*	78.33	−2.70
Dynamic reconstructed models				
Anger	90	.40	79.17	25.39
Disgust	100	1.21	73.33	21.03
Happy	100	.41	98.33	3.89
Fear	90	.60	75.00	23.93
Surprise	100	.75	89.17	13.79
Sad	100	.66	86.66	19.23

*$p < .05$.

4. General discussion

Influential theoretical (Bruce & Young, 1986) and neuroanatomical (Haxby et al., 2000) models of face processing have suggested the existence of distinct cortical pathways for face identification and expression categorization, a view that has also been challenged (Calder & Young, 2005). The main goal of the present study was to clarify whether the face information of identity and emotional expression categorization tap into common or distinct representational systems. To tackle this issue, brain-damaged patients can be very informative, as from their lesions, their specific behavioural impairments and information use it is possible to infer the critical role played by the damaged regions in the healthy operating system. We first assessed the ability of PS – an acquired case of pure prosopagnosia – to categorize *static* facial expressions. PS was impaired for many facial expressions of the Ekman and Friesen's faces. Secondly, we modelled her mental representations of happy, surprise, fear, disgust, anger and sad. Our overarching goal was thus to map out the facial features used by the patient to achieve this biologically relevant task, given that we previously reported a suboptimal use of the mouth for face identification in the same patient (Caldara et al., 2005). Surprisingly, her *dynamic* mental models of facial expressions revealed an appropriate use of *all* facial features and Action Units (AUs – facial muscles), for all facial expressions, with the exception of fear. Since PS is using more than the mouth during this task, these results suggest that the mental representations of facial expressions are anatomically separate, or they are common but can be accessed from a distinct (cortical) route from face identification, as shown in memory models (Banks, 2000). Regardless of either potential explanation, our data support the view of a discrete (neural) coding for expression and identity.

The normal representations of *dynamic* facial expressions in PS, coupled with the impairment in the categorization of many of the *static* Ekman faces, came as a surprise to us and raised unexpected novel questions. How could PS have appropriate dynamic models of facial expressions and not be able to recognize them when presented in static images? We thus designed subsequent verification tasks in which the patient was asked to categorize *her* and *average static* and *dynamic* reconstructed mental models of facial expressions of emotion. These experiments revealed a clear-cut dissociation. PS was *selectively* impaired in the categorization of many facial expressions of her and the average *static* reconstructed models. In stark contrast, she excelled with the very same *dynamic* models, a pattern of results that can be explained by her particular set of lesions. Moreover, in general, this result points to the use of dynamic stimuli as being critical in he assessment of facial expression recognition with brain-damaged patients and questions the sole use of static face images to this aim. We now discuss in turn each of these findings and their implications.

4.1. *Does the face system rely on common or distinct representations for identity and expression?*

In order to investigate whether facial identity and expression decoding is tapping into common or distinct representational systems, we mapped out the different facial features/AUs used by a pure case of acquired prosopagnosia to categorize facial expressions. PS showed abnormal performance in categorizing most of the classic facial expressions (i.e., anger, fear, surprise and sad) of the well known Ekman and Friesen database (Ekman & Friesen, 1976, 1978), whereas the age-matched control group showed normal range performance (Calder et al., 2003). The analysis of the reconstructed models clearly revealed that PS is comparable to the age-matched control observers and uses similar facial muscles (i.e., AUs) and similar temporal dynamics to represent the six classic emotions. Thus, contrary to our previous observations for face recognition (Caldara et al., 2005), PS used *all* facial features/AUs to reconstruct facial expressions, favouring the view of distinct representations for expression and identity.[1] In line with these positions, neuroimaging studies have shown that the fusiform gyrus is sensitive both to facial identity and facial expression information (e.g., Cohen Kadosh, Henson, Cohen Kadosh, Johnson, & Dick, 2010; Fox, Moon, Iaria, & Barton, 2009; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001). Calder (2011) suggested that the fusiform gyrus contributes primarily to the analysis of the *visual form* of faces for both tasks, whereas the pSTS would be involved in the coding of the *changeable aspects* of faces (Haxby et al., 2000). PS would thus rely on the fusiform gyrus during face identification and the pSTS during facial expression recognition. This explanation could be partially accounted by a previous neuroimaging study using a neural adaptation paradigm with the patient. Schiltz et al. (2006) showed that contrary to normal observers, the neural activations of PS's right fusiform gyrus could not discriminate between the repetition of identical and different faces. This result suggests that the fine-grained visual form analysis necessary to effectively perform face identification requires the integrity of the face network and/or an optimal use of all the facial features. In contrast, the pSTS is anatomically and functionally spared in PS (Sorger et al., 2007) and could account for her normal facial information use for facial expression categorization. Despite favouring this view, we cannot completely and firmly rule out an alternative scenario in which the face system has a common set of representations, as the access could occur from distinct cortical pathways – one for face *identification* (through the inferior occipital gyrus) and one for *expressions* (through the pSTS). Importantly, both explanations suggest the existence of a discrete coding for expression and identity, and a future neuroimaging study is necessary to provide a clear-cut picture of those scenarios and precisely isolate the brain regions dedicated to the decoding of *static* and *dynamic* faces in PS, for both face *identity* and *expression* categorization.

On a general note, the use of dynamic reverse correlation techniques represents a unique tool for the understanding of patient impairments and their rehabilitation. For instance, growing studies indicate that schizophrenic patients are impaired in the recognition of the six basic facial emotional expressions (e.g., Kohler, Bilker, Hagendoorn, Gur, & Gur, 2000; Kohler et al., 2003; Kohler, Turner, Gur, & Gur, 2004; Martin, Baudouin, Tiberghien, & Franck, 2005; Sachs, Steger-Wuchse, Kryspin-Exner, Gur, & Katschnig, 2004). A selective impairment in recognizing fear and disgust has also been shown for unaffected relatives (Mendoza et al., 2011). Revealing the precise (defective) facial information use in these populations might help to tailor rehabilitation-training programs. Gaze-contingent eye tracking paradigms (Caldara, Zhou, & Miellet, 2010; Miellet, Caldara, & Schyns, 2011; Miellet, He, Zhou, Lao, & Caldara, 2012) will be well suited for this scope, as they can force the viewing of a particular diagnostic features during a categorization task (see also Adolphs et al. 2005), hopefully improving performance.

4.2. *Advantage in decoding* dynamic *facial expression in prosopagnosia*

Our study clearly points to an advantage in decoding *dynamic* versus *static* images for the categorization of facial expressions in PS only. Dynamic facial expressions provide observers with richer, unique and ecologically valid representations, which should facilitate their processing (e.g., Giard & Peronnet, 1999; Johnston et al., 2013; LaBar, Crupain, Voyvodic, & McCarthy, 2003; Paulmann, Jessen, & Kotz, 2009; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004; Trautmann, Fehr, & Herrmann, 2009). However, the advantage in the processing of dynamic over static emotional stimuli in healthy observers is controversial (for a review see, Fiorentini & Viviani, 2011). Some studies have showed an advantage (e.g., Ambadar, Schooler, & Cohn, 2005;

[1] According to this scenario, it could be possible that there are shared mechanisms represented in a multiple node network, with nodes being responsible for the processing of identity and others for the recognition of facial expressions. Some of the nodes related to face identification would be strongly damaged in PS.

Cunningham & Wallraven, 2009; Giard & Peronnet, 1999; Knappmeyer, Thornton, & Bulthoff, 2003; Paulmann et al., 2009; Wehrle, Kaiser, Schmidt, & Scherer, 2000), whereas others have revealed that the benefits of dynamic properties in processing facial information might be minimal (e.g., Gold et al., 2013) or inexistent (e.g., Fiorentini & Viviani, 2011). A study by Palermo et al. (2011) also revealed that congenital prosopagnosic patients showed normal recognition of static facial expressions but less efficient and weaker holistic coding for both identity and expressions. These results suggest that compensatory strategies could play a role in the normal recognition of static facial expressions and that the perceptual representations of identity and expression may not be separate at all stages. But more importantly, this observation can be accounted for by the set of lesions in the patient PS. It has been recently shown that the right inferior occipital gyrus – anatomically damaged in PS – is causally engaged in the processing of *static* face images (Pitcher et al., 2014) and expressions (Pitcher, 2014). On the contrary, the pSTS – anatomically spared in PS – has been related to the processing of *dynamic* faces (Pitcher et al., 2014) and expressions (Pitcher, 2014). Consequently, our data suggest that the inferior occipital gyrus plays a critical role in the decoding of *static* facial expressions (as the patient shows an impairment), but the pSTS is sufficient to effectively decode facial expressions from dynamic visual inputs (for which the patient shows normal performance). Greater responses for dynamic compared to static facial expressions have been found in the fusiform gyrus and the pSTS in the right hemisphere (e.g., Johnston et al., 2013; Kessler et al., 2011; LaBar et al., 2003; Sato et al., 2004; Schultz & Pilz, 2009), as well as the visual motion area in occipitotemporal regions (more commonly referred to as V5/MT) (Johnston et al., 2013). Our observations also reinforce the existence of a direct and functionally distinct cortical pathway connecting the early visual cortex to the pSTS, which would not require structural information from the right inferior occipital gyrus (since this region is damaged in PS) to decode expressions effectively. This advantage for directly processing dynamic visual inputs seems to be specific to facial expressions, as the patient cannot recover identity through dynamic visual information in everyday life. However, this hypothesis remains to be clarified with a future functional neuroimaging study measuring the extent to which the activations observed in the pSTS in PS (Sorger et al., 2007) would be significantly modulated by the presentations of dynamic faces, as well as static facial expressions.

Our results also feed the debate of the dynamic versus static advantage with new data, by suggesting that dynamic information might give an advantage to patients only. In fact, our results are in line with those by Humphreys et al. (1993) with an agnostic patient. This patient was impaired at identifying facial identity and facial expressions when exposed to *static* images, whereas he was performing normally when asked to judge a subset of facial expressions (i.e., smiling, frowning, or surprise) and gender from *dynamic* faces animated by light dots. However, whether this agnostic patient could correctly categorize *all* the basic facial expressions and his fine-grained information use was not assessed. In spite of these methodological and theoretical differences, the observation that emerges from both studies is that the recognition of emotions seems to imply a complex mechanism being facilitated by dynamic information. In fact, patients suffering from depression or schizophrenia also benefit from dynamic presentation of facial emotional expressions (e.g., Atkinson, Dittrich, Gemmell, & Young, 2004; Kan, Mimura, Kamijima, & Kawamura, 2004; Schaefer, Baumann, Rich, Luckenbaugh, & Zarate, 2010). Dynamic stimuli contain information that cannot be completely rendered by static representations and force the observers to shift their attention to different facial features. This might enhance attention and motor simulations particularly in fragile or neurologically impaired face systems, explaining increased performance for dynamic faces in those populations.

We should acknowledge that we did not objectively assess whether the amount of physical information conveyed by static and dynamic stimuli is identical or different for facial expressions categorization. We therefore cannot completely rule out the hypothesis that temporal properties provide a wealth of information that cannot be completely rendered by static facial cues. Interestingly, Gold et al., 2013 have shown that dynamic stimuli do not seem to provide additional information for the recognition of facial expressions than what is already offered by static facial cues in normal observers, by measuring the amount of information carried by static and dynamic facial expressions. In our study we created a static version of the stimuli by keeping only the highest amplitudes of each AU involved in the model, a procedure that should have led to the representation of 'optimal' static signals. In fact, by using a comparable approach, Fiorentini and Viviani (2011) have shown the absence of an advantage between the categorization of static and dynamic facial expressions in normal observers. In line with those results, our findings show equal performance for our healthy control observers between static and dynamic stimuli, with the exception of surprise. Thus, PS's ability to correctly categorize dynamic facial expressions does not seem to stem from the physical information available, but rather from an adequate psychological ability to make use of this information; a process that is most probably occurring in the pSTS.

4.3. *The special case of* "fear"

Our results support the hypothesis of a defective processing of fear in brain-damaged patients. PS was strongly impaired in recognizing the dynamic facial expressions of fear from her mental model, the static version from Ekman and Friesen's faces, and average mental model. It is worth pointing out that our age-matched control group showed an effective categorization of emotions from PS's *static* and *dynamic* reconstructed models, for all facial expressions but fear. This observation suggests defective internal representations for this expression in the patient. However, when PS was stimulated by optimal fear *dynamic* inputs (i.e., the average dynamic mental models) she achieved correct categorization.

The impairment for fear categorization with static images resonates with findings obtained with another brain-damaged patient. Adolphs et al. (2005) found selective impairment in fear recognition with a patient presenting bilateral damage of the amygdala: SM. SM did not spontaneously use the eyes during fear decoding in static images, but the mouth, which resulted in impairment in fear recognition. SM was able to categorize fear only when forced to look at the diagnostic region for this expression: the eye (Smith et al., 2005). Similarly, the analysis comparing PS's model for fear with the Ekman model showed a clear tendency to emphasize information from the mouth region in PS, compared to the eyes. However, PS's lesions are anatomically sparing the amygdala (Sorger et al., 2007) and cannot account for this deficit. In fact, Adolphs (2013) suggests that the processing of fear involves a complex distributed network featuring interactions among diverse cortical regions, rather than a single, localized "fear center". Very little is however known about which structures play a key role in this brain circuit and how these different regions interact together. Thus, PS's selective impairment in fear recognition could also stem from her brain lesions, micro-lesions such as axonal shearing (Sorger et al., 2007) or the missing interactions between her lesions and other cortical structures.

PS's impairment for fear might also appear in contrast with a previous fMRI result on her emotional attention (Peelen, Lucas, Mayer, & Vuilleumier, 2009). In a visual search task, a target face was presented among an array of distractor faces. The target differed from the distractor either by identity, identity and emotional expression (fear or happy), or identity and colour. PS and the controls showed a faster detection for fear and happy compared to the neutral face conditions. PS showed also a similar advantage for fear in a second change detection task, detecting significantly more changes when the changed face was fearful, as compared to when it was neutral. This behavioural pattern of results was parallelled with according neural responses biases indicating emotional attention in the brain areas coding for faces, suggesting a normal processing for fear. However, paying attention to a particular facial expression of emotion does not necessarily involve an *explicit* correct categorization for this expression. PS could have reached this pattern of results by using low-level cues distinguishing fear from neutral or happy signals, as she is relatively preserved for those expressions. PS's deficit for fear might also be clarified by recording her brain activation during the decoding of *her* and *average* models with in a future neuroimaging study.

5. Conclusions

The adequate categorization of facial expressions is a critical feature for adaptive social interactions. Our general goal was to understand whether face information used for identity and emotional expression categorization tap into common or distinct representational systems. We isolated information use for facial expressions in a pure case of acquired prosopagnosia with a lesion encompassing the right inferior occipital gyrus. PS's reconstructed mental models showed a normal use of *all* of the face features and muscles (i.e., AUs of the FACS coding system) for the representation of facial expressions, with the exception of fear. This is in stark contrast with the suboptimal information she uses for retrieving face identity (i.e., the mouth and the external contours). These data suggest that the face system does not rely on a unique representational system to code face features for identity and expression, or at least it relies on distinct cortical pathways to access them, flexibly adapting to visual and task constraints. In addition, our observations indicate that those cortical routes are modulated by the use of dynamic information, which facilitates the correct categorization of facial expressions in the patient. The inferior occipital gyrus plays a critical role for the decoding of *static* images, and the patient presents a selective impairment in the decoding of static expressions. On the contrary, the patient shows normal performance to effectively decode facial expressions from dynamic faces. The pSTS, which is spared in the patient, would be sufficient to effectively achieve this task. This result reinforces the view of the existence of a cortical pathway carrying out directly face signals from the early visual cortex to the pSTS, thus providing novel insights on the normal face operating system. Altogether, our data question also the conclusions obtained with patients by using unnatural static images and emphasize the need for a future neuroimaging study on the same patient to consolidate and provide a fine-grained picture of the present findings.

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REFERENCES

Adolphs, R. (2013). The biology of fear. *Current Biology, 23*(2), 79–93.

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature, 433*(7021), 68–72.

Ambadar, Z., Schooler, J. W., & Cohn, J. F. (2005). Deciphering the enigmatic face: the importance of facial dynamics in interpreting subtle facial expressions. *Psychological Science, 16*(5), 403–410.

Atkinson, A. P., Dittrich, W. H., Gemmell, A. J., & Young, A. W. (2004). Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception, 33*(6), 717–746.

Banks, W. P. (2000). Recognition and source memory as multivariate decision processes. *Psychological Science, 11*(4), 267–273.

Benton, A., & Van Allen, M. (1972). Prosopagnosia and facial discrimination. *Journal of the Neurological Sciences, 15*, 167–172.

Bodamer, J. (1947). Die Prosopagnosie. *Archiv fuer Psychiatrie und Nervenkrankheiten, 179*, 6–54.

Bouvier, S. E., & Engel, S. A. (2004). Patterns of cortical damage in achromatopsia and prosopagnosia. *Journal of Vision, 4*(8), 205a.

Bowers, D., Bauer, R. M., Coslett, H. B., & Heilman, K. M. (1985). Processing of faces by patients with unilateral hemisphere lesions. *Brain and Cognition, 4*(3), 258–272.

Brown, E., & Perrett, D. I. (1993). What gives a face its gender? *Perception, 22*(7), 829–840.

Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology, 77*(3), 305–327.

Bruyer, R., Laterre, C., Seron, X., Feyereisen, P., Strypstein, E., Pierrard, E., et al. (1983). A case of prosopagnosia with some preserved covert remembrance of familiar faces. *Brain and Cognition, 2*(3), 257–284.

Busigny, T., Graf, M., Mayer, E., & Rossion, B. (2010). Acquired prosopagnosia as a face-specific disorder: ruling out the general visual similarity account. *Neuropsychologia, 48*(7), 2051–2067.

Caldara, R., & Abdi, H. (2006). Simulating the 'other-race' effect with autoassociative neural networks: further evidence in favor of the face-space model. *Perception, 35*(5), 659–670.

Caldara, R., Rossion, B., Bovet, P., & Hauert, C. A. (2004). Event-related potentials and time course of the "other-race" face classification advantage. *NeuroReport, 15*(5), 905–910.

Caldara, R., Schyns, P., Mayer, E., Smith, M. L., Gosselin, F., & Rossion, B. (2005). Does prosopagnosia take the eyes out of face representations? Evidence for a defect in representing diagnostic facial information following brain damage. *Journal of Cognitive Neuroscience, 17*(10), 1652–1666.

Caldara, R., Zhou, X., & Miellet, S. (2010). Putting culture under the 'spotlight' reveals universal information use for face recognition. *PLoS One, 5*(3), e9708.

Calder, A. J. (2011). Does facial identity and facial expression recognition involve separate visual routes? In A. J. Calder, G. Rhodes, M. H. Johnson, & J. V. Haxby (Eds.), *The Oxford handbook of face perception* (pp. 427–448) Oxford: Oxford University Press.

Calder, A. J., Burton, A. M., Miller, P., Young, A. W., & Akamatsu, S. (2001). A principal component analysis of facial expressions. *Vision Research, 41*(9), 1179–1208.

Calder, A. J., Keane, J., Manly, T., Sprengelmeyer, R., Scott, S., Nimmo-Smith, I., et al. (2003). Facial expression recognition across the adult life span. *Neuropsychologia, 41*(2), 195–202.

Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews Neuroscience, 6*(8), 641–651.

Campbell, R., Landis, T., & Regard, M. (1986). Face recognition and lipreading. A neurological dissociation. *Brain, 109*, 509–521.

Cohen Kadosh, K., Henson, R. N., Cohen Kadosh, R., Johnson, M. H., & Dick, F. (2010). Task-dependent activation of face-sensitive cortex: an fMRI adaptation study. *Journal of Cognitive Neuroscience, 22*(5), 903–917.

Cole, M., & Perez-Cruet, J. (1964). Prosopagnosia. *Neuropsychologia, 2*, 237–246.

Crawford, J. R., & Garthwaite, P. H. (2002). Investigation of the single case in neuropsychology: confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia, 40*(8), 1196–1208.

Cunningham, D. W., & Wallraven, C. (2009). Dynamic information for the recognition of conversational expressions. *Journal of Vision, 9*(13), 1–17.

Damasio, A. R., Damasio, H., & Van Hoesen, G. W. (1982). Prosopagnosia: anatomic basis and behavioral mechanisms. *Neurology, 32*(4), 331–341.

De Gelder, B., Pourtois, G., Vroomen, J., & Bachoud-Levi, A. C. (2000). Covert processing of faces in prosopagnosia is restricted to facial expressions: evidence from cross-modal bias. *Brain and Cognition, 44*, 425–444.

De Renzi, E., & Di Pellegrino, G. (1998). Prosopagnosia and alexia without object agnosia. *Cortex, 34*(3), 403–415.

Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.

Ekman, P., & Friesen, W. V. (1978). *Facial action coding system*. Palo Alto, CA: Consulting Psychologists Press.

Farah, M. J. (1990). *Visual agnosia*. Cambridge: MIT Press.

Fiorentini, C., & Viviani, P. (2011). Is there a dynamic advantage for facial expressions? *Journal of Vision, 11*(3), 1–15.

Fox, C. J., Moon, S. Y., Iaria, G., & Barton, J. J. (2009). The correlates of subjective perception of identity and expression in the face network: an fMRI adaptation study. *NeuroImage, 44*(2), 569–580.

George, P. A., & Hole, G. J. (1995). Factors influencing the accuracy of age estimates of unfamiliar faces. *Perception, 24*(9), 1059–1073.

Giard, M. H., & Peronnet, F. (1999). Auditory-visual integration during multimodal object recognition in humans: a behavioral and electrophysiological study. *Journal of Cognitive Neuroscience, 11*(5), 473–490.

Gill, D., Garrod, O. G., Jack, R. E., & Schyns, P. G. (2014). Facial movements strategically camouflage involuntary social signals of face morphology. *Psychological Science, 25*(5), 1079–1086.

Gold, J. M., Barker, J. D., Barr, S., Bittner, J. L., Bromfield, W. D., Chu, N., et al. (2013). The efficiency of dynamic and static facial expression recognition. *Journal of Vision, 13*(5), 1–12.

Gosselin, F., & Schyns, P. G. (2001). Bubbles: a technique to reveal the use of information in recognition tasks. *Vision Research, 41*(17), 2261–2271.

Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. (1989). The role of expression and identity in face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research, 32*, 203–218.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*(6), 223–233.

Humphreys, G. W., Donnelly, N., & Riddoch, M. J. (1993). Expression is computed separately from facial identity, and it is computed separately for moving and static faces: neuropsychological evidence. *Neuropsychologia, 31*(2), 173–181.

Jack, R. E., Blais, C., Scheepers, C., Schyns, P. G., & Caldara, R. (2009). Cultural confusions show that facial expressions are not universal. *Current Biology, 19*(18), 1543–1548.

Jack, R. E., Caldara, R., & Schyns, P. G. (2012a). Internal representations reveal cultural diversity in expectations of facial expressions of emotion. *Journal of Experimental Psychology General, 141*(1), 19–25.

Jack, R. E., Garrod, O. G., Yu, H., Caldara, R., & Schyns, P. G. (2012b). Facial expressions of emotion are not culturally universal. *Proceedings of the National Academy of Sciences of the United States of America, 109*(19), 7241–7244.

Johnston, P., Mayes, A., Hughes, M., & Young, A. W. (2013). Brain networks subserving the evaluation of static and dynamic facial expressions. *Cortex, 49*, 2462–2472.

Kan, Y., Mimura, M., Kamijima, K., & Kawamura, M. (2004). Recognition of emotion from moving facial and prosodic stimuli in depressed patients. *Journal of Neurology Neurosurgery & Psychiatry, 75*(12), 1667–1671.

Kessler, H., Doyen-Waldecker, C., Hofer, C., Hoffmann, H., Traue, H. C., & Abler, B. (2011). Neural correlates of the perception of dynamic versus static facial expressions of emotion. *Psycho-social Medicine, 8*, 1–8.

Knappmeyer, B., Thornton, I. M., & Bulthoff, H. H. (2003). The use of facial motion and facial form during the processing of identity. *Vision Research, 43*(18), 1921–1936.

Kohler, C. G., Bilker, W., Hagendoorn, M., Gur, R. E., & Gur, R. C. (2000). Emotion recognition deficit in schizophrenia: association with symptomatology and cognition. *Biological Psychiatry, 48*(2), 127–136.

Kohler, C. G., Turner, T. H., Bilker, W. B., Brensinger, C. M., Siegel, S. J., Kanes, S. J., et al. (2003). Facial emotion recognition in schizophrenia: intensity effects and error pattern. *American Journal of Psychiatry, 160*(10), 1768–1774.

Kohler, C. G., Turner, T. H., Gur, R. E., & Gur, R. C. (2004). Recognition of facial emotions in neuropsychiatric disorders. *CNS Spectrums, 9*(4), 267–274.

LaBar, K. S., Crupain, M. J., Voyvodic, J. T., & McCarthy, G. (2003). Dynamic perception of facial affect and identity in the human brain. *Cerebral Cortex, 13*(10), 1023–1033.

Landis, T., Regard, M., Bliestle, A., & Kleihues, P. (1988). Prosopagnosia and agnosia for noncanonical views. An autopsied case. *Brain, 111*(6), 1287–1297.

Malone, D. R., Morris, H. H., Kay, M. C., & Levin, H. S. (1982). Prosopagnosia: a double dissociation between the recognition

of familiar and unfamiliar faces. *Journal of Neurology Neurosurgery & Psychiatry, 45*(9), 820–822.
Martin, F., Baudouin, J. Y., Tiberghien, G., & Franck, N. (2005). Processing emotional expression and facial identity in Schizophrenia. *Psychiatry Research, 134*, 43–53.
Mattson, A. J., Levin, H. S., & Grafman, J. (2000). A case of prosopagnosia following moderate closed head injury with left hemisphere focal lesion. *Cortex, 36*(1), 125–137.
Mendoza, R., Cabral-Calderin, Y., Dominguez, M., Garcia, A., Borrego, M., Caballero, A., et al. (2011). Impairment of emotional expression recognition in schizophrenia: a Cuban familial association study. *Psychiatry Research, 185*, 44–48.
Miellet, S., Caldara, R., & Schyns, P. G. (2011). Local Jekyll and global Hyde: the dual identity of face identification. *Psychological Science, 22*(12), 1518–1526.
Miellet, S., He, L., Zhou, X., Lao, J., & Caldara, R. (2012). When East meets West: gaze-contingent Blindspots abolish cultural diversity in eye movements for faces. *Journal of Eye Movement Research, 5*(2), 1–12.
Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research, 12*(2), 225–231.
Palermo, R., O'Connor, K. B., Davis, J. M., Irons, J., & McKone, E. (2013). New tests to measure individual differences in matching and labelling facial expressions of emotion, and their association with ability to recognise vocal emotions and facial identity. *PLoS One, 8*(6), 1–16.
Palermo, R., Willis, M. L., Rivolta, D., McKone, E., Wilson, C. E., & Calder, A. J. (2011). Impaired holistic coding of facial expression and facial identity in congenital prosopagnosia. *Neuropsychologia, 49*(5), 1226–1235.
Paulmann, S., Jessen, S., & Kotz, S. A. (2009). Investigating the multimodal nature of human communication: an ERP study. *Journal of Psychophysiology, 23*(2), 63–76.
Peelen, M. V., Lucas, N., Mayer, E., & Vuilleumier, P. (2009). Emotional attention in acquired prosopagnosia. *Social Cognitive and Affective Neuroscience, 4*(3), 268–277.
Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature Reviews Neuroscience, 9*(2), 148–158.
Pitcher, D. (2014). Facial expression recognition takes longer in the posterior superior temporal sulcus than in the occipital face area. *Journal of Neuroscience, 34*(27), 9173–9177.
Pitcher, D., Duchaine, B., & Walsh, V. (2014). Combined TMS and fMRI reveal dissociable cortical pathways for dynamic and static face perception. *Current Biology, 24*(17), 2066–2070.
Quaglino, A. (1867). Emiplegia sinistra con amaurosi—Guarigione—Perdita totale della percezione dei colori e della memoria della configurazione degli oggetti. *Giornale d'Oftalmologia Italiano, 10*, 106–112.
Rossion, B. (2008). Constraining the cortical face network by neuroimaging studies of acquired prosopagnosia. *NeuroImage, 40*(2), 423–426.
Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain, 126*, 2381–2395.
Sachs, G., Steger-Wuchse, D., Kryspin-Exner, I., Gur, R. C., & Katschnig, H. (2004). Facial recognition deficits and cognition in schizophrenia. *Schizophrenia Research, 68*(1), 27–35.
Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., & Matsumura, M. (2004). Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study. *Cognitive Brain Research, 20*(1), 81–91.
Schaefer, K. L., Baumann, J., Rich, B. A., Luckenbaugh, D. A., & Zarate, C. A., Jr. (2010). Perception of facial emotion in adults with bipolar or unipolar depression and controls. *Journal of Psychiatric Research, 44*(16), 1229–1235.
Scherer, K. (2005). What are emotions? And how can they be measured? *Social Science Information, 44*(4), 695–729.
Schiltz, C., Sorger, B., Caldara, R., Ahmed, F., Mayer, E., Goebel, R., et al. (2006). Impaired face discrimination in acquired prosopagnosia is associated with abnormal response to individual faces in the right middle fusiform gyrus. *Cerebral Cortex, 16*(4), 574–586.
Schultz, J., & Pilz, K. S. (2009). Natural facial motion enhances cortical responses to faces. *Experimental Brain Research, 194*(3), 465–475.
Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding recognition from the use of visual information. *Psychological Science, 13*(5), 402–409.
Schyns, P. G., Petro, L. S., & Smith, M. L. (2009). Transmission of facial expressions of emotion co-evolved with their efficient decoding in the brain: behavioral and brain evidence. *PLoS One, 4*(5), e5625.
Sergent, J., & Signoret, J. L. (1992). Varieties of functional deficits in prosopagnosia. *Cerebral Cortex, 2*(5), 375–388.
Sergent, J., & Villemure, J. G. (1989). Prosopagnosia in a right hemispherectomized patient. *Brain, 112*, 975–995.
Shuttleworth, E. C. J., Syring, V., & Allen, N. (1982). Further observations on the nature of prosopagnosia. *Brain and Cognition, 1*(3), 307–322.
Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science, 16*(3), 184–189.
Sorger, B., Goebel, R., Schiltz, C., & Rossion, B. (2007). Understanding the functional neuroanatomy of acquired prosopagnosia. *NeuroImage, 35*(2), 836–852.
Tranel, D., Damasio, A. R., & Damasio, H. (1988). Intact recognition of facial expression, gender, and age in patients with impaired recognition of face identity. *Neurology, 38*(5), 690–696.
Trautmann, S. A., Fehr, T., & Herrmann, M. (2009). Emotions in motion: dynamic compared to static facial expressions of disgust and happiness reveal more widespread emotion-specific activations. *Brain Research, 1284*, 100–115.
Vizioli, L., Foreman, K., Rousselet, G. A., & Caldara, R. (2010a). Inverting faces elicits sensitivity to race on the N170 component: a cross-cultural study. *Journal of Vision, 10*(1), 1–23.
Vizioli, L., Rousselet, G. A., & Caldara, R. (2010b). Neural repetition suppression to identity is abolished by other-race faces. *Proceedings of the National Academy of Sciences of the United States of America, 107*(46), 20081–20086.
Warrington, E. K. (1984). *Recognition memory test*. Windsor, Berkshire: NFER.
Wehrle, T., Kaiser, S., Schmidt, S., & Scherer, K. R. (2000). Studying the dynamics of emotional expression using synthesized facial muscle movements. *Journal of Personality and Social Psychology, 78*(1), 105–119.
Wigan, A. L. (1844). *The duality of the mind: Proved by the structure, functions, and diseases of the brain, and by the phenomena of mental derangement, and shown to be essential to moral responsibility*. London: Longman, Brown, Green, and Longmans.
Winston, J. S., Henson, R. N., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of Neurophysiology, 92*(3), 1830–1839.
Young, A. W., Newcombe, F., de Haan, E. H., Small, M., & Hay, D. C. (1993). Face perception after brain injury. Selective impairments affecting identity and expression. *Brain, 116*, 941–959.
Yu, H., Garrod, O. G. B., & Schyns, P. G. (2012). Perception-driven facial expression synthesis. *Computer & Graphics, 36*(3), 152–162.