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Holistic processing of shape cues in face identification: Evidence from face inversion, composite faces, and acquired prosopagnosia

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Face recognition is based on two main sources of information: Three-dimensional (3-D) shape and two-dimensional surface reflectance (colour and texture). The respective contribution of these two sources of information in face identity matching task is usually equal, suggesting that there is no functional dissociation. However, there is recent evidence from electrophysiology and neuroimaging that contribution of shape and surface reflectance can be dissociated in time and neural localization. To understand the nature of a potential functional dissociation between shape and surface information during face individualization, we used a 3-D morphable model (Blanz & Vetter 1999) to generate pairs of face stimuli that differed selectively in shape, reflectance, or both. In three experiments, we provided evidence that the processing of shape and surface reflectance can be functionally dissociated. First, participants performed a delayed face matching task, in which discrimination between the sample and distractor faces with the same orientation (either upright or inverted) was possible based on shape information alone, reflectance information alone, or both. Inversion decreased performance for all conditions, but the effect was significantly larger when discrimination was based on shape information alone. Second, we found that participants' composite face effect, a marker of holistic processing, was caused primarily by the presence of interfering shape cues, with little interference from surface reflectance cues. Finally, contrary to

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normal observers, a well-known patient with acquired prosopagnosia suffering from holistic face perception impairment performed significantly better when discriminating faces based on reflectance than on shape cues. Altogether, these observations support the view that the diagnosticity of shape information for individualizing faces depends relatively more on holistic face processing than that of surface reflectance cues.

Keywords: Acquired prosopagnosia; Composite faces; Face inversion; Shape and surface reflectance.

The human brain's efficiency in recognizing people from their face relies on multiple potential sources of diagnostic information, i.e., variations between faces that characterize identity. A large amount of studies have emphasized the distinction between local feature variations (e.g., eye colour, mouth shape, . . .) as opposed to relative distances (e.g., interocular distance, . . .) between these features concerning their roles in face identity recognition (e.g., Maurer, Le Grand, & Mondloch, 2002; Rhodes, 1988). However, perhaps a more basic distinction to make is between the three dimensional (3-D) shape of the face, defined essentially but not exclusively by the bone structure of the head, and the two dimensional (2-D) surface information (brightness, colour, and texture variations), defined by the reflectance of light on the skin (Bruce & Young, 1998). Individual faces vary tremendously in both shape and surface reflectance information (Figure 1).

Recognizing individuals from their face is a challenging task, so that all kinds of facial cues are potential diagnostic sources of information. Several studies have shown that face shape and reflectance can be about equally useful in face recognition (Jiang, Blanz, & O'Toole, 2006; O'Toole, Vetter, & Blanz, 1999; Russell, Biederman, Nederhouser, & Sinha, 2007; Russell, Sinha, Biederman, & Nederhouser, 2006). Using computer graphics, O'Toole et al. (1999) manipulated 3-D shape and 2-D surface reflectance independently of each other, creating faces that varied selectively in shape or reflectance. They found roughly equal performance in an old/new recognition task for these two types of faces, showing the importance of both shape and surface reflectance for the recognition of unfamiliar faces. Russell et al. (2006, 2007) reported similar results in a matching task, in which participants matched the target and distractor faces on the basis of shape or reflectance properties. Jiang et al. (2006) tested the role of shape and reflectance information in face identity adaptation, where prolonged exposure to a face alters the perception of a subsequently presented face with opposite features (Leopold, O'Toole, Vetter, & Blanz, 2001; Webster & MacLin, 1999). Significant aftereffects were found after adaptation to face morphs that varied selectively in reflectance or shape. Moreover, identity aftereffects induced by shape-varying or reflectance-varying faces both

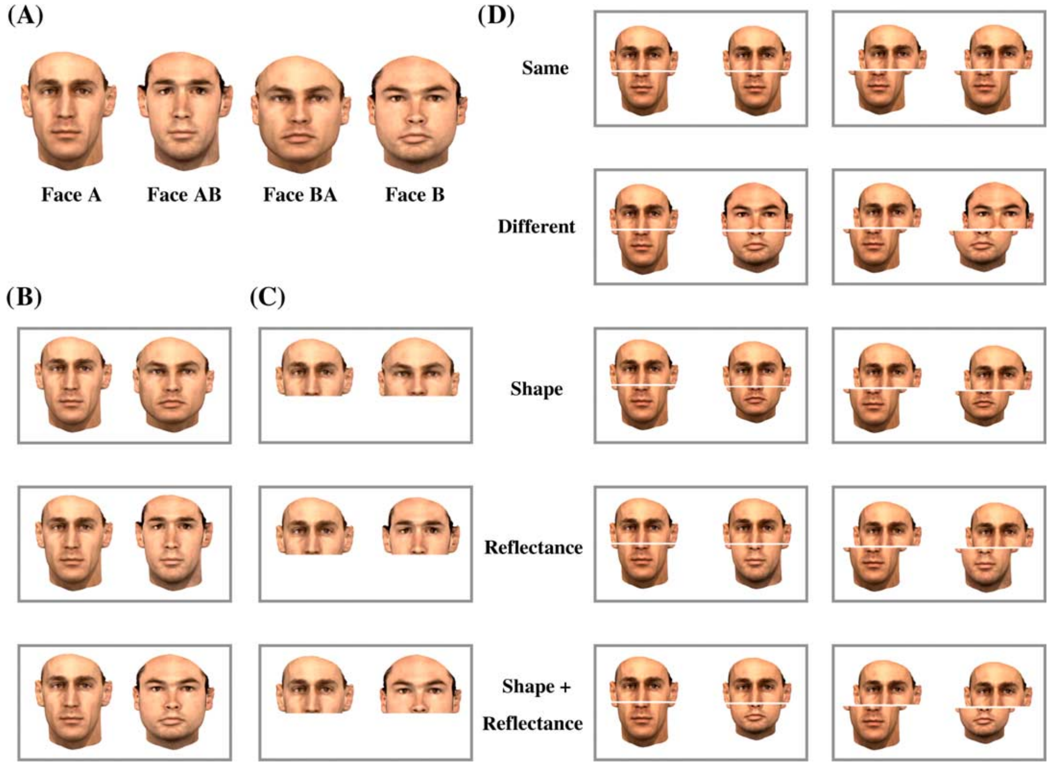

Figure 1. Example stimuli. (A) Illustration of an example pair of original faces (A and B) and corresponding faces (AB and BA) created with a 3-D morphable model (Blanz & Vetter, 1999) by swapping the 3-D shape/surface reflectance between two original faces. Face AB was created by mapping the reflectance of Face B onto Face A's shape, and Face BA was created by mapping the reflectance of Face A onto Face B's shape. (B) Example stimuli used in a delayed match-to-sample task in Experiment 1. The inverted stimuli were not shown here. (C) Example stimuli used in a delayed match-to-sample task in Experiment 3. Only top parts of the faces were presented to minimize patient PS' use of mouth cue. (D) Example composite face stimuli used in Experiment 2, with aligned face stimuli shown in the left column and misaligned in the right column. To view this figure in colour, please see the online issue of the Journal.

survived a substantial viewpoint change between the adapting and test faces. These results indicated that shape and reflectance information in faces are equally important not only for identity adaptation but also for its transfer across changes in 3-D viewpoint.

Despite their differential nature, there is little data suggesting a dissociation, or quantitative difference, between the respective contributions of these two sources of information (i.e., shape being more important than surface reflectance for a given function in general, or the opposite). This, at least, as far as face identity judgements are concerned (for different contributions of shape and surface reflectance in age, sex, and race categorization of faces, see Bruce et al., 1993; Burt & Perrett, 1995; Hill, Bruce, & Akamatsu, 1995). However, this lack of differential contribution between shape and surface-based information for face recognition performance does not necessarily mean that these two types of information are processed the same way when we identify faces. For instance, shape and surface reflectance may lead to the same overall performance in face identity judgements (Jiang et al., 2006; O'Toole et al., 1999; Russell et al., 2006, 2007), yet performance is impaired by contrast negation when faces vary in surface reflectance but not when they vary in shape (Russell et al., 2006). Along these lines, the present study sought to test the hypothesis of a functional dissociation between the role of shape and surface reflectance cues when individualizing faces. Precisely, we hypothesized that the observer relies relatively more on holistic/configural processes when faces vary primarily in shape, as opposed to a more local, feature-based, analysis of the face when surface reflectance carry the most diagnostic cues for individualization.

This hypothesis, and the general goal of the present study, was inspired by the outcome of two recent studies. First, in an event-related potential (ERP) study using a face identity adaptation paradigm (Jacques, d'Arripe, & Rossion, 2007), we found that a target face differing in shape alone from the adapter face led to a larger amplitude of the early N170 face-sensitive visual ERP than when the same face was repeated (Caharel, Jiang, Blanz, & Rossion, 2009). However, a face differing in reflectance alone did not modulate the N170 significantly, and adding reflectance to shape did not increase the N170 face-identity effect (Caharel et al., 2009).

The early (N170) face identity adaptation effect driven primarily by shape was found only in the right hemisphere, at occipitotemporal electrode sites. This study suggested that diagnostic information for face individualization is extracted earlier—or accumulates at a faster rate—from shape than from surface reflectance, even when behavioural performance indicates that the two kinds of cues are equally useful for individual face discrimination (Caharel, Jiang et al., 2009). Second, in a functional magnetic resonance imaging (fMRI) variant of this experiment we also found that shape was the main source of information for discriminating pictures of individual faces within the occipitotemporal network of face-sensitive areas in the human brain. This is especially evident in the right hemisphere (Jiang, Dricot, Blanz, Goebel, & Rossion, 2009).

The dominance of the right hemisphere in individual face processing has been associated to holistic processing (e.g., Hillger & Koenig, 1991; Schiltz & Rossion, 2006; Sergent, 1988). Consequently, under the theoretical framework of a coarse-to-fine processing of faces (Sergent, 1986), these recent findings led us to suggest that the initial representation of an individual face is holistic, and is based primarily on shape rather than on reflectance information. In the face processing literature, "holistic" or "configural" processing usually refers to the fact that humans seem to perceive the face as a whole stimulus, a single entity whose multiple features are perceived simultaneously and interdependently (Galton, 1883; Rossion, 2008, 2009; Sergent, 1984; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). This view stands in contrast with an analytical view of face processing, according to which local elements of the face (an eye, the mouth, ...) would be analysed and represented separately (e.g., Gosselin & Schyns, 2001; Haig, 1985, 1986; Sadr, Jarudi, & Sinha, 2003; Yarbus, 1967). In this context, we hypothesized that individual faces varying only in terms of shape would be more dependent on the ability to process holistically/configurally[1] than individual faces varying only in terms of their surface reflectance properties.

This hypothesis was tested behaviourally in the present study, in three experiments. First, we compared the processing of upright and inverted individual faces differing in shape or surface information. Given that the well-known decrement of performance for recognizing inverted faces (e.g., Yin, 1969) has been associated with a loss of holistic face processing (e.g., Farah, Tanaka, & Drain, 1995; for reviews see Rossion, 2008, 2009), we predicted that the face inversion effect would be larger for faces varying only in shape as compared to those varying only in surface reflectance information. Note that this prediction stands in contrast to recent observations (Russell et al., 2007), an aspect we discuss later.

[1] The term "configural" was originally used to refer to the interactive or interdependent processing of facial features (e.g., Hole, 1994; Sergent, 1984; Young et al., 1987). This meaning can be considered largely as a synonym of the term "holistic face processing" introduced later (Tanaka & Farah, 1993). However, other authors (e.g., Leder & Bruce, 2000; Leder & Carbon, 2006; Maurer et al., 2002) have attributed a specific meaning to the term "configural" as reflecting the relative distances between features (e.g., interocular distance, mouth–nose distance). In this framework, "configural processing" then would refer exclusively to the sensitivity of the system to these relative distances. We have argued elsewhere against making such a distinction, which we believe to be unnecessary (Rossion, 2008, 2009; see also McKone & Yovel, 2009). Here the terms "configural" and "holistic" will be used throughout the paper as synonyms, reflecting the processing of all facial features, including relative distances, as an integrated whole.

Second, in Experiment 2, we tested our hypothesis more directly by comparing how observers' performance of matching the top (cut above the tip the nose) half of a face would be influenced by the aligned bottom half of another face. This composite face paradigm, developed originally by Young and colleagues (1987) is well known and widely used to test the extent to which an individual face is processed holistically (e.g., de Heering & Rossion, 2008; Hole, 1994; Le Grand, Mondloch, Maurer, & Brent, 2004). Again, in line with our general hypothesis, we predicted to observe a larger composite face effect for faces varying in shape than for faces varying in surface reflectance.

Finally, in Experiment 3, we tested a well-known acquired prosopagnosic patient in a face matching task with faces varying either in shape or in surface reflectance information. This patient, PS (Rossion et al., 2003), has difficulties recognizing individual faces following brain damage, and her difficulties have been associated with an impairment in holistic face processing in several studies (Busigny & Rossion, 2010; Ramon, Busigny, & Rossion, 2010; van Belle, de Graef, Verfaillie, Busigny, & Rossion, 2010). Hence, we reasoned that, in contrast to normal observers, this case of prosopagnosia would be relatively more impaired in her ability to process faces differing by shape alone.

These three experiments were considered as different approaches, and meant to bring converging evidence, for a dominant reliance of shape diagnostic information on holistic face processing.

GENERAL EXPERIMENTAL METHODS

Stimuli were generated with a three-dimensional (3-D) morphable model (Blanz & Vetter, 1999). This model implemented a multidimensional face space based on 200 3-D face scans. Constructed from 75,000 surface points in correspondence with a reference face, the 3-D shape (x, y, z) and surface reflectance (r, g, b) of a face were transformed into separate vectors. With this correspondence established, the reflectance of one face can be mapped on to the shape of another face, resulting in a realistically looking new face with both physical and perceptual differences.

Using this model, we created our stimulus set based on 40 original faces (20 female and 20 male) from the face space. These 40 original faces were paired into 20 gender-matched pairs in order to generate additional stimuli by exchanging the shape and surface reflectance properties between a pair of original faces. Specifically, for each pair of original faces (A and B), a Face AB was created by mapping the reflectance of Face B onto the shape of Face A, and a Face BA was created by mapping the reflectance of Face A onto the shape of Face B. Note that here we used two letters to label the additional face stimuli created from original faces, with the first letter indicating the origin of the face shape and the second indicating the origin of the surface reflectance. This procedure resulted four faces per pair (A, AB, BA, B; Figure 1A), totalling 80 face stimuli.

As seen in Figure 1A, Face AB differed from Face A in reflectance, and Face BA differed from Face B in reflectance. On the other hand, Face AB and Face B, as well as Face BA and Face A, differed in 3-D shape. When both 3-D shape and surface reflectance were considered, the two faces of the original face pair (A and B) were different, so were the pair of two additional face stimuli (AB and BA). Therefore, for each set of four faces (A, B, AB, BA), there were two possible pairings for each of the three conditions, in which two faces differed in shape, reflectance, and shape + reflectance, respectively (see Figure 1B for example pairing). Both pairings were used to access the relative contribution of shape and reflectance information in all three experiments.

To quantify the physical difference induced by changes in shape, reflectance, and both, we calculated intensity-based (range 0–255) Euclidean distance per pixel between all pairs of faces. There were 40 distinct pairings of face per condition. The averaged distance between face pairs (mean $\pm$ *SD*) was 35.71 ± 6.26 in the shape condition, 22.89 ± 5.05 in the reflectance condition, and 45.63 ± 7.27 in the shape + reflectance condition.

EXPERIMENT 1

In the first experiment, using a paradigm similar to that used in Russell et al. (2007), we examined how performance on the sole basis of shape or reflectance information would be affected by inversion.

Method

Participants. A total of 22 students participated Experiment 1. Two participants were excluded, one due to the use of wrong answer keys and the other due to the incompleteness caused by computer crash. This left 20 participants (14 females) with a mean age of 21 years ($\pm$ 3 years). All participants were naïve to the purpose of the study. Data from the first 12 participants have been reported as postscanning behavioural test results in Jiang et al. (2009).

Stimuli. Stimuli used in Experiment 1 were original faces and their shape/reflectance exchanged counterparts (Figure 1B). Inverted stimuli were created by rotating faces upside-down.

Procedure. Participants performed a delayed match-to-sample, two-alternative forced-choice task. In each trial, a sample face was presented for 150 ms, followed by a blank screen for 500 ms. A noise mask were then presented for 200 ms, followed by a 1000 ms blank screen. Finally, the sample face and a distractor were shown side by side on the screen for 500 ms. All face stimuli were presented in colour with white background. Participants were then given a 2000 ms window to judge which one (the left vs. the right) matched the sample face they saw before the noise mask and press a corresponding key. They were instructed to perform the task as fast as possible while being as accurate as possible. The matching task could be performed based on face shape (shape condition), surface reflectance (reflectance condition), or both (shape + reflectance condition).

Each participant performed a total of 480 trials (20 original face pairs $\times$ 3 conditions $\times$ 2 pairings per pair per condition $\times$ 2 orientations $\times$ 2 left–right key counterbalance) grouped in eight blocks. Four blocks consisted of trials in which faces were presented upright, and another four consisted of trials in which faces were presented inverted. All faces within a trial were presented either upright or inverted. Upright and inverted blocks were interleaved and the starting block (upright vs. inverted) was counterbalanced between participants. Each block included 60 trials (20 from each of the three conditions), which were randomized for each participant. In between the blocks, participants were given the chance to take a self-paced pause.

Results

Accuracy (percentage correct response) and response time (correct trials only) were calculated for 20 participants. Correct response time data were additionally cleaned for each participant by removing response that were more than three standard deviations above the participant's mean response time (frequency (mean $\pm$ SD) 1.06% $\pm$ 0.37%).[2] The effect of counterbalanced order of the starting block (upright vs. inverted) was not significant and was not included as a factor. Both accuracy and correct response time data were tested with a 2×3 ANOVA, with orientation (upright, inverted) and diagnosticity (shape, reflectance, shape + reflectance) being two within-subjects factors.

As seen in Figure 2, there was a main effect of orientation on accuracy, $F(1, 19) = 48.32$, $p < .001$, as indicated by higher performance for upright than inverted trials. There was also a main effect of diagnosticity on accuracy, $F(2, 38) = 77.69$, $p < .001$, with highest accuracy in the shape + reflectance condition. Most importantly, the interaction between orientation

[2] For all participants, no response time was found more than three standard deviations below the their mean response time.

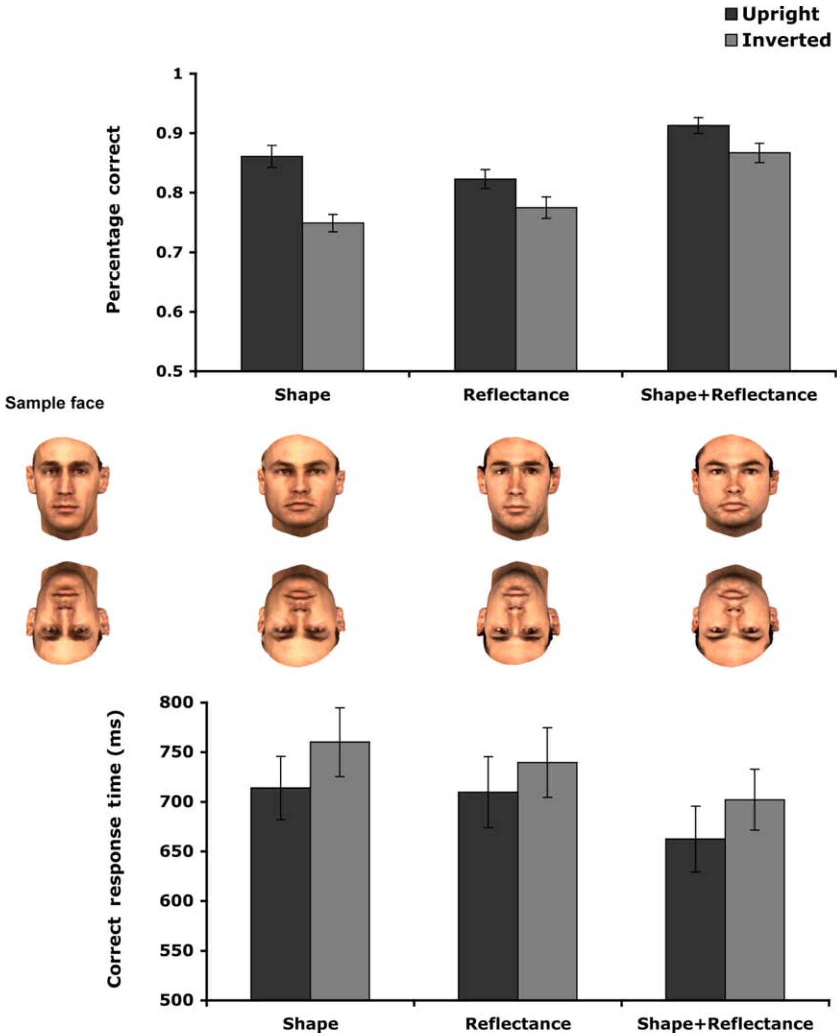

Figure 2. Results of Experiment 1. Accuracy is shown in percentage correct and response time is calculated based on correct trials only. A larger inversion effect was found for faces differing in shape than for faces differed in surface reflectance. Note that adding surface reflectance cues to shape cues (shape + reflectance condition) improves overall performance but reduces the face inversion effect. A sample face and distractor faces used in different conditions were shown for both upright and inverted orientation. To view this figure in colour, please see the online issue of the Journal.

and diagnosticity reached significance, $F(2, 38) = 7.59$, $p < .002$, with inversion causing a greater performance impairment in the shape condition than in the other two conditions (Figure 2).

To further examine the interaction, we calculated the accuracy difference between upright and inverted trials for all three conditions and submitted the differences into a one factor ANOVA. This analysis showed a significant effect of diagnosticity, $F(2, 38) = 7.59$, $p < .002$. The accuracy difference caused by inversion in the shape condition was indeed greater than those in the reflectance and shape + reflectance conditions, $t(19) = 3.12$, $p < .003$, Cohen's $d = 0.88$, effect size $r = .40$, and $t(19) = 3.76$, $p < .001$, Cohen's $d = 1.16$, effect size $r = .50$, respectively. These results indicate that inversion disrupted shape information more than reflectance information or than the combination of shape and reflectance information.

For correct response time data, there was a main effect of orientation, $F(1, 19) = 8.59$, $p < .009$, with faster response time when faces were presented upright than inverted. The main effect of diagnosticity was also significant, $F(2, 38) = 30.37$, $p < .001$. Overall, participants were faster in the shape + reflectance condition than in the shape and reflectance conditions, $F(1, 38) = 57.96$, $p < .0001$, with no significant difference between these latter two conditions, $F(1, 38) = 2.78$, *ns.* Unlike for accuracy data, correct response time data did not show a significant interaction between orientation and diagnosticity, $F(2, 38) = 1.41$, *ns.*

Discussion

We found an inversion effect for all conditions in this face matching task, replicating numerous previous studies (see, for reviews, Rossion, 2008, 2009). Most importantly, as predicted, we found a larger inversion effect for faces differing in shape than for faces differing in surface reflectance. The amount of decrement in performance caused by inversion cannot be explained or predicted by a speed–accuracy tradeoff, or by the performance at upright orientation. Indeed, participants' performance in the condition that led to the largest inversion effect (i.e., shape condition) was neither the best nor the worst of all three conditions at upright orientation (Figure 2). These observations stand in contrast to a previous study performed by Russell et al. (2007), in which an equal decrement in performance with inversion was reported for shape and reflectance conditions. We suspect that the nature of the stimuli used in the two studies might account for this discrepancy. Russell et al. used face stimuli varying in 2-D-shape in the image plane, and which were cropped in a homogenous way, minimizing a number of shape diagnostic cues (see Figure 1 in that study). Supporting this suggestion, with colour stimuli, performance at upright orientation in the shape condition was substantially lower than in the reflectance condition in their study (about 7% accuracy and 30 ms slower on average; see Exp. 2 in Russell et al., 2007), whereas it was slightly—but not significantly—higher for shape-varying than for reflectance-varying faces in the present study. This suggests that Russell et al. may have reduced the diagnosticity of certain shape variations whose diagnosticity depends heavily on observers' ability to process the face holistically.

Since the face inversion effect reflects the inability to perceive inverted faces holistically (Farah et al., 1995; Rossion, 2008, 2009), our results indicate a stronger dependence on holistic processing for face shape as compared to face reflectance cues. When full faces are upright, one is able to rely on not only information conveyed at a local level (e.g., shape of the mouth, colour of the eyebrow) but also at a global level, using for instance global head shape as a diagnostic cue to individualize faces. However, when faces are presented upside-down, global faces cues, primarily supported by face shape, become less available to the perceiver, since his/her perceptual field—in the Gestaltist sense the spatial region over which vision functions—would be constricted to one feature at a time (Rossion, 2009; van Belle, de Graef, Verfaillie, Rossion, & Lefèvre, 2010). In contrast, local face cues are less affected by inversion, resulting in a smaller face inversion effect when diagnostic reflectance cues are present.

The largest inversion effect found when shape was the only diagnostic cue of individuality can be attributed to the fact that shape cues convey information which is not only *available* at a global scale, but whose diagnosticity also *depends* on a perception of the face at a global scale (e.g., the overall head shape for instance; see Figure 1). However, even at the local level, shape information may be more dependent on holistic processing than surface based cues when upright faces are considered (McKone & Yovel, 2009). For instance, for upright faces, a difference in the shape of the mouth changes the expression of the whole face as well as the relative distances between the mouth and the other facial features. In contrast, a change in the texture and colour of the mouth does not affect the whole facial expression, or any relative distances between features. Thus, the loss of holistic face perception following inversion may also affect indirectly the diagnosticity of local face shape cues (for a discussion of this issue, see Rossion, 2008, 2009).

The finding that inversion can affect differently the processing of different face cues, such as shape and reflectance, supports the qualitative view of face inversion (Rossion, 2008). However, this observation should not be taken as evidence that these two kinds of cues are dissociated within the holistic representation of faces, but rather that one kind of information is more dependent on this holistic mode of representing faces than the other.

EXPERIMENT 2

In Experiment 2, we further examined the relative dependence of shape and surface reflectance information on holistic face processing using the well-known composite face effect, which was originally demonstrated by Young et al. (1987) with famous faces. Here, participants were asked to make same/different judgements on the top halves of unfamiliar face pairs (Hole, 1994). A top half of a face combined with different bottoms creates a visual illusion ("composite face illusion"; Rossion & Boremanse, 2008) that the top part appears different in each composite face. Hence, when observers are asked to match two identical top parts of faces (ignoring the bottom parts), they tend to wrongly respond "different" more often, and take longer to respond than if the bottom parts are also the same (e.g., de Heering & Rossion, 2008; Le Grand et al., 2004; Michel, Rossion, Han, Chung, & Caldara, 2006).[3] This effect, however, is disrupted when the top and bottom are spatially misaligned (e.g., Young et al., 1987).

The composite face effect is considered, and widely used, as a marker of holistic face perception. It has been demonstrated that the composite face effect is disrupted by inversion (e.g., Young et al., 1987), and depends more on low than high spatial frequencies of the stimulus (Goffaux & Rossion, 2006). The effect is not found for nonface stimuli such as dog pictures (Robbins & McKone, 2007), but can be found for other-species nonhuman faces (Taubert, 2009), and requires the face stimuli to be biologically plausible (Taubert & Alais, 2009). The magnitude of the composite face effect is larger both for same-race than other-race faces (Michel et al., 2006), and for same-age than other-age faces (de Heering & Rossion, 2008; Kuefner, Cassia, Vescovo, & Picozzi, 2010). However, the effect may not be present in patients suffering from acquired prosopagnosia (Ramon et al., 2010) or lacking early visual experience with faces (Le Grand et al., 2004). Here, in line with our main theoretical view, we predicted that the composite face effect in matching top face halves would be larger when bottom halves differed in shape than when they differed in surface reflectance.

[3] This procedure introduces a response bias specifically for same (aligned) trials: Participants respond more often by pressing the "different" response keys. Although this bias has been taken by some as being problematic or supporting evidence that the composite face effect is primarily a decisional rather than a perceptual effect (Richler, Gauthier, Wenger, & Palmeri, 2008), the large majority of authors disagree with this view and consider that this response bias is created by the set-up of a visual illusion in a "same/different" response paradigm. It is in fact exactly what researchers aim at measuring (see, e.g., McKone & Robbins, 2007; Rossion & Boremanse, 2008).

Method

Participants. Fifteen participants (six male, 21 ± 2) participated in Experiment 2 and all were naïve to the purpose of the experiment.

Stimuli. Composite faces were created with the stimuli used in Experiment 1. Faces were split in half horizontally above the tip of the nose. The top half of each face was then combined with the original bottom half (same face condition), or with bottom halves that differed with respect to the original bottom half in shape only, reflectance only, or both (see Figure 1D). To properly align the top and bottom halves, the size of the bottom half was altered proportionally in some cases (only in the shape and the shape + reflectance conditions[4]). In the misaligned condition, the bottom half was further shifted horizontally to the left by a nose width. For both aligned and misaligned faces, we added a small spacing between the top and bottom halves. This small spacing was used so that even in the aligned condition the border separating the top and bottom halves could be well identified and participants could define exactly what was meant by "the top part of the face" to match.

Procedure. A sequential matching paradigm (e.g., Le Grand et al., 2004) was used to test the composite face effect. In each trial, we presented a pair of faces sequentially. The study face was presented in the centre of the screen for 150 ms, followed by a blank screen for 300 ms. The test face was then presented and remained on the screen until participants' response occurred. To avoid pixel-based matching, the location of the test face was shifted approximately 15 pixels upper and 20 pixels to the left ($\sim$0.61 cm/0.7° horizontally and 0.46 cm/0.5° vertically) of the study face. Participants were asked to judge whether the top half of a test face was the same as or different than the study face. Five conditions were included. In the "same" condition, the two subsequently presented faces had the identical top and bottom halves. In the "different" condition, both the top and bottom halves of the two faces were of a different identity. In the other three conditions, the study and test face shared an identical top half. However, their bottom halves differed in terms of shape (shape condition), reflectance (reflectance condition), or both (shape + reflectance condition, see Figures 1 and 3).

Each participant performed a total of 640 trials, grouped into eight blocks. Within each block, half of the 80 trials consisted of face pairs with

[4] If anything, the fact that the bottom halves of the stimuli were adjusted in width for these two conditions increased the similarity of the two different bottom halves in these two conditions. Therefore, if this (indispensable) manipulation has an effect, it would be to slightly reduce the composite face effect in these two conditions, an effect that runs counter to our hypothesis.

different top halves and thus required a "different" answer (i.e., different condition). The other half of the trials (40) consisted of face pairs with an identical top half, including 10 trials for each of the remaining four conditions (i.e., same, shape, reflectance, and shape + reflectance, in which the two bottom halves were the same, differed in shape, reflectance, or both, respectively). These 40 trials required a "same" answer, representing all the relevant trials for this experiment. This is because the composite face illusion is present on "same" trials only, reflecting the fact that observers perceive identical top halves of faces as being different if they are aligned with different bottom halves (see Le Grand et al., 2004; Robbins & McKone, 2007; Rossion & Boremanse, 2008). Since observers do not perceive different top halves of faces as being more similar if they are associated with identical bottom halves, "different" trials do not reflect the composite face illusion and should not be used in this paradigm to measure holistic processing (see, e.g., Le Grand et al., 2004; Robbins & McKone, 2007; Rossion & Boremanse, 2008). Trials within each block were presented randomly for each participant. In between the blocks, participants were given the chance to take a self-paced pause.

Results

We computed the percentage correct and mean response time. Only correct trials were included to compute the mean response time and trials with response time greater than three standard deviations were further excluded from the computation. As seen in Figure 3, participants performed the matching task successfully, with an average of 95% accuracy for trials in the different condition. The main analysis was concentrated on the remaining four conditions that required a "same" response (i.e., conditions in which the tops of the two faces were identical). This gave a 4 (same, shape, reflectance, shape + reflectance) $\times$ 2 (aligned, misaligned) two-factor repeated measure design.

We found a main effect of diagnosticity, $F(3, 42) = 9.45$, $p < .001$, and a main effect of alignment, $F(1, 14) = 18.60$, $p < .001$, on accuracy. The accuracy for aligned trials was lower than for misaligned trials, but the effect of alignment was only evident in shape and shape + reflectance conditions (Figure 3). This was reflected in the significant interaction between diagnosticity and alignment, $F(3, 42) = 12.55$, $p < .0001$. We further computed the accuracy difference between the misaligned and aligned trials as an index of the composite effect size. Only the indexes in the shape and shape + reflectance conditions were significantly greater than zero (both *ps* $< .005$). The composite effect size is larger in the shape + reflectance condition than in the shape condition, $t(14) = 2.38$, $p < .02$. However, as

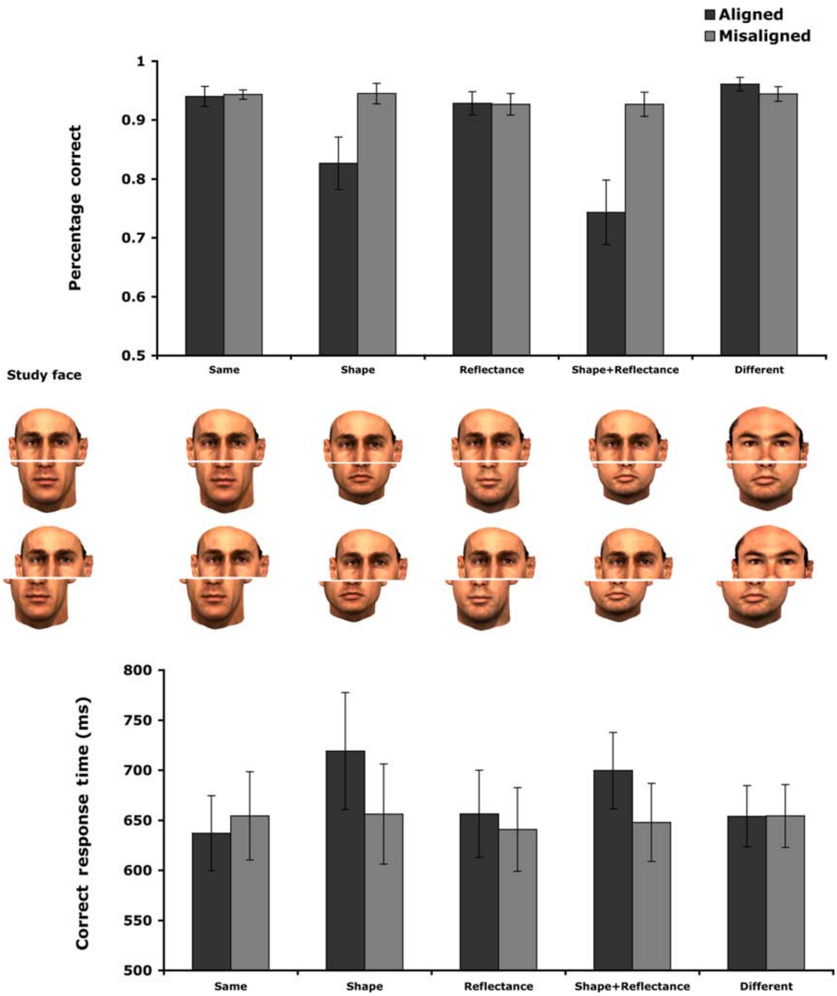

Figure 3. Results of Experiment 2, with accuracy and correct response time data for both aligned and misaligned trials. The composite face effect, as indicted by an increase of both error rates and correct response time, was evident in both shape and shape + reflectance conditions, being primarily driven by shape information. Here, adding reflectance cues increased (slightly) the composite face effect since these cues were not added to the parts that had to be distinguished but to the interfering parts. A study face and test faces used in different conditions were shown both as aligned and misaligned. To view this figure in colour, please see the online issue of the Journal.

shown in Figure 3, it is clear that the composite effect was driven primarily by face shape.

For correct response time, there was a main effect of alignment, $F(1, 14) = 14.05$, $p < .002$, as well as a nonsignificant trend for a main effect of diagnosticity, $F(3, 42) = 2.29$, $p < .09$. A significant interaction was also found, $F(3, 42) = 3.23$, $p < .04$. As seen in Figure 3, the alignment increased the participants' response time, an effect that was only evident in the shape and shape + reflectance conditions (ps $< .01$ and $< .03$, respectively). The amount of increase in correct response time was not different between these two conditions, $t(14) = 0.28$, *ns*.

For both accuracy and correct response time, we further computed a relative index of composite face effect, as defined by the formula

$$(\text{Aligned X} - \text{Aligned Same}) - (\text{Misaligned X} - \text{Misaligned Same})$$

where X represented one of the three conditions in which the bottom halves differed (i.e., shape, reflectance, shape + reflectance). This relative index took into account any effect that different bottoms may have had in the misaligned trials. A greater composite face effect was indicated by a more negative relative index for accuracy (i.e., larger decrease in accuracy) and a more positive relative index for correct response time (i.e., larger increase in response time).

As seen in Figure 4, the relative index for accuracy was significantly negative in both shape and shape + reflectance conditions, $t(14) = -2.96$, $p < .006$, and $t(14) = -4.46$, $p < .0005$, respectively (one tailed), but not in the reflectance condition, $t(14) = 0.34$, *ns.* As predicted, the magnitude of the composite effect as reflected by accuracy relative index was larger in both shape and shape + reflectance conditions than in the reflectance condition (both ps $< .01$). Furthermore, the effect was significantly larger in the shape + reflectance condition than in the shape condition, $t(14) = -2.38$, $p < .02$, indicating a possible contribution from the reflectance information presented in the shape + reflectance condition.

The relative index for correct response times was significantly positive in all three conditions including the reflectance condition (all ps $< .03$). Compared to the reflectance condition, there was a trend for a larger composite effect in both shape and shape + reflectance conditions, $t(14) = 1.54$, $p < .07$, and $t(14) = 1.65$, $p < .06$, respectively. There was no difference in relative correct response time index between the shape and shape + reflectance condition, $t(14) = 0.28$, *ns.*

Discussion

With full faces (i.e., shape + reflectance condition in which faces differed in both shape and reflectance cues), we replicated the well-known composite

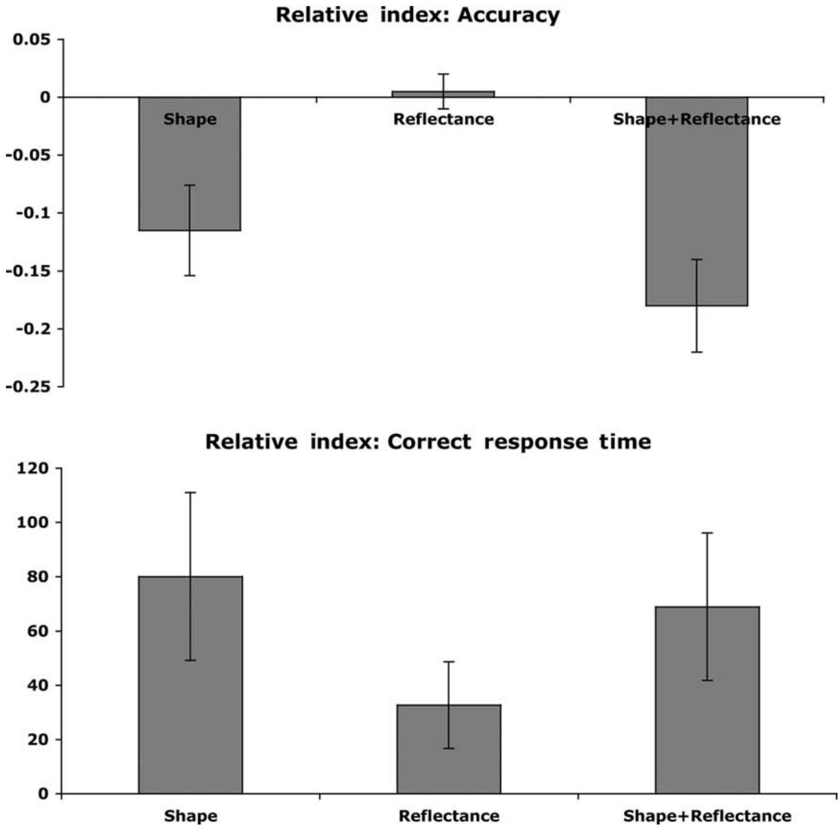

Figure 4. Relative index of composite face effect for both accuracy and correct response time. The relative index of composite face effect was computed following the formula [(Aligned X – Aligned Same) – (Misaligned X – Misaligned Same)], where X represents one of the three conditions in which the bottom halves differs (i.e., shape, reflectance, shape + reflectance).

face effect, showing an increase of both error rates and correct response time when the identical top halves to be matched were paired with different bottom halves of faces. This composite face effect was also found in the shape condition, where the bottom halves differed only in terms of face shape. The increase of error rates was slightly smaller in the shape condition than in the shape + reflectance condition but the increase of response time was comparable between these two conditions. Strikingly, there was no evidence of a composite face effect both in accuracy and correct response time, when the bottom halves differed only in terms of surface reflectance, even though the analysis of relative index revealed a small composite effect in correct response time. Taken together, these observations support the prediction that the composite face effect is driven primarily, if not exclusively, by face shape. This is, to the best of our knowledge, a new observation about the composite face effect, and one that we believe will contribute to a better understanding of the nature of this effect.

At first glance, one might believe that the data of Experiment 2 does not fit completely with the data obtained in Experiment 1. Indeed, in Experiment 1, adding reflectance diagnostic cues to shape cues reduced the inversion effect (shape + reflectance < shape only). In contrast, in Experiment 2, adding reflectance diagnostic cues to shape cues increased the composite face effect (shape + reflectance > shape only). In other words, when compared to the shape only condition, the shape + reflectance condition led to a smaller inversion effect in Experiment 1 (Figure 2), whereas in Experiment 2 it led to a slightly larger composite face effect. We believe that this observation makes perfect sense. In Experiment 1, the information added to the face is not there to play an interfering role in participants' performance. When surface reflectance cues are added to shape cues, as in the shape + reflectance condition, they can be used to minimize the decrease of performance for inverted faces. In contrast, in Experiment 2, any reflectance information added to the bottom half is not there to help but rather interferes with the participant's judgement of the top half. Hence, the presence of reflectance cues in the bottom halves may not be sufficient enough to induce composite illusion by itself, but nevertheless could result in a slightly larger composite effect when combined with shape cues (shape + reflectance condition) as compared to effect by shape cues alone (shape condition). This suggests that even if the mere presence of shape cues in the bottom halves largely accounts for the effect, reflectance cues may also contribute by providing additional information (e.g., shadows defined by local intensity).

Altogether, these observations support the view that the diagnosticity of shape cues, compared to that of surface reflectance cues, rely more on our ability to perceive a face holistically. In our last experiment, we tested this hypothesis once again, with a brain-damaged prosopagnosic patient who does not process individual faces holistically.

EXPERIMENT 3

In Experiment 3, we compared the performance of a case of acquired prosopagnosia, the patient PS (Rossion et al., 2003), to normal observers on a delayed match to sample task with faces differing only in shape or surface reflectance. The rationale for testing the patient was the following. Acquired prosopagnosia corresponds to a massive impairment in face recognition following brain damage (e.g., Bodamer, 1947; Quaglino & Borelli, 1867). The impairment cannot be explained by intellectual deficiencies or low-level visual problems. For most patients, prosopagnosia is embedded in a more general visual recognition defect that encompasses nonface object categories (e.g., Levine & Calvanio, 1989). However, there are rare cases of prosopagnosia whose visual recognition difficulties appear to be truly restricted to faces (e.g., Busigny, Graf, Mayer, & Rossion, 2010; de Renzi, 1986; Henke, Schweinberger, Grigo, Klos, & Sommer, 1998; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008). Whether the visual recognition impairment is restricted to faces or not, most, if not all, cases of acquired prosopagnosia are characterized by difficulties at integrating individual components of a face into a global percept, i.e., they are impaired at holistic/configural face processing (e.g., Boutsen & Humphreys, 2002; Joubert et al., 2003; Levine & Calvanio, 1989; Saumier, Arguin, & Lassonde, 2001; Sergent & Villemure, 1989; see Ramon et al., 2010, for a review). The impairment of holistic/configural face processing has been demonstrated through different paradigms measuring the interdependence of processing between facial features. Whereas normal observers cannot process a specific feature of a face without being influenced by other features (e.g., Sergent, 1984; Tanaka & Farah, 1993; Young et al., 1987), patients suffering from prosopagnosia appear to process a face feature by feature. In other words, their perceptual field seems to be constrained and limited to one feature at a time.

In this context, we have recently demonstrated such a holistic face processing impairment in a pure case of prosopagnosia, the patient PS, through various paradigms. Specifically, contrary to normal observers, PS does not show any face inversion effect (Busigny & Rossion, 2010), or whole–part interference or composite face effect (Ramon et al., 2010) when matching faces. Moreover, there is also evidence from gaze-contingency that her perceptual field is limited to one facial feature at a time (van Belle, de Graef, Verfaillie, Busigny, & Rossion, 2010).

The patient is thus particularly well suited to test our hypothesis and strengthen the findings of our first two experiments performed by normal observers. That is, we reasoned that if the discrimination of individual faces differing in shape depends more on our ability to perceive faces holistically than the discrimination of individual faces differing in reflectance, the patient should be relatively more impaired in discriminating faces based on shape than on reflectance information alone.

Method

Participants. PS was born in 1950. She suffered a closed head injury in 1992, causing bilateral asymmetric lesions mainly in the occipital and occipitotemporal regions (see Sorger, Goebel, Schiltz, & Rossion, 2007, for a detailed description). She represents a case of pure acquired prosopagnosia, as her ability to identify and discriminate nonface objects is intact, even when fine-grained discrimination is required (Busigny et al., 2010; Rossion et al., 2003). To recognize individual faces, PS relies heavily on single features, the mouth in particular (Caldara et al., 2005), which she fixates much more than any other feature of the face (Orban de Xivry, Ramon, Lefèvre, & Rossion, 2008).

We tested PS twice (approximately 2 months apart). Her performance was compared to those of 10 young controls (nine females, 21 ± 2 years). We also included two age-matched female (54 and 64 years old) controls, in order to ensure that the effects observed for PS were not due to age, and that the age-matched participants showed the same profile of performance as the young controls.

Stimuli. We used the same set of stimuli that we used in Experiment 1. However, we only presented the top part of the faces in this experiment (Figure 1C). This was done to avoid PS' heavy reliance on the mouth when performing face recognition tasks (Caldara et al., 2005; Orban de Xivry et al., 2008; Rossion, Kaiser, Bub, & Tanaka, 2009).

Procedure. Each task consisted of a total of 240 trials (20 original face pairs $\times$ 3 conditions $\times$ 2 pairings per pair per condition $\times$ 2 left–right key counterbalance). A sample face was presented for 1000 ms, followed by a blank screen for 500 ms. Then a noise mask were presented for 200 ms, followed by a 1000 ms blank screen. The target and distractor faces were shown side by side up to 5000 ms and were terminated by participants' key response. In all trials, only the top parts of the faces were presented.

Because here PS was tested as a single case, we measured the reliability of our matching task. Cronbach's alpha value (Cronbach, 1951) was computed separately for three experimental conditions. For each condition, we computed a Cronbach's alpha value based on 12 control participants' accuracy data on its 40 distinctive pairings. High task reliability was found in all three conditions, with a Cronbach's alpha value of .69 for the shape condition, .76 for the reflectance condition, and .8711 for the shape + reflec-reflectance condition.

Results

Young controls. A one-factor (condition) repeated measure ANOVA was used to analyse the data from young control participants (Figure 5). For accuracy, there was a main effect of condition, $F(2, 18) = 16.78$, $p < .0001$. The best performance occurred in the shape + reflectance condition (ps $< .001$ compared to shape and reflectance condition, respectively). There was no accuracy difference between the shape and the reflectance conditions

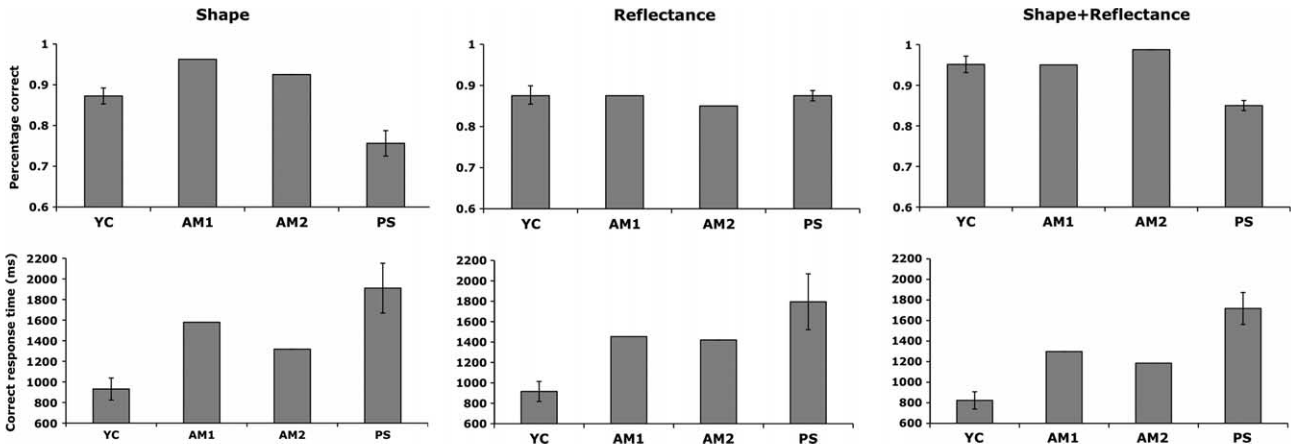

Figure 5. Results of Experiment 3 for acquired prosopagnosia patient PS and normal controls (including both young controls (YC) and age-matched controls (AM1 and AM2). In contrast to normal controls, PS performed significantly less well based on shape cues alone than reflectance alone. Note the increase of correct RTs for PS in all conditions.

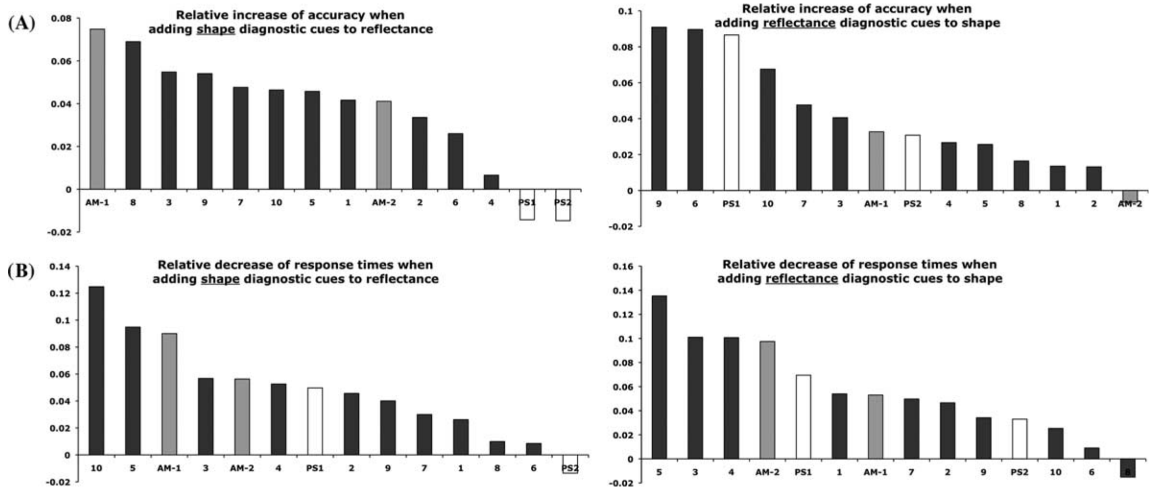

Figure 6. Individual index showing the relative increase in accuracy (A) and decrease in response time (B) as a result of additional shape(reflectance) diagnostic cues to the existing reflectance(shape). In contrast to controls, PS (recorded twice, PS1 and PS2) showed little benefit from the presence of additional shape information (left side of the figure). However, the benefit provided by the presence of additional reflectance information was in the normal range for PS (right part of the figure). AM-1 = age-matched control 1.

($p = .89$). For response times, there was also a significant effect of condition, $F(2, 18) = 7.87$, $p < .0035$, participants being again faster in the shape + reflectance condition than in the other two conditions (ps $< .001$). There was no response time difference between the shape and reflectance conditions ($p = .60$).

Patient PS. As seen in Figure 5, PS' average accuracy rate was much lower in the condition where faces differed only in shape (75.6%) than in the condition where faces differed in both shape and reflectance (85%; chi-square test of two proportions, $p = .036$), or where faces differed only in reflectance (87.5%; $p = .007$). The last two conditions did not differ from each other ($p = .43$). For correct response times, PS was tested against herself in different conditions by considering the number of correct trials (unpaired t-tests, 160 trials/condition; 121 correct trials in the shape condition, 136 in the shape + reflectance condition, and 140 in the reflectance condition). She was faster in the reflectance condition than in the shape condition, although this difference failed to reach significance, $t(259) = 1.21$, $p = .11$. However, in line with our hypothesis, she was significantly faster when both shape and reflectance information were present compared to when only shape information was available, $t(255) = 2.25$, $p = .013$. This advantage was not found when the shape + reflectance condition was compared to the reflectance condition, $t(274) = 1.00$, $p = .15$.

In summary, PS was already able to perform the task above chance level when only one kind of information, either face shape or surface reflectance, was diagnostic. However, in contrast to normal controls, she performed significantly less well when only shape cues were present than when only reflectance cues were present on the faces. Moreover, unlike normal controls, when reflectance cues were present already, she did not benefit further from the shape cues that were added to the existing reflectance cues.

PS vs. controls. We compared PS' performance to those of normal controls (including both young and age-matched) using Crawford and Howell's (1998) modified t-test (one tailed) for single-case studies. This was done for PS' two sessions' data separately. When considering accuracy rates, PS performed lower than the controls in the shape, $t(11) = 2.884$, $p = .017$, and $t(11) = 1.43$, $p = .085$, and shape + reflectance condition, $t(11) = 1.49$, $p = .082$, and $t(11) = 1.897$, $p = .042$. However, this was not true for the reflectance condition, for which there was no difference in accuracy between PS and controls, $t(11) = 0.20$, $p = .42$, and $t(11) = 0.32$, $p = .38$. For correct response times, PS was significantly slower than controls in all three conditions across two sessions, except in the first session of the reflectance condition where she only showed a trend, $t(11) = 1.44$, $p = .088$.

In order to compare the advantage gained by being able to use shape in addition to reflectance information between patient PS and individual controls, we normalized data for each participant using the following formula

$$(\text{Shape} + \text{Reflectance} \; - \text{Reflectance})/(\text{Shape} + \text{Reflectance} + \text{Reflectance})$$

This was done for the accuracy rates and correct response times separately. The indexes, reflecting the contribution of shape cues to participants' performance, are displayed in Figure 6A (accuracy) and 6B (correct response times). For accuracy, PS was the only participant whose performance did not increase by the diagnostic shape cues added to the existing reflectance cues. Her indexes were significantly below normal controls, $t(11) = 3.13$, $p < .0047$, and $t(11) = 3.15$, $p < .0046$, for two sessions respectively. For correct response times, her index was also negative and below all control participants the second time that she performed the task, $t(11) = 1.92$, $p < .04$; first time, $t(11) = -0.1995$, *ns.* Importantly, both for accuracy rates and correct response times, the age-matched controls did not differ from the young controls, and were, in fact, among the participants who gained substantially from the additional presence of shape cues (Figure 6).

When reflectance was added to existing shape, as measured by [(Shape + Reflectance − Shape)/(Shape + Reflectance + Shape)], all control participants but one showed an improvement in accuracy rates, and all controls but another one showed an improvement in correct response times (Figure 6). Here, the prosopagnosic patient PS' indexes were in the normal range, both for accuracy rates and correct response times, the two times that she performed the task: Accuracy, $t(11) = 0.62$, $p = .27$, and $t(11) = -0.20$, $p = .42$; correct response times, $t(11) = -0.54$, $p = .30$, and $t(11) = -0.27$, $p = .40$. This finding indicates that PS' performance was improved to a similar degree as those of normal controls by the additional reflectance cues.

Discussion

In summary, our data suggest that an acquired prosopagnosic patient who is unable to perceive faces holistically relied relatively more on reflectance than on shape when matching individual faces. On the contrary, normal participants, on average, appeared to rely on both kinds of cues to the same extent. Moreover, unlike controls, PS did not benefit substantially from the presence of additional shape information when diagnostic reflectance was already present. These observations support the hypothesis that a loss of the ability to perceive faces holistically in acquired prosopagnosia leads to a reduced reliance on diagnostic facial cues conveyed by 3-D shape information.

GENERAL DISCUSSION

Across three behavioural experiments, we first replicated previous evidence that both 3-D shape and surface reflectance information contribute to the individualization of faces (Bruce et al., 1991; Jiang et al., 2006; O'Toole et al., 1999; Russell et al., 2006, 2007). Having both kinds of cues present makes us performing better and faster at individualizing faces than when only one of these two kinds of cues is present. Moreover, in agreement with these previous studies (Jiang et al., 2006; O'Toole et al., 1999; Russell et al., 2006, 2007), we found that shape and reflectance as defined in our stimulus set were roughly equally diagnostic for individual faces at upright orientation (Experiment 1), even when the lower part of the face is removed (Experiment 3).

Most interestingly, despite their equal contribution to the discrimination of faces at upright orientation in normal observers, we found converging evidence for a functional dissociation between these two kinds of cues in our three experiments. The data of Experiments 1 and 3 shows that when an observer's capacity to process an individual face holistically is disrupted, either by inverting the faces or because of prosopagnosia caused by brain lesion, shape cues become significantly less diagnostic. In contrast, the diagnosticity of surface reflectance cues is only mildly, if at all, affected. Moreover, Experiment 2 showed that while the presence of interfering shape cues in the to-be-ignored bottom half induces the composite face effect, the presence of interfering reflectance cues alone does not. Altogether, these observations support the view that whereas both shape and reflectance cues are used to individualize faces, shape cues depend much more on holistic face perception than surface reflectance cues.

Why would shape cues be particularly dependent on holistic face perception? A simple look at our stimuli (Figure 1) shows that when faces differ by shape information, the shape of the global contour of the face and the relative size of the head are highly salient cues for individual face matching/discrimination. Moreover, relative distances between internal features of the face (e.g., mouth–nose, interocular distance, etc.) can also be diagnostic. These potentially diagnostic facial cues, in particular the head shape and long-range distances between facial features (e.g., eyes–mouth distance; see Sekunova & Barton, 2008), are relatively easy to detect, if the stimulus is perceived at a global scale. However, if perception is restricted to a local scale (i.e., at the level of a single feature), cues such as global head shape and long-range relations between features are no longer salient. If faces differing in shape alone have then to be analysed more locally, they can still be individualized based on, for instance, the shape of the left eye, of the mouth, etc. However, a great deal of global information would be discarded. With these stimulus-specific considerations, it is rather logical that the disruption of holistic perception, as in the case of acquired prosopagnosia or following inversion of the face stimulus in normal observers, affects relatively more the processing of faces differing by shape than by reflectance alone. Moreover, when having to judge top halves of composite faces, the presence of different bottom halves also changes the kinds of large-scale cues that are generally supported by shape information. Even if the observer attempts to rely on local cues in the composite task (i.e., using only the top part the face), his/her perception of these "local cues" is necessarily influenced by the shape of the whole face. Thus, the diagnosticity of shape cues for individualizing faces appears to depend on our ability to perceive faces at a global scale. In contrast, the reflectance cues that are diagnostic for face individualization either have to be resolved locally (e.g., colour of the lips), or *can* be resolved locally (e.g., darkness of eyebrows, colour of the eyes, skin colour).

This interpretation is in agreement with recent findings of larger effects of inversion for global shape modifications of the face stimuli (head contour) as opposed to local modification (internal features; van Belle, de Smet, de Graef, van Gool, & Verfaillie, 2009). It may also explain the discrepancy between our observations in Experiment 1, and the results of Russell et al. (2007), who found equally large inversion effects for shape- and reflectance-varying faces in a similar face matching paradigm as we used here. In that study, faces varied in 2-D-shape in the image plane and shape variations between faces at a global scale were minimal (see Figure 1 in Russell et al., 2007). For instance, the top of the head was artificially cut above the eyebrows the same way for all faces (i.e., a flat line). Moreover, at least for the few example stimuli provided by the authors, the shape of the chin and cheeks was highly similar between faces, and the variations in long-range distances between internal features were almost nonexistent. The shape variations, in general, were mainly present at a local level (nose, eye shape, etc.). Hence, in that study, we argue that inversion could not disrupt the diagnosticity of shape cues at a global scale, because global shape cues were minimized in the upright stimuli.

Note that our findings do not dismiss the observations of Russell and colleagues, but rather complement them. Indeed, we also found an inversion effect for faces differing in terms of reflectance cues alone, even though it was smaller than for faces differing in shape cues alone. Moreover, although Russell et al. (2007) chose to equalize the physical similarity of all the pairs of faces in their different conditions, we decided to respect the natural variations of shape and surface reflectance as captured by the laser scans. As a result, face pairs were not matched for physical similarity in our study, and it could be that by equating physical similarity and apply cropping to our face stimulus set, our results would have been more similar to those of

Russell et al.[5] Nevertheless, faces differing in shape or reflectance alone led to equal performance at upright orientation. Therefore, the physical dissimilarity cannot explain the present findings of a dissociation between these two types of faces at inverted orientation, in a composite paradigm, or with acquired prosopagnosic patient. Our observations supports the finding that global head shape contour plays a significant role in the magnitude of the face inversion effect (van Belle et al., 2009). Studies using faces with a homogenous face contour (e.g., schematic faces, cropped faces in an oval, or a single head shape), and/or with normalized long-range relative distances between features, may not be adequate to fully capture the implication of holistic face processing and of its disruption by inversion.

In another previous study, Russell and colleagues (2006) showed that contrast negation of faces affects performance of faces differing in reflectance but not in shape only. Here we showed that disruption of holistic face processing through picture-plane inversion and prosopagnosia affects performance for faces differing in shape but not in reflectance alone. Considering these observations altogether, they reinforce the view that contrast negation and inversion—two manipulations that are detrimental for recognizing faces—do not affect face processing the same way (Hole, George, & Dunsmore, 1999; Itier & Taylor, 2002; Kemp, McManus, & Pigott, 1990; Lewis & Johnston, 1997). Yet, these previous studies were unable to clarify how contrast negation and inversion affects distinct face processes, whereas the combined observations of Russell et al. (2006) and of the present study offer a clearer view on this issue: Contrast negation affects primarily surface reflectance cues which are resolved more analytically, whereas inversion affects mainly shape-related cues which are resolved more holistically.

More importantly, these observations indicate that shape and surface reflectance diagnostic cues are functionally dissociated. Electrophysiological data also support this view, showing that early representations of individual faces in the right hemisphere are based largely on shape rather than surface reflectance cues (Caharel et al., 2009). Moreover, representation of individual faces in face-sensitive areas in the right hemisphere as identified in fMRI is based primarily on shape information (Jiang et al., 2009). Diagnostic surface reflectance cues play a role later in the individualization of faces, and with a lesser involvement of face-sensitive areas of the right hemisphere (Caharel et al., 2009). These (neuro)functional dissociations indicate that, although the two kinds of cues lead to equal performance in

[5] Note that there is no "absolute" way to quantify the physical variance in shape and texture. Pixel-by-pixel image comparisons would certainly be nonoptimal, because a simple global shift of the face would cause a huge image difference, even though it is the same face (and looks like the same face, too).

face matching tasks, our expertise in face perception is based more on shape than on surface reflectance information. Indeed, when these expert face processes cannot be sufficiently recruited, as in the case of acquired prosopagnosia or following inversion, the diagnosticity of shape-related information is much more affected than surface-reflectance information. This conclusion is compatible with the view that what makes faces special kinds of stimuli, for which we are expert, is that, contrary to other object classes, individual members of the face category are perceived holistically (Biederman & Kalocsai, 1997; Robbins & McKone, 2007; Tanaka & Farah, 1993). In contrast, our findings do not support the view that surface reflectance contribute substantially to our specific expertise for faces. Thus, although the reflectance cues contribute significantly to face recognition performance, this may be through more general mechanisms that would also play a significant role in nonface object recognition (Tanaka, Weiskopf, & Williams, 2001; Vuong, Peissig, Harrison, & Tarr, 2005).

In summary, the current study provides evidence in support of the view that shape plays a more important role than reflectance cues in holistic face processing. Note that we are not claiming from our observations that the representation of faces is reflectance-less, or that shape and reflectance are completely separated. Their representations appear to be partially separated along the time course of face processing, with information about shape heading and accumulating faster than reflectance (Caharel et al., 2009), and being particularly important for holistic face processing (the present study). Yet, representation of faces is likely to integrate both shape and surface reflectance in the human brain, two fundamental sources of information for face recognition.

REFERENCES

Biederman, I., & Kalocsai, P. (1997). Neurocomputational bases of object and face recognition. *Philosophical Transactions of the Royal Society B*, *352*, 1203–1219.

Blanz, V., & Vetter, T. (1999). A morphable model for the synthesis of 3D faces. In *SIGGRAPH '99: Proceedings of the 26th annual conference on computer graphics and interactive techniques* (pp. 187–194). New York, NY: ACM Press/Addison-Wesley.

Bodamer, J. (1947). Die Prosop-agnosie. *Archiv für Psychiatrie und Nervenkrankheiten*, *179*, 6–54.

Bousten, L., & Humphreys, G. W. (2002). Face context interferes with local part processing in a prosopagnosic patient. *Neuropsychologia*, *40*, 2305–2313.

Bruce, V., Burton, A. M., Hanna, E., Healey, P., Mason, O., Coombes, A., et al. (1993). Sex-discrimination: How well do we tell the difference between male and female faces. *Perception*, *22*, 131–152.

Bruce, V., Healey, P., Burton, M., Doyle, T., Coombes, A., & Linney, A. (1991). Recognising facial surfaces. *Perception*, *20*, 755–769.

Bruce, V., & Young, A. W. (1998). *In the eye of the beholder: The science of face perception*. Oxford, UK: Oxford University Press.

Burt, D. M., & Perrett, D. I. (1995). Perception of age in adult Caucasian male faces: Computer graphic manipulation of shape and colour information. *Proceedings of the Royal Society of London*, *259B*, 137–143.

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*, 2051–2067.

Busigny, T., & Rossion, B. (2010). Acquired prosopagnosia abolishes the face inversion effect. *Cortex*, *46*, 965–981.

Caharel, S., Jiang, F., Blanz, V., & Rossion, B. (2009). Recognizing an individual face: 3D shape contributes earlier than 2D surface reflectance information. *NeuroImage*, *47*, 1809–1818.

Caldara, R., Schyns, P., Mayer, E., Smith, M., Gosselin, F., & Rossion, B. (2005). Does prosopagnosia take the eyes out from faces? Evidence for a defect in the use of diagnostic facial information in a brain-damaged patient. *Journal of Cognitive Neurosciences*, *17*, 1652–1666.

Crawford, J. R., & Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. *The Clinical Neuropsychologist*, *12*, 482–486.

Cronbach, L. J. (1951). Coefficient alpha and the internal structure of tests. *Psychometrika*, *16*(3), 297–334.

De Heering, A., & Rossion, B. (2008). Prolonged visual experience in adulthood modulates holistic face perception. *PLOS One*, *3*(5), e2317.

De Renzi, E. (1986). Current issues on prosopagnosia. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. W. Young (Eds.), *Aspects of face processing* (pp. 243–252). Dordrecht, The Netherlands: Martinus Nijhoff.

Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 628–634.

Galton, F. (1883). *Inquries into human faculty and its development*. London, UK: Macmillan.

Goffaux, V., & Rossion, B. (2006). Faces are "spatial"—Holistic face perception is supported by low spatial frequencies. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 1023–1039.

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

Haig, N. D. (1985). How faces differ—a new comparative technique. *Perception*, *14*, 601–615.

Haig, N. D. (1986). Investigating face recognition with an image processing computer. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. W. Young (Eds.), *Aspects of face processing* (pp. 410–425). Dordrecht, The Netherlands: Martinus Nijhoff.

Henke, K., Schweinberger, S. R., Grigo, A., Klos, T., & Sommer, W. (1998). Specificity of face recognition: Recognition of exemplars of non-face objects in prosopagnosia. *Cortex*, *34*, 289–296.

Hill, H., Bruce, V., & Akamatsu, S. (1995). Perceiving the sex and race of faces: The role of shape and colour. *Proceedings of the Royal Society of London*, *261B*, 367–373.

Hillger, L. A., & Koenig, O. (1991). Separable mechanisms in face processing: Evidence from hemispheric specialization. *Journal of Cognitive Neurosciences*, *3*, 42–58.

Hole, G. J. (1994). Configural factors in the perception of unfamiliar faces. *Perception*, *23*, 65–74.

Hole, G. J., George, P., & Dunsmore, V. (1999). Evidence for holistic processing of faces viewed as photographic negative. *Perception*, *28*, 341–359.

Itier, R. J., & Taylor, M. J. (2002). Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: A repetition study using ERPs. *NeuroImage*, *15*, 353–372.

Jacques, C., d'Arripe, O., & Rossion, B. (2007). The time course of the inversion effect during individual face discrimination. *Journal of Vision*, *7*(8), 1–9.

Jiang, F., Blanz, V., & O'Toole, A. J. (2006). Probing the visual representation of faces with adaptation: A view from the other side of the mean. *Psychological Sciences*, *17*, 493–500.

Jiang, F., Dricot, L., Blanz, V., Goebel, R., & Rossion, B. (2009). Neural correlates of shape and surface reflectance information in individual faces. *Neuroscience*, *163*, 1078–1091.

Joubert, S., Felician, O., Barbeau, E., Sontheimer, A., Barton, J. J., Ceccaldi, M., et al. (2003). Impaired configurational processing in a case of progressive prosopagnosia associated with predominant right temporal lobe atrophy. *Brain*, *126*, 2537–2550.

Kemp, R., McManus, C., & Pigott, T. (1990). Sensitivity to the displacement of facial features in negative and inverted images. *Perception*, *19*, 531–543.

Kuefner, D., Cassia, V. M., Vescovo, E., & Picozzi, M. (2010). Natural experience acquired in adulthood enhances holistic processing of other-age faces. *Visual Cognition*, *18*(1), 11–25.

Leder, H., & Bruce, V. (2000). When inverted faces are recognized: The role of configural information in face recognition. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *53A*(2), 513–536.

Leder, H., & Carbon, C.-C. (2006). Face-specific configural processing of relational information. *British Journal of Psychology*, *97*, 19–29.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2004). Impairment in holistic face processing following early visual deprivation. *Psychological Sciences*, *15*, 762–768.

Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, *4*, 89–94.

Levine, D. N., & Calvanio, R. (1989). Prosopagnosia: A defect in visual configural processing. *Brain Cognition*, *10*, 149–170.

Lewis, M. B., & Johnston, R. A. (1997). The Thatcher illusion as a test of configural disruption. *Perception*, *26*, 225–227.

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Science*, *6*, 255–260.

McKone, E., & Robbins, R. (2007). The evidence rejects the expertise hypothesis: Reply to Gauthier & Bukach. *Cognition*, *103*, 331–336.

McKone, E., & Yovel, G. (2009). Why does picture-plane inversion sometimes dissociate perception of features and spacing in faces, and sometimes not? *Psychonomic Bulletin and Review*, *16*(5), 778–797.

Michel, C., Rossion, B., Han, J., Chung, C. S., & Caldara, R. (2006). Holistic processing in finely tuned for faces of our own race. *Psychological Sciences*, *17*, 608–615.

Orban de Xivry, J. J., Ramon, M., Lefèvre, P., & Rossion, B. (2008). Reduced fixation on the upper area of personally familiar faces following acquired prosopagnosia. *Journal of Neuropsychology*, *2*, 245–268.

O'Toole, A. J., Vetter, T., & Blanz, V. (1999). Three-dimensional shape and two-dimensional surface reflectance contributions to face recognition: An application of three-dimensional morphing. *Vision Research*, *39*, 3145–3155.

Quaglino, A., & Borelli, G. (1867). Emiplegia sinistra con amaurosi-guarigione-perdita totale della percezione dei colori e della memoria della configurazione degli oggetti. *Giornale d'Oftalmologia Italiano*, *10*, 106–117.

Ramon, M., Busigny, T., & Rossion, B. (2010). Impaired holistic processing of unfamiliar individual faces in acquired prosopagnosia. *Neuropsychologia*, *48*, 933–944.

Rhodes, G. (1988). Looking at faces: First-order and second-order features as determinants of facial appearance. *Perception*, *17*, 43–63.

Richler, J. J., Gauthier, I., Wenger, M. J., & Palmeri, T. J. (2008). Holistic processing of faces: Perceptual and decisional components. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*, 328–342.

Riddoch, M. J., Johnston, R. A., Bracewell, R. M., Boutsen, L., & Humphreys, G. W. (2008). Are faces special? A case of pure prosopagnosia. *Cognitive Neuropsychology*, *25*(1), 3–26.

Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, *103*(1), 34–79.

Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica*, *128*, 274–289.

Rossion, B. (2009). Distinguishing the cause and consequence of face inversion: The perceptual field hypothesis. *Acta Psychologica*, *132*, 300–312.

Rossion, B., & Boremanse, A (2008). Nonlinear relationship between holistic processing of individual faces and picture-plane rotation: Evidence from the face composite illusion. *Journal of Vision*, *8*(4), 1–13.

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.

Rossion, B., Kaiser, M. D., Bub, D., & Tanaka, J. W. (2009). Is the loss of diagnosticity of the eye region of the face a common aspect of acquired prosopagnosia? *Journal of Neuropsychology*, *3*, 69–78.

Russell, R., Biederman, I., Nederhouser, M., & Sinha, P. (2007). The utility of surface reflectance for the recognition of upright and inverted faces. *Vision Research*, *47*, 157–165.

Russell, R., Sinha, P., Biederman, I., & Nederhouser, M. (2006). Is pigmentation important for face recognition? Evidence from contrast negation. *Perception*, *35*, 749–759.

Sadr, J., Jarudi, I., & Sinha, P. (2003). The role of eyebrows in face recognition. *Perception*, *32*, 285–293.

Saumier, D., Arguin, M., & Lassonde, M. (2001). Prosopagnosia: A case study involving problems in processing configural information. *Brain Cognition*, *46*, 255–259.

Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *NeuroImage*, *32*(3), 1385–1394.

Sekunova, A., & Barton, J. J. S. (2008). The effects of face inversion on the perception of long-range and local spatial relations in eye and mouth configuration. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 1129–1135.

Sergent, J. (1984). An investigation into component and configural processes underlying face perception. *British Journal of Psychology*, *75*, 221–242.

Sergent, J. (1986). Microgenesis of face perception. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. W. Young (Eds.), *Aspects of face processing* (pp. 17–33). Dordrecht, The Netherlands: Martinus Nijhoff.

Sergent, J. (1988). Face perception and the right hemisphere. In L. Weiskrantz (Ed.), *Thought without language* (pp. 108–131). Oxford, UK: Clarendon Press.

Sergent, J., & Villemure, J. G. (1989). Prosopagnosia in a right hemispherectomized patient. *Brain*, *112*, 975–995.

Sorger, B., Goebel, R., Schiltz, C., & Rossion, B. (2007). Understanding the functional neuroanatomy of prosopagnosia. *NeuroImage*, *35*, 852–856.

Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology*, *46A*, 225–245.

Tanaka, J. W., Weiskopf, D., & Williams, P. (2001). The role of color in high-level vision. *Trends in Cognitive Sciences*, *5*(5), 211–215.

Taubert, J. (2009). Chimpanzee faces are "special" to humans. *Perception*, *38*(3), 343–356.

Taubert, J., & Alais, D. (2009). The composite illusion requires composite face stimuli to be biologically plausible. *Vision Research*, *49*, 1877–1885.

van Belle, G., de Graef, P., Verfaillie, K., Busigny, T., & Rossion, B. (2010). Whole not hole: Expert face recognition requires holistic perception. *Neuropsychologia*, *48*, 2609–2620.

van Belle, G., de Graef, P., Verfaillie, K., Rossion, B., & Lefèvre, P. (2010). Face inversion impairs holistic perception: Evidence from gaze-contingent stimulation. *Journal of Vision*, *10*(5), 1–13. doi:10.1167/10.5.10

van Belle, G., de Smet, M., de Graef, P., van Gool, L., & Verfaillie, K. (2009). Configural and featural processing during face perception: A new stimulus set. *Behavior Research Methods*, *41*, 279–283.

Vuong, Q. C., Peissig, J. J., Harrison, M. C., & Tarr, M. J. (2005). The role of surface pigmentation for recognition revealed by contrast reversal in faces and Greebles. *Vision Research*, *45*, 1213–1223.

Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin and Review*, *6*, 647–653.

Yarbus, A. L. (1967). *Eye movements and vision*. New York, NY: Plenum Press.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*, 141–145.

Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception*, *16*, 749–759.

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