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Picture-plane inversion leads to qualitative changes of face perception

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Abstract

Presenting a face stimulus upside-down generally causes a larger deficit in perceiving metric distances between facial features ("configuration") than local properties of these features. This effect supports a qualitative account of face inversion: the same transformation affects the processing of different kinds of information differently. However, this view has been recently challenged by studies reporting equal inversion costs of performance for discriminating featural and configural manipulations on faces. In this paper I argue that these studies did not replicate previous results due to methodological factors rather than largely irrelevant parameters such as having equal performance for configural and featural conditions at upright orientation, or randomizing trials across conditions. I also argue that identifying similar diagnostic features (eyes and eyebrows) for discriminating individual faces at upright and inverted orientations by means of response classification methods does not dismiss at all the qualitative view of face inversion. Considering these elements as well as both behavioral and neuropsychological evidence, I propose that the generally larger effect of inversion for processing configural than featural cues is a mere consequence of the disruption of holistic face perception. That is, configural relations necessarily involve two or more distant features on the face, such that their perception is most dependent on the ability to perceive simultaneously multiple features of a face as a whole.

PsycINFO classification: 2323

Keywords: Face perception; Inversion effect; Holistic

1. Introduction: holistic perception and face inversion

An inverted face is extremely difficult to recognize. This rather old observation (e.g., Hochberg & Galper, 1967) has become widely documented in the face processing literature, for several reasons. First, the effect of inversion is much larger for faces than for other object categories, a phenomenon known as the 'face inversion effect' (Yin, 1969). Together with the observation of recognition impairments limited for faces following brain injury (prosopagnosia: Bodamer, 1947; Wigan, 1844) and of neurons responding selectively to faces in the monkey inferotemporal cortex (Gross, Rocha-Miranda, & Bender, 1972), this face inversion effect is one of the first (and most compelling) sources of evidence that faces are processed by specific brain mechanisms (i.e., those that are particularly affected by inversion, Yin, 1969). Second, the effect of face inversion is extremely robust, and has been observed in a variety of conditions: for processing familiar and unfamiliar faces, in old/new recognition tasks or matching tasks, with or without delay between the stimuli to match, with upright and inverted trials blocked or randomized (for a review see Rossion & Gauthier, 2002; for more recent references: e.g., Barton, Keenan, & Bass, 2001; Barton, Zhao, & Keenan, 2003; Goffaux, in press; Goffaux & Rossion, 2007; Jacques, d'Arripe, & Rossion, 2007; Leder & Carbon, 2006; Le Grand, Mondloch, Maurer, & Brent, 2001; Mondloch, Le Grand, & Maurer, 2002; Rhodes, Hayward,

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& Winkler, 2007; Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Russell, Biederman, Nederhouser, & Sinha, 2007; Yovel & Kanwisher, 2004).

Third and most importantly, since Yin (1969) reported that the participants of his experiment were unable to "*get a general impression of the whole picture*" (p. 145) for inverted faces, a number of empirical studies have supported this intuition. When a face stimulus is presented at upright orientation, the processing of a facial feature (e.g., eyes, nose, mouth,...) is affected by alterations to the identity or the position of one or several other features of the face (e.g., Farah, Wilson, Drain, & Tanaka, 1998; Homa, Haver, & Schwartz, 1976; Mermelstein, Banks, & Prinzmetal, 1979; Sergent, 1984; Suzuki & Cavanagh, 1995; Tanaka & Farah, 1993; Tanaka & Sengco, 1997; Young, Hellawell, & Hay, 1987). The most compelling illustration of this phenomenon comes from an adaptation of the so-called face composite effect (Young et al., 1987) to create a visual illusion in which identical top halves of faces are perceived as being slightly different if they are aligned with different bottom parts, even when the bottom parts are irrelevant and not attended to (Fig. 1a). This face composite illusion is a particularly clear demonstration that the features of a face (here the two halves of a single face) cannot be perceived in isolation. That is, the perception of the attended top part in this example *depends* on the identity of the bottom part and its position (since the illusion vanishes when the two parts are misaligned spatially; for empirical demonstrations in face matching tasks see e.g., Goffaux & Rossion, 2006; Hole, 1994; Le Grand, Mondloch, Maurer, & Brent, 2004; Michel, Rossion, Han, Chung, & Caldara, 2006; Rossion & Boremanse, in press). This empirical observation is generally interpreted as a deficit in the integration of the facial features into a Gestalt, a global picture, a so-called 'configural' (Sergent, 1984; Young et al., 1987) or 'holistic' (Farah et al., 1998; Tanaka & Farah, 1993) representation.

Strikingly, the face composite illusion is abolished or strongly reduced when faces are presented upside-down (Fig. 1b; e.g., Goffaux & Rossion, 2006; Hole, 1994; Le Grand et al., 2004; Michel et al., 2006; Rossion & Boremanse, in press). This dramatic impairment of the interdependence of facial features with inversion has been demonstrated in other behavioral paradigms measuring the interdependence between facial features (e.g., Farah et al., 1998; Leder & Carbon, 2005; Suzuki & Cavanagh, 1995; Tanaka & Farah, 1993; Tanaka & Sengco, 1997; see also Sergent, 1984; Thompson, 1980): the location and/or the identity of one or several facial feature(s) does not modulate the processing of a target feature when the face is presented upside-down.

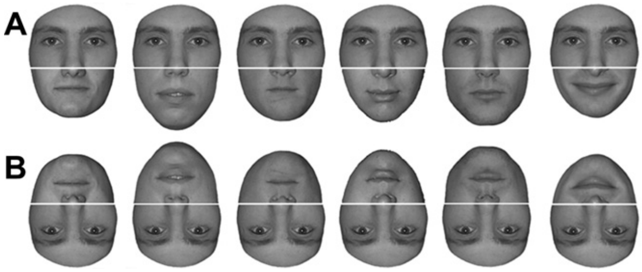

Fig. 1. The face composite illusion is a nice demonstration of the integrative nature of face perception and how it is affected by inversion. Above, upright faces: all top halves of the faces (above the white line) are identical, yet they are perceived as slightly different due to the presence of the different bottom parts. This illustrates how facial features influence each other for upright faces. Below, the illusion vanishes or is strongly reduced when the same stimuli are presented upside-down.

These observations have been particularly important in the field because an extremely simple stimulus transformation like inversion, while preserving the low-level visual information of the stimulus, can be used to reduce the interdependence of facial features during face processing tasks. They have also supported the view that faces are perceived more holistically/configurally than other objects, and thus could be relatively more, or even selectively, impaired (i.e., by inversion, or following brain damage, prosopagnosia, e.g., Sergent & Signoret, 1992). More recently, neuroimaging (Mazard, Schiltz, & Rossion, 2006; Yovel & Kanwisher, 2004, 2005) and electrophysiological (Jacques et al., 2007) studies in humans have compared the discrimination of individual upright and inverted faces in order to clarify the neural underpinnings of this holistic/configural face processing.

It is important to stress that the terms 'holistic' or 'configural', which are sometimes used interchangeably in the literature among other terms, refer here to a perceptual *process* and not a cue that can be manipulated on a single face stimulus. In line with recent reviews on this topic (Maurer, Le Grand, & Mondloch, 2002; Rossion & Gauthier, 2002), I will only use the term 'holistic' in the remaining part of the text to refer to this process. Indeed, the term 'configural' seems more ambiguous to me, since various authors in the field have used 'configural' to refer either to a process (e.g., Sergent, 1984; Young et al., 1987), *or* to physical information that can be measured and manipulated on a stimulus (metric distances between features or configural relations, e.g., Rhodes, 1988). To avoid any ambiguity, in the remaining part of this paper, the term 'configural' will always refer to the metric distances between features (see Section 2 below).

Even though there is no formal and widely accepted definition of holistic face processing in the literature, the term 'holistic' has been widely used. In line with early (Galton, 1883) and more recent (e.g., Farah et al., 1998; Ingvalson & Wenger, 2005) proposals, most researchers would probably agree with a definition of holistic face processing as *the simultaneous integration of the multiple features of a face into a single perceptual representation*. Yet, admittedly, the empirical evidence collected so far and cited above essentially shows that facial features are *interdependent*. Empirical studies have not shown that the *whole* of the face stimulus is necessarily involved in this process, or that features are processed *simultaneously* (i.e., in parallel), two assumptions that remain largely hypothetical.[1]

Although the interdependence between features can lead to response biases (Wenger & Ingvalson, 2002) in face matching tasks (e.g., responding "different" to two top parts of a face that are identical but are aligned with different bottom parts, see Fig. 1a), there is evidence that the primary locus of this effect is at the perceptual level. This is illustrated by the fact that the face composite effect corresponds to a visual illusion, and takes place predominantly in high-level visual areas responding preferentially to faces such as the right 'fusiform face area' ('FFA', Schiltz & Rossion, 2006). Similarly, the onset of the effect of inversion on individual face discrimination takes place in the same cortical areas (Mazard, Schiltz, & Rossion, 2006; Yovel & Kanwisher, 2005), and event-related potential studies indicate an early onset of this effect (160 ms), on the occipito-temporal N170 component (Jacques et al., 2007).

2. A disproportionate effect of inversion on the perception of metric distances between facial features?

In parallel to these observations, numerous behavioral studies have shown that the perception of *metric distances* between features (e.g., interocular distance, mouth-nose distance…) is more affected by inversion than the perception of local cues (e.g., shape of the mouth, color of the eyes…) (e.g., Barton et al., 2001; Cabeza & Kato, 2000; Collishaw & Hole, 2000; Freire, Lee, & Symons, 2000; Goffaux, in press; Goffaux & Rossion, 2007; Le Grand et al., 2001; Leder & Bruce, 2000; Leder, Candrian, Huber, & Bruce, 2001; Rhodes, Brake, & Atkinson, 1993; Rhodes et al., 2007). The former type of manipulation has largely been referred to as "configural information", while the latter is usually referred to as "featural information", with both types of cues considered as being important to characterize an individual face (e.g., Cabeza & Kato, 2000; Rhodes, 1988). Following the review of Maurer et al. (2002), most researchers consider that inversion of the stimulus leads to a dramatic impairment of both holistic face perception and the perception of configural relations, in addition to a weaker effect on featural perception. That is, according to these and other authors, holistic face perception is conceptually distinguished from the perception of metric distances between features ("the many faces of configural processing", Maurer et al., 2002).

Since inversion does not affect the processing of all face cues equally but is more devastating for configural than featural information, it is generally considered to affect face processing *qualitatively* rather than *quantitatively*. This statement does not imply that different representations and/or neural populations support the processing of upright and inverted faces, but rather that for the very same amount of transformation (i.e., a 180° rotation), the processing of certain cues (configural) is more affected than others (featural).

However, quite interestingly and surprisingly, several recent behavioral studies have cast strong doubts on this view. In contrast to previous studies, Riesenhuber et al., 2004 as well as Yovel and Kanwisher (2004) found equivalent inversion effects for individual discrimination of faces differing by local features and by metric distances between features. These authors concluded that *"there is no difference between 'featurally' and 'configurally' transformed faces in terms of inversion effect"* (e.g., Riesenhuber et al., 2004, p. 448).

Along the same lines, Sekuler, Gaspar, Gold, and Bennett (2004) stimulated an observer during thousands of discrimination trials with two pairs of face stimuli embedded in noise. Performance was better for upright faces. However, classification of the images based on subject's responses showed that the same area of the face, mostly around the eyes, was used to perform individual discrimination, irrespective of orientation. These authors concluded that "*inversion leads to quantitative, not qualitative, changes in face processing*" (Sekuler et al., 2004, title, p. 391), and argued that the relationship between the configural/featural distinction in face recognition and the inversion effect is merely speculative. That is, information would simply be extracted more efficiently from upright faces than inverted faces, using the same cues.

These recent studies are interesting because they challenge a widely accepted view in the face literature (e.g., Bruce & Young, 1998), i.e., that the effect of face inversion is related to a particular disruption of configural cues. They have the merit to force researchers in this area not only to reconsider their views, but also to think more deeply about the various notions of the relations between facial features that have been used in the literature (sometimes admittedly in an extremely confusing way). Yet, irrespective of the theoretical issues, the empirical observations of these studies remain at odds with quite a large number of previous experiments on face inversion, as indicated above.

In this paper, my first objective will be to provide a critical account of these last studies, and suggest that they present methodological and conceptual shortcomings that do not allow to reach general conclusions such as *"there is no difference between 'featurally' and 'configurally' transformed faces in terms of inversion effect"* (Riesenhuber et al., 2004; Yovel & Kanwisher, 2004). I believe that such a statement is erroneous and potentially misleading for researchers in the field. In short, I will argue that inversion indeed generally affects relatively more the perception of metric distances between features (configural information) than the processing of local features. That is, inversion affects face perception qualitatively. Rather than dismissing it, there is a need to clarify this issue in order to understand

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[1] While Tanaka, Farah and colleagues have essentially emphasized the notion of a single representation of the whole face as characterizing holistic face processing (Farah et al., 1998; Tanaka & Farah, 1993), other authors (e.g., Ingvalson & Wenger, 2005) have also pointed to the parallel aspect of the processing of the features, in line with early empirical work in the field (e.g., Bradshaw & Wallace, 1971).

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better the nature of the face inversion effect. My second goal here was prompted by the fact that Sekuler et al. (2004) went further than the statement above, arguing against the view that there is a differential coding of configural cues of the face, or of the stimulus *as a whole*, between upright and inverted faces. I will challenge this claim by indicating how the findings of this study are not relevant to this issue. Finally, in a more constructive perspective, I will then propose that the larger effect of inversion observed for configural than featural face information is, in fact, merely a natural *consequence* of the disruption of holistic face perception by inversion as described in the first section of the present paper. That is, it is precisely because inversion disrupts holistic perception that the processing of metric distances between features, which involves two or more distant elements, is particularly impaired.

One note of caution is needed before proceeding to this argumentation. I am aware that ‘‘holistic processing’’ and ‘‘configural information’’ are loaded terms that have become quite confusing in the face processing literature. In addition, there are many different terms that have been introduced and used throughout the years to refer to similar concepts, such as ‘‘configural processing’’ (e.g., Sergent, 1984), ‘‘first and second-order spatial relations’’ (e.g., Diamond & Carey, 1986), ‘‘relational information’’ (Leder & Bruce, 1998) etc. For the sake of clarity and in keeping with the conceptual distinctions made in two relatively recent reviews (Maurer et al., 2002; Rossion & Gauthier, 2002), I will avoid using these latter terms. On the one hand, I will refer here only to ‘‘holistic’’ as an integrative perceptual *process* (i.e., which cannot be measured or manipulated on a stimulus independent of the observer) as defined in Section 1. On the other hand, I will refer to ‘‘configural’’ as a manipulation on a stimulus that consists in increasing or decreasing the metric distances between features, and which can be opposed to a ‘‘featural’’ manipulation (changing the shape or surface property of a local feature). While acknowledging this *conceptual* distinction, a point that will be developed at the end of this manuscript is that holistic perception and the processing of configural information cannot be dissociated *empirically* by studies of face inversion.

3. Early challenges on qualitative effects of face inversion

Interestingly, it is not the first time that the idea of a larger effect of inversion on relations between facial features is challenged in the literature. In his seminal review of the face inversion effect, Valentine (1988) pointed to the lack of evidence supporting this view. However, Valentine's (1988) review was written before the majority of experiments showing such effects were reported. The author also reasoned that if inversion affected face processing qualitatively, there should be a sudden shift in the function relating the face processing performance and the angle of rotation of the face, from 0° to 180°. That is, the variable measured during face processing tasks (e.g., accuracy, correct response time) should be non-linearly related to the angle of rotation, the departure from linearity occurring at the angle at which the process of interest (e.g., feature integration) could not be applied to the face anymore. Valentine and Bruce (1988) tested this hypothesis in a number of experiments using faces presented at 45° increments (45°, 90°, 135° and 180°) and found a strict linear relationship between response time and the degree of disorientation. They interpreted this finding as supporting the quantitative view of the face inversion effect.

However, a linear relationship between orientation of the face and performance at an individual discrimination task is not at all an evidence against the qualitative view of face inversion. It may well be that *both* the perception of configural relations and featural relations show a linear relationship with orientation of the stimulus, but that the slope is steeper for the configural condition for instance. In this situation, we would observe an interaction between orientation and the type of information manipulated on the face stimulus, i.e., a difference of a difference, or a non-linearity. Such an observation would support the qualitative view of face inversion. In any case, many studies with similar paradigms have rather revealed non-linear relationships between orientation and face processing (e.g., Carbon, Grueter, Weber, & Lueschow, 2007; Jacques & Rossion, 2007; Murray, Yong, & Rhodes, 2000; Stürzel & Spillmann, 2000). I will briefly come back to this issue at the end in this paper (see also Rossion & Boremanse, in press).

Tanaka and Farah (1991) also challenged the view that inversion dramatically affected the perception of metric distances by using dot patterns. The recognition of dot patterns sharing an overall organization and differing by metric distances did not suffer more from inversion than the recognition of very distinct patterns. However, these authors did not compare the equivalent of ‘‘configural’’ and ‘‘featural’’ manipulations as applied to faces in many studies. Most importantly, by using configurations of simple dots rather than face stimuli, their conclusions could only be of very limited scope, especially if one considers that the same authors, as many researchers, have argued that face processing is qualitatively different than nonface object processing (Farah et al., 1998).

In contrast to these studies, both Riesenhuber et al. (2004) and Yovel and Kanwisher (2004) used a same/different discrimination task, with two sequentially presented individual face stimuli. This paradigm is similar in most respects to previous studies that found the strongest inversion costs for configural trials (e.g., Barton et al., 2001; Collishaw & Hole, 2000; Freire et al., 2000; Le Grand et al., 2001; Leder & Bruce, 2000; Mondloch et al., 2002; Rhodes et al., 1993). Thus, at first glance, the discrepancy between these studies and previous work appears rather puzzling.

4. Differences between conditions at upright orientation: an important factor?

According to Yovel and Kanwisher (2004), there was one key difference with previous studies that might explain

Fig. 2. Example of so-called 'featural' trials used by Riesenhuber et al. (2004). These authors swapped the whole area of the eyes to create these stimuli. However, as illustrated here on our own stimuli (see also Fig. 1 of Riesenhuber et al., 2004) the distance between the eyes and eyes/eyebrows was also very different between face stimuli. Hence, these stimuli led to large inversion costs, but this effect cannot be attributed to featural manipulations only.

their peculiar results: performance on configural and featural trials for upright faces was equalized (about 80%) in their study using pilot experiments, whereas configural trials were generally harder than featural trials in other studies (Freire et al., 2000; Mondloch et al., 2002; see also Leder & Carbon, 2006). These authors argued that the lack of equal baselines (for upright trials) may explain the largest inversion effects found for configural trials in previous studies. This is rather surprising because, if anything, a higher performance for featural than configural trials at upright orientation leaves more room for inversion costs in the former condition. Furthermore, Yovel and Kanwisher's (2004) claim is not always substantiated: a number of studies compared the effect of inversion on featural and configural trials when the performance at upright orientation was equal and not at ceiling (e.g., Barton et al., 2001; Le Grand et al., 2001; Leder & Bruce, 2000). For instance, participants in the study of Le Grand et al. (2001) performed at 80% for both configural and featural upright trials, but their performance dropped to 60% for configural trials only. Finally, Riesenhuber et al. (2004) did *not* equalize performance for configural and featural trials upright in the experiment showing equal effects of inversion for both conditions: featural trials were performed substantially better than configural trials (about 85% *vs.* 77%, Fig. 2 in Riesenhuber et al., 2004), even though the direct statistical comparison was not provided. This indicates that equalizing performance for configural and featural trials is not a critical factor accounting for discrepancies between Yovel and Kanwisher's (2004) results and the findings of other studies.

5. Blocking *vs.* randomization of trials

Riesenhuber et al. (2004) offered a different explanation for the discrepancies between their results and previous observations. According to these authors, a potentially significant shortcoming of studies finding larger effects for configural trials is that they used blocked designs: trials were either grouped by change type (e.g., Mondloch et al., 2002) or different groups of subjects were tested for featural and configural trials (e.g., Freire et al., 2000, experiment 1). According to Riesenhuber et al. (2004), these designs would not control for subject's expectations and may lead to artificially small effects of inversion for featural trials in which subjects could focus on detecting a local change. In the main experiment (2) of their study, these authors showed that when presenting stimuli with featural and configural trials randomized, the effect of inversion was equally large for both types of trials. Thus, according to these authors, randomizing conditions would be the key: when this is done, equivalent costs of inversion would be found for featural and configural trials. However, there are several elements that contradict this claim.

First, the claim of the authors is not founded with respect to previous studies. For instance, Freire et al. (2000) randomized the configural and featural trials in their last two delayed matching experiments (3 and 4). This also holds for the study of Leder and Bruce (2000), using a learning paradigm. These two studies found a cost of inversion for configural trials only, reported in accuracy rates. More recent studies have also shown larger effects for configural trials than featural trials when these conditions were randomized (e.g., Goffaux, in press; Goffaux & Rossion, 2007; Rhodes et al., 2007).

Second, Riesenhuber et al. (2004) did not compare the right conditions in their study to make the conclusion that blocking of conditions was an important factor. When subjects were presented with change types randomized, there was indeed no interaction between change type and orientation (experiment 2). When subjects were presented with change types in block, only the main effects were reported for each group ('featural first' and 'configural first'), but not the critical interaction. According to the authors' reasoning, this interaction should have been significant, but it was not reported. In fact, when change types were blocked (experiment 3, supplementary Fig. 1 of Riesenhuber et al., 2004), the effects for configural and featural trials looked of equivalent magnitude, contrary to their suggestion. Moreover, to support their claim, the authors should have demonstrated a triple interaction between change *type* (featural *vs.* configural), *orientation* (upright *vs.* inverted) and *design* (block *vs.* random). This analysis was not reported in the paper, but data from supplemental figures suggest that it would have been far from significant.

In short, there is no evidence whatsoever that this blocking factor plays any role in the absence of significantly larger inversion costs for configural than featural trials reported by Riesenhuber and colleagues (2004). As a matter of fact, Yovel and Kanwisher (2004) found equally large effects of inversion for featural and configural trials, whether these conditions were presented randomly and subjects were unaware of the type of changes, or if the conditions were presented in blocks and subjects were

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informed about which change types they should pay attention in the coming block. This seriously undermines Riesenhuber et al.'s (2004) assertion that subject's expectations play a key role in observing the largest effects for configural trials in previous studies.

To summarize, none of these two studies (Riesenhuber et al., 2004; Yovel & Kanwisher, 2004) can offer a reasonable account for their failure to disclose larger inversion costs of performance for configural than featural conditions. In fact, the explanations proposed in either of these studies contradict each other: Yovel and Kanwisher's (2004) results indicate that randomizing or blocking configural and featural trials did not matter in their experiment, while Riesenhuber et al.'s (2004) results show that equal baselines between these two conditions at upright orientation did not matter either. These two studies simply failed to replicate an otherwise widely demonstrated phenomenon.

6. The interaction between featural and configural manipulations

There may be many reasons why these two studies failed to replicate a basic effect, such as the size of the spacing change in configural trials, the duration of stimulus presentation and ISI. However, if a behavioral effect is robust, it should not vanish completely with such modifications, unless the participants perform tasks at ceiling or floor, which was not the case in these experiments. Rather, a careful look at these studies indicates that there are other methodological factors that may explain this lack of replication. Most importantly, Riesenhuber et al.'s (2004) featural trials were made of faces differing by the mouth as well as the *whole* eye area, including eyebrows. Thus, as can be seen on one of the stimuli presented (Fig. 2; see also Fig. 1 in Riesenhuber et al., 2004), the faces in these 'featural' trials could be distinguished based on metric distances between features: eye-eyebrow distance could be used as a cue alone to differentiate the faces, just like mouth-nose distance for instance. In other words, so-called 'featural' trials in that study were in fact 'featural + configural trials'. Given this, it is not surprising that for upright stimuli this condition was performed better than the other conditions. Most importantly, it gave rise to large effects of inversion since local configural variations such as eye-eyebrow distance or mouth-nose distance are strongly affected by inversion (e.g., Leder & Bruce, 2000, experiment 5).

Researchers in the field have noted for long that configural and featural manipulations applied to face stimuli are not independent, since changing the shape of local features necessarily modifies the distances between features (e.g., Rhodes et al., 1993). Yet, this effect can be minimized either by carefully selecting the face parts to swap between trials (i.e., not the whole superior part of the face), or by using surface changes (eye/mouth brightness, texture, color...) for the featural condition, as in many studies (e.g., Barton et al., 2001; Freire et al., 2000; Leder & Bruce, 2000; Rhodes et al., 2007; Searcy & Bartlett, 1996). For instance, Rhodes et al. (2007), made featural changes by simultaneously altering eye and lip brightness and making the end of the nose more or less bulbous. This latter modification of feature shape does not change its distance from the eyes and mouth. When local shape changes also affect distances, inversion costs in performance are intermediate for this condition, in between configural manipulations (larger inversion costs) and local color changes, the latter type of trials being unaffected by inversion (Leder & Carbon, 2006). Thus, unfortunately, Riesenhuber et al.'s (2004) non-replication of previous data, rather than being accounted for by a better control of observers' expectations (randomized conditions) appears to be due to 'featural' manipulations of stimuli that were not done properly: they included major changes in metric distances between features as well (Fig. 2).

A final note on this stimulus issue is that using variations in color or brightness for featural changes cannot simply be dismissed as invalid tests because surface discrimination tasks would be '*primarily mediated by lower level processes*' (Yovel & Kanwisher, 2004, p. 895). Indeed, human faces vary according to both local shape and surface variations, as well as metric distances between features, all of which are potential diagnostic cues for individual face perception. Diagnostic local cues include color, which is helpful to differentiate and categorize face stimuli (e.g., Hill, Bruce, & Akamatsu, 1995; Lee & Perrett, 1997), and is potentially processed by high-level face processing mechanisms, just like local variations in shape. In short, I believe that it is important to specify if the features of the faces are modified according to shape (generally not orientation-invariant) or texture/color (generally orientation-invariant) cues in any paradigm given that they may involve distinct processes. However, the latter kinds of transformations cannot be simply dismissed as being of lower-level, and they have the advantage of leaving the metric distances between features unaffected, contrary to local shape transformations.[2]

7. The importance of considering correct response times (RTs)

There were other limitations in Riesenhuber et al. (2004)' study. Most importantly, the correct response times (RTs) were not reported. In fairness, very few of the studies comparing inversion effects for configural and featural conditions report correct RTs. However, this may not be strictly needed in these studies, precisely since they usually report much stronger (or exclusive) effects of inversion for configural trials in accuracy (e.g., Freire et al., 2000; Le

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[2] In this context, it is interesting to note that when pigmentation and shape information for individuality are manipulated separately over the whole face, both kinds of cues are equally affected by inversion (Russell et al., 2007).

Grand et al., 2001; Leder & Bruce, 2000; Leder & Carbon, 2006). Several studies show inversion costs larger for metric distances than features *both* in accuracy and RTs (Barton et al., 2001, 2003; Goffaux & Rossion, 2007), whereas some studies reporting both variables simply show this effect in performance (e.g., Mondloch et al., 2002; Rhodes et al., 2007). However, when differences in accuracy are *not* found, as in Riesenhuber et al. (2004), considering RTs may become critical: for inverted faces, participants may take much longer to achieve the same level of performance for configural trials than featural trials. Unfortunately, response times were not reported either in Yovel and Kanwisher's (2004) experiments, preventing to assess speed accuracy trade-offs, in or simple effects of inversion larger for configural trials in that study as well. In fact, the absence of reported RTs even prevented to assess whether featural and configural conditions were, as claimed by the authors, of equal difficulty.

8. Disentangling horizontal and vertical metric distances between features

In attempting to understand why Riesenhuber et al. (2004) and Yovel and Kanwisher (2004) did not find even a hint of a larger inversion effect for configural manipulations, we noted an interesting aspect of their study: in half of the configural trials in Yovel and Kanwisher's (2004) study the difference between faces concerned the interocular distance, a manipulation in the *horizontal* direction, while in the other half the difference concerned the mouth-nose distance, a *vertical* manipulation. These two types of trials were mixed in the analyses. In Riesenhuber et al. (2004), they were mixed on the stimuli, as in most studies. However, several studies by Barton, Keenan, and Bass (2001) and Barton, Zhao, and Keenan (2003) dissociated these trials and reported larger inversion effects for vertical displacement of the mouth than for horizontal displacement of the eyes. Together with Valérie Goffaux, we reasoned that this difference might be partly due to the displacement direction (vertical vs. horizontal) rather than the face region under study (eyes *vs.* mouth). To test this hypothesis, we distinguished two types of configural conditions: those for which the metric variations were made horizontally (interocular distance) and those for which the metric variations were made in the vertical direction (eyes height) (Fig. 3; Goffaux & Rossion, 2007). We observed a dramatic performance decline for discriminating inverted faces in the vertical–configural condition, whereas, as also shown by others (Malcom, Leung, & Barton, 2005), an equally moderate impairment was found in the featural and the horizontal–configural conditions (Goffaux & Rossion, 2007). These effects were observed both in performance and correct RTs (Fig. 3) and were recently replicated across several bands of spatial frequencies (Goffaux, in press). They were observed irrespective of the randomization of conditions and with equal performance for the different conditions at upright orientation, again showing that these latter factors are not critical to obtain qualitative effects of face inversion. Thus, these results provide further evidence that inversion dramatically disrupts the

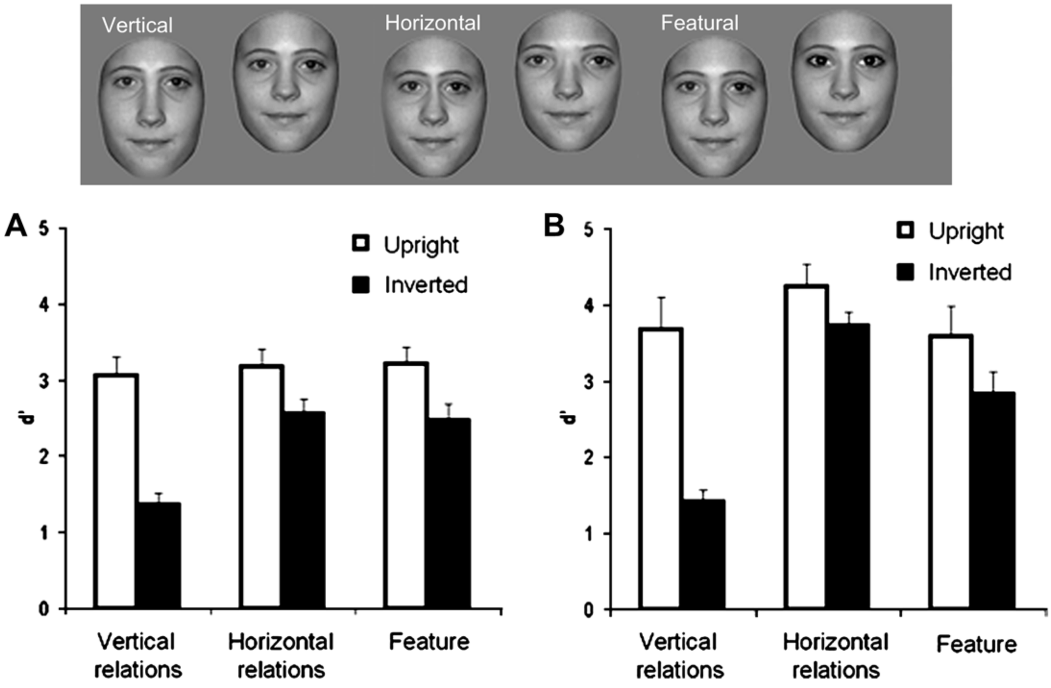

Fig. 3. Results obtained by Goffaux and Rossion (2007) in a delayed matching task of individual faces presented upright and inverted. Inversion costs were significant for all kinds of manipulations, but were much larger when faces differed according to vertical relations (eyes height) than for featural differences or interocular distance (horizontal relations). These results were observed while the performance for upright conditions was equal across conditions, and did not differ for trials presented in block (A) or randomized (B).

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ability to extract distances between facial features, particularly vertical distances, supporting the view that inversion *qualitatively* changes face perception by rendering some of these cues available for upright faces particularly difficult to perceive. Interestingly, the larger decrement of performance for vertical distances between features was also found when faces were tilted in the horizontal plane (90°) indicating that these observations were not due to purely geometric aspects, but to the dominant vertical organization of features in a face stimulus (Goffaux & Rossion, 2007).

Since the vertical and horizontal manipulations of distances were mixed in Riesenhuber et al. (2004) as well as in Yovel and Kanwisher (2004), these studies should still have found larger costs of inversion for the configural trial manipulations than featural conditions if variables such as correct RTs were considered. Most importantly, these observations (Goffaux & Rossion, 2007; Malcom et al., 2005) indicate that before concluding that inversion would not affect more the processing of configural than featural information (Riesenhuber et al., 2004; Yovel & Kanwisher, 2004), one needs to take into account stimulus manipulations that are directly related to the nature of our face processing system (i.e., horizontal/vertical directions of distances between features), and are far more important than tangential factors such as blocked *vs.* randomization of trials or equal performance at upright orientation.

In summary, the bulk of the evidence indicates that following inversion of a face stimulus, both the perceptions of configural information of featural information are impaired, but the former is generally more affected. In the final section of this paper, I will attempt to provide an account of this larger effect of inversion for configural trials. Before that, in the next section, I will address the limitations of the study of Sekuler et al. (2004), which offered a different type of challenge to this qualitative view of face inversion.

9. The diagnosticity of the eye regions during impoverished face stimulation: against a qualitative view of face inversion?

> "*I reasoned that, if I were to truly discover what constituted a facial recognition feature, I must make no assumptions whatever when dividing up a face with a mask... some preliminary experiments quickly established that very few apertures would be required to achieve reliable recognition... looking at the overall result, notice the very high proportion of correct responses across the eyes/eyebrows...* (Haig, 1986b)".

Sekuler et al. (2004) designed an experiment in which they sought to identify the nature of the cues used by human observers when matching upright *vs.* inverted faces. During a block of trials, participants were presented with a 2-alternative forced choice task in which a first face stimulus – the target – was presented for 1 s, followed by a pair of stimuli containing the target and a distractor. In each trial, white Gaussian noise was added to the first face stimulus, revealing only a small amount of information that the participant had to encode to take a decision on the following pair of faces. The pair of stimuli that followed was presented in high contrast, without noise. Response accuracy was maintained at about 71% throughout the experiment by adjusting stimulus contrast of the first stimulus with a staircase procedure. For each face stimulus, a classification image was computed by adding all the noise fields – during thousands of trials – leading to the subject's choice of that stimulus and subtracting the noise fields that are associated with the choice of the other stimulus. In the end, the classification image revealed the areas of the face stimulus where the noise affects the decision (face A or face B). This way, if the noise was located on an area of the face that is highly diagnostic to discriminate between faces A and B (i.e., the eyes), it would always lead to strong response biases.

The main result of that experiment was that, as indicated by classification images, participants relied largely on a restricted area to discriminate the two faces of a pair: the eyes and eyebrows. This was found whether faces were presented upright or inverted. As noted by the authors, this is not surprising because the eyes and eyebrows were the regions of the face stimuli used in the experiment that differed most from one another. However, and importantly, even if observers used as much information from this area of the face for upright and inverted orientations, they required much more contrast in the stimulus (i.e., information surviving the noise) to perform at the same level for inverted faces than upright faces. In addition, the correlation between their classification images and an ideal observer's classification images (i.e., the most discriminative pixels in the images) was lower for inverted than upright faces.

The conclusion of the authors is that human observers rely on the same cues for discriminating upright or inverted faces, even though these cues are used most efficiently for upright faces. Up to this point, I can agree with Sekuler et al.'s (2004) conclusions. As a matter of fact, eye movement recordings have also shown that the same features, mostly the eyes, can be fixated during long duration encoding and recognition of faces at upright and inverted orientations (Henderson, Falk, Minut, Dyer, & Mahadevan, 2001; Williams & Henderson, 2007), despite the observers performing better with upright faces.[3] As Sekuler et al. (2004) acknowledge, it is not surprising that the participants used the eyes and eyebrows for both upright and inverted faces in their experiment. This is particularly true considering that only two faces are presented during thousands of trials and they differ maximally on the eyebrows

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[3] This does not mean that eye movements are necessarily identical for upright and inverted faces (e.g., Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006). Yet, location of gaze *can* remain identical despite a loss of holistic face perception following inversion (Henderson et al., 2001; Williams & Henderson, 2007) or misalignment of the two face parts as in the composite face effect (de Heering, Rossion, Turati, & Simion, in press).

(pair 1) or the eyes (pair 2). Moreover, contrary to other areas of the face such as the mouth, the difference at this location is of a very high contrast, suggesting that these are the only regions that survive the amount of noise used to maintain performance at 71%. In doing the discrimination task, the observers rapidly know that these localized areas are the most (or only) diagnostic locations to extract information, irrespective of orientation.

However, Sekuler et al. (2004) take this observation as an evidence against the view that the inversion effect is related to a loss of holistic face perception, or to a detrimental effect on the perception of configural cues. That is, they claim that inversion does not affect face processing qualitatively but simply quantitatively. Here, I disagree with these authors. In drawing this conclusion, it seems to me that they ignore solid empirical evidence in favor of such a qualitative account from experimental work, as discussed above. Moreover, they over-interpret their observations. Let me try to clarify this latter point.

To start, it is interesting to ask the following question: what kind of result in this experiment could have led the authors to conclude that there *are* indeed qualitative differences between the processing of upright and inverted faces? Presumably, if classification images revealed *different* areas of the faces for upright and inverted faces (e.g., the eyes for upright faces, the mouth for inverted faces). However, this is not a prediction that necessarily follows from the hypothesis that inversion affects mainly holistic face perception and/or the processing of configural cues. What the qualitative view predicts is that for upright faces, but not for inverted faces, processing a given facial feature is influenced by the other features' position and identity, and the perception of metric distances between features is most dramatically impaired. It is unclear how these predictions could be refuted from the findings of Sekuler et al. (2004).

Presumably, another result that could have been interpreted by the authors in favor of the qualitative view would have been the presence of *multiple* features for one condition *vs.* only local features for the other condition. For instance, if relations between features are more important for upright faces, one may reason that multiple features might have been present in the response classification images at upright orientation, with only local features observed for inverted faces. However, alternatively, the presence of multiple features may reveal an analytic (featural) strategy and may have been observed for inverted faces but not for upright faces. This illustrates a major problem with the experiment of Sekuler et al. (2004): there were no predictions of an outcome that would have favored a qualitative view of face inversion. The authors reported roughly identical locations for diagnostic information in discriminating upright and inverted faces, and took this result against a qualitative view of face inversion, but the reason why the qualitative view would be incompatible with these results is unclear.

Sekuler et al. (2004) also showed that their participants performed slightly more efficiently than what could be predicted from their classification images, indicating that they used information that was not revealed in the classification images built from the linear association between each pixel's contrast and the observer's responses. However, the contribution of these non-linearities was of equal amount for upright and inverted faces, suggesting that the information not captured by classification images was also identical for upright and inverted faces. Unfortunately, this analysis is irrelevant to the question of whether features relations (interdependence of features, or metric distances) contribute to the differential performance for upright and inverted faces. Rather, a non-linearity effect that could be potentially relevant to this question would be an analysis of the *conjunctions* emerging between face features during a response classification experiment based on categorization performance (i.e., when the amount of Gaussian noise is not too high, such that several features are revealed simultaneously). Yet, even when this kind of analysis is performed on response classification images (e.g., Schyns, Bonnar, & Gosselin, 2002), it cannot determine whether the contribution of features in a given conjunction is additive or interactive, or if the observer relies on the distances between features.

In the experiment of Sekuler et al. (2004), the participants did not have many stimulus features presented simultaneously (i.e., most of the face was covered by noise), and they focused on the area where the most diagnostic local features (around the eyes and eyebrows) were located to perform the task. This is in fact quite trivial and expected, especially if only two pairs of faces upright and inverted were presented during thousands of trials. However, and critically, observers were less efficient for inverted faces. Why is this? After all, since the observers are presented always with the same two faces, differing by localized information, they should perhaps be equally efficient for upright and inverted faces. To understand this effect, it should be first reminded that inversion does not affect only the processing of configural cues, but it also affects the perception of featural cues, albeit to a lesser extent (e.g., Goffaux & Rossion, 2007; Rhodes et al., 2007). Hence, when the stimulus is presented upside-down, the local shape of the eyes may be less well perceived to compare to an internal representation of the face. This, in itself, may explain the reduced efficiency found for inverted faces in Sekuler et al.'s (2004) study. Second, as mentioned above, when the stimulus is presented upside-down, local configural information such as the eye-eyebrow distance (which was highly diagnostic in the face stimuli used in the experiment, see Fig. 1 of Sekuler et al., 2004) or the interocular distance, is less well encoded (Leder & Carbon, 2005; Leder et al., 2001). That is, the 'local configural' information is processed less efficiently on inverted faces. How could this be revealed in the different classification images for upright and inverted faces, which only show localized patches of pixels? In other words, what is the evidence from Sekuler et al.'s (2004) data that the distance between the two eyes, or between the eyes and eyebrows, were not perceived better for upright faces than inverted faces in their experiment and contributed to the differential performance? As a matter of fact, the diagnostic pixels were not located on the features, but around or in between the features. That is, the eye-eyebrows distance (face pair 1) and the height of the eyes in the face (pair 2) were the highest diagnostic regions in the pairs of stimuli to discriminate in that study. Moreover, in the classification images, whereas borders were sharply defined for the eyes and the distances between diagnostic noise fields (on the eyes and eyebrows) for the upright faces, they were not for inverted faces (Fig. 2 in Sekuler et al., 2004). This suggests indeed that subjects could not appreciate precisely the relational information for inverted faces that was left available by the noise procedure.

To sum up this point, while Sekuler et al. (2004) considered that using roughly the same area around the eyes for upright and inverted faces is evidence against a qualitative view of face inversion, this result is in fact entirely compatible with this latter view. In particular, participants may have been able to extract local configural information (eye–eyebrows distance, height of the eyes in the face, interocular distance) better for upright faces than inverted faces. Clarifying this issue would require manipulating the discriminability of the faces in terms of local and configural information separately. Moreover, the higher efficiency of observers for identical localized pixels on an upright as compared to an inverted face image is perfectly compatible with a holistic account of face perception. Indeed, holistic processing of the face does not require the whole face stimulus to be presented: the simultaneous extraction of information from multiple elements of the face can be applied to a small area, and to a partially revealed or a degraded face stimulus. Providing that observers apply such a holistic process to the stimulus, they will be more efficient at processing upright than inverted faces, even if the face stimulus is degraded or if only limited areas of the face (e.g., the eyes) are revealed (Boutsen & Humphreys, 2003; Leder & Carbon, 2005; Leder et al., 2001; Rakover & Teucher, 1997). Thus, even though the kind of psychophysical experiment performed by Sekuler and colleagues (2004; or as in 'Bubbles', Gosselin and Schyns 2001) with very few degraded stimuli that are repeated extensively certainly encourages a local and analytical strategy, it may not be insensitive to qualitative changes of face perception with inversion. However, the findings cannot be unequivocally attributed to holistic or analytic face perception, or to a differential reliance on featural and configural cues.

10. Featuralism *vs.* Holism in face processing: a revisited debate

Today a large amount of research is devoted to understanding the nature of our tremendous face processing abilities, using the most sophisticated tools of psychophysics and cognitive neuroscience. This interest in face processing started to expand dramatically in the seventies (Ellis, 1986). The major part of the research carried out until the mid-eighties in the field was devoted to clarify the facial features that were important for various face processing tasks. Most experiments carried out early on to measure the relative importance of different internal facial features for individual face recognition revealed the dominance of the eye/eyebrow combination, followed by the mouth and then the nose (e.g., Davies, Ellis, & Shepherd, 1977; Haig, 1986a; Sheperd, Davies, & Ellis, 1981; Walker-Smith, Gale, & Findlay, 1977). These studies were based on simple methods of masking or isolating facial features to address their respective contribution in various face processing tasks. The peak of this approach can be identified with the remarkable work of Haig (1985, 1986b), who introduced a simple computational method that he called the "distributed aperture technique" to define which features of a face were optimally used for recognition, in an unbiased way. Briefly, Haig (1985) equally divided four face pictures into square grids of 8 × 8 apertures that were revealed or masked randomly. The number of apertures revealing facial features was also randomly selected, and observers were asked to recognize the faces revealed through a subset of apertures on each trial. Classification images were obtained by representing each aperture as a square having a brightness that was a linear function of the percentage correct at that aperture address. The results showed that very few apertures were needed to achieve a good performance. Most importantly, the method identified a very high proportion of correct responses across the eyes/eyebrows and across the hairline at the forehead (which varied a lot across faces in that experiment), with fewer correct responses on the mouth and lower chin area. This remarkable invention, especially considering the weak computational power of computers available at the time, was later refined to a higher resolution (Haig, 1986b) and tested with thousands of trials in a few observers. It led to the same observation of a large dominance of the eyes and eyebrows among internal features for face recognition.

However, it was soon realized that this part-based approach performed on a few stimuli, revealing local features during thousands of trials, could only lead to the identification of localized features as diagnostic for face processing tasks. That is, it was missing a fundamental aspect of face perception (Endo, 1986; Valentine, 1988): that facial features are heavily interdependent. Since then, researchers in this field have largely shifted their interest to the investigation of the *integrative* aspects of face perception, with various paradigms (e.g., Bartlett & Searcy, 1993; Cabeza & Kato, 2000; Farah et al., 1998; Hole, 1994; Hosie, Ellis, & Haig, 1988; Leder & Bruce, 1998; Leder & Carbon, 2005; Malcom et al., 2005; Rhodes, 1988; Rhodes et al., 1993; Sergent, 1984; Suzuki & Cavanagh, 1995; Tanaka & Farah, 1993; Tanaka & Sengco, 1997; Young et al., 1987).

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The previous section has illustrated the recent revival of similar methods as the distributed aperture technique developed by Haig (1985, 1986b) to identify diagnostic cues for face perception, with more computationally powerful and sophisticated tools available (e.g., "reverse correlation in noise", Sekuler et al., 2004; "Bubbles", Gosselin & Schyns, 2001). These methods are based on the same principles of confronting a few observers during thousands of trials with visual information randomly sampled (or masked by noise) on the stimulus on each trial. The stimulus samples leading to optimal performance – maintained at a certain level in the experiment – reveal the face cues that are relevant to resolve a given task. These studies have by and large replicated Haig's original observations of the dominance of the eyes/eyebrows region during face identification tasks (Gosselin & Schyns, 2001; Schyns et al., 2002; Sekuler et al., 2004). Unfortunately, the experiments of Haig (1985, 1986b) were not performed with inverted faces, but it is likely that with the same stimuli they would have revealed the same observation as in the experiment of Sekuler et al. (2004): the eyes/eyebrows were used predominantly, irrespective of orientation.

These sophisticated methods developed and used by psychophysicists can be very useful to reveal diagnostic cues for face categorization (e.g., Smith, Cottrell, Gosselin, & Schyns, 2005). More generally, it is interesting to note that their revival parallels the return of a featuralist approach in face perception, coincident with a toning down of the integrative views of face perception in more conventional studies that we discussed earlier (Riesenhuber et al., 2004; Yovel & Kanwisher, 2004).

However, the point that I want to make here is that it is important that one remembers the history of the field in order to avoid over-interpreting the outcome of such response classification experiments driven by a featuralist approach: their results should not be taken as being against the fundamental integrative nature of face perception. As indicated in the section above, I do not claim that these methods are inherently insensitive to the integrative aspects of face perception. However, they are currently implemented and used with very few stimuli repeated during a large number of trials, and local diagnostic information that can be easily identified (see also Yovel & Kanwisher, 2004, who used a single face stimulus in their whole experiment). Moreover, the face stimulus is covered by noise or only revealed in fragments, such that a whole face is rarely or never presented (or only in a few trials at a very low resolution, Gosselin & Schyns, 2001). Consequently, there is a risk of minimizing the integrative aspect of face processing: holistic face perception and the extraction of metric distances between features, which require several elements of a face to be presented concurrently (or with a short delay, Anaki, Boyd, & Moscovitch, 2007; Singer & Sheinberg, 2006).

Another issue to consider is that, even when revealing localized areas of the face as being diagnostic for individual face discrimination or identification, as in the study of Sekuler et al. (2004); see also Gosselin & Schyns, 2001, the outcome of such experiments can be easily mistaken for evidence of a strict featural and sequential analysis of faces. One major reason is that these computational methods have been developed to deal with identifiable parts of the face (i.e., pixels), but not to deal with distances between parts ('configural information'). Most importantly, since holistic face perception is a process, it cannot be manipulated physically on the stimulus, but it requires an experiment in which explicit behavioral measures of the interdependence between features are collected (as in the face composite effect for instance). Such behavioral experiments are more difficult to conceptualize, and their results are, in principle, more open to interpretation. Hence, while psychophysicists and low-level visual scientists rather approach the problem of understanding face perception from a computational and feature-oriented point of view, the holistic approach is more popular among those who adhere to less formal theories (Uttal, 2001; although see Biederman & Kalocsai, 1997; Ingvalson & Wenger, 2005). Despite this lack of formalization, the integrative approach of face perception, with the diagnosticity of information manipulated most often on whole face stimuli, has provided solid evidence both for the integrated nature of face perception and for its spectacular disruption by picture-plane inversion, as summarized in Sections 1 and 2. Therefore, even though this approach is theoretically underdeveloped and may have generated a certain degree of confusion in the literature, psychophysicists and computational scientists would do well to consider both the empirical evidence and the historical development of the field of face processing to avoid throwing the baby (facial feature integration) out with the bath water (the theoretical confusion in this field).

11. The face inversion effect as a defect in holistic perception

> "*They seemed to use two alternative strategies, either searching for some distinguishing feature or attempting to get a general impression of the whole picture. The first tended to be used for most of the materials; the second was used mostly for faces, with subjects trying to remember some personal impression made by the face. None of the subjects, however, reported being able to use the second strategy when looking at the inverted face* (Yin, 1969)".

Having been recently concerned by the rather strong and negative conclusions about the relation between face inversion and feature integration reached by a few behavioral studies (Riesenhuber et al., 2004; Sekuler et al., 2004; Yovel & Kanwisher, 2004) and the confusion they generated in the field, I have presented a detailed criticism of these studies, arguing that they concluded against the qualitative view of face inversion based on rather limited and questionable evidence. However, in a more constructive perspective, I would like to take advantage of the elements that have been reviewed here to offer my own view in

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a few paragraphs on the inversion effect and its relationship to holistic/configural face processing. In a nutshell, the point that I would like to make here is the following: the detrimental effect of inversion on what is called configural information in the literature (i.e., metric distances between features) is merely a *by-product* of the disruption of holistic face perception with inversion.

In order to make this point, let me come back to the definition proposed in Section 1, in line with earlier accounts (e.g., Galton, 1883; Ingvalson & Wenger, 2005; Tanaka & Farah, 1993): holistic face perception refers to *the simultaneous integration of the multiple features of a face into a single perceptual representation*. The empirical marker of this phenomenon, as we have seen, is the *interdependence* of facial features. If the stimulus is inverted, this interdependence disappears or drops down, indicating a loss of holistic face perception. The observer thus has to process the face stimulus element by element. Moreover, what I would call the face *perceptual field* shrinks with inversion: the observer cannot focus on one feature of the inverted face and yet be influenced by another, distant, feature of this face.

When the inverted visual stimulus is well segmented from the background and can be detected as a face through its local elements, its individuality will not be perceived readily: it will have to be derived by a detailed analysis, local element by local element. In this context of analytical processing and reduction of the face perceptual field with inversion, if two individual faces differ by local elements (i.e., the shape of the mouth), the effect of face inversion on the performance will be substantial. This will be especially true when there is an uncertainty about the identity and localization of the diagnostic feature on the face. However, even in this situation of uncertainty, it is easy to understand that a feature-by-feature processing associated with a reduction of the perceptual field will usually affect most dramatically the perception of metric distances between features. This is simply because the perception of a metric distance requires to consider *two* elements at least, or more, across a larger space of the face. Hence, a defect in holistic perception should logically lead to a larger impairment at perceiving distances between features than local features.

According to this view, even if ‘holistic face perception’ and ‘configural information’ can be distinguished at the conceptual level (e.g., Maurer et al., 2002), from an empirical point of view it does not make sense to claim that inversion affects both holistic face perception and the balance between configural and featural information. The larger effect of face inversion on configural than featural information appears to be merely a consequence of the loss of holistic face perception. This proposal has the advantage of being more parsimonious, and it is in agreement with a qualitative view of face inversion. However, what is the evidence from the current literature that it may be correct, and how could it be tested further? Here are a few suggestions.

11.1. Vertical vs. horizontal relations and holistic face perception

First, we have seen that even when the same feature (the eyes) is concerned, inversion affects more the perception of manipulations of the position of features in the vertical direction than in the horizontal direction (Goffaux, in press; Goffaux & Rossion, 2007). One interpretation of this observation is that a modification of the eyes of a face stimulus in the vertical direction affects more than two features across the whole face, and thus taxes holistic face processes more importantly than a modification of the interocular distance for instance, which can be assessed more locally (Goffaux & Rossion, 2007). This hypothesis was tested recently by Sekunova and Barton (2007), who showed a larger effect of inversion for vertical distances only when the eyes and eyebrows of the faces were moved together. If the position of the eyes is modified in the vertical direction but the eyebrows are not moved, observers can use local configural information (i.e., eye–eyebrow distance) to resolve the task and show a reduced inversion effect. As the authors put it, this result suggests that the larger effect of inversion for vertical–configural relations in the study of Goffaux and Rossion (2007) is due to an inefficient sampling of the whole face structure for inverted faces, i.e., a defect in holistic face perception. The observation that the largest effects of inversion are found when the mouth is manipulated vertically (Barton et al., 2001; Malcom et al., 2005) is also consistent with a holistic interpretation. Indeed, if the eyes of the face stimulus are fixated for both upright and inverted faces (Henderson et al., 2001; Williams & Henderson, in press) but if our perceptual system is unable to perceive the whole of an inverted face, modifications applied further away (the mouth) from the fixation point will be extremely hard to detect.

An interesting prediction of this holistic account of the configural information defect with inversion is the following: increasing the stimulus size should lead to an increase in the disproportionate effect of face inversion on individual faces for configural manipulations relative to featural changes (as long as the stimulus is not *too* large, preventing to see it as a whole). This is a natural prediction which follows from the fact that inversion leads to a reduction of the face perceptual field.

11.2. Configural information and holistic face perception across multiple orientations

As indicated earlier, a number of studies have tested holistic face perception across multiple angles of rotation of the face rather than just two orientations. Most of these studies aimed at isolating holistic perception by asking viewers to judge the grotesqueness of “Thatcherized faces” (e.g., Murray et al., 2000; Sjoberg & Windes, 1992; Stürzel & Spillmann, 2000), an estimation of the degree of integration between facial features. These studies reported deviations from linearity at orientations around 90° (e.g., Murray et al., 2000; Sjoberg & Windes, 1992; Stürzel & Spillmann, 2000). Other experiments tested the effect of orientation on holistic face perception using tasks such as the categorical perception of faces in noise (McKone, Martini, & Nakayama, 2001), the perception of a "Mooney" face stimulus (McKone, 2004), the matching of Thatcherized faces (Edmonds & Lewis, 2007). In general, these studies reported departure from linearity around the horizontal orientation of the face, but also described significant differences among adjacent angles of rotation (e.g., between 90 and 120°; see also Jacques & Rossion, 2007). In a recent study, we showed that the face composite illusion described in Fig. 1 remains equally strong until at least 60° rotation of the stimulus, and drops down abruptly at 90° orientation (Rossion & Boremanse, in press; see Fig. 4). Interestingly, there is an evidence that this tuning function is similar for the processing of configural information, with a massive drop of performance and RT increase between 60° and 90° during individual face discrimination (Schwaninger & Mast, 2005). In other words, the function relating performance at discrimination and angle of rotation of the face appears to be non-linear, and similar for measures of holistic processing and for the processing of configural information. This observation strongly suggests a commonality of mechanisms (see also Rossion & Boremanse, in press for a discussion of this point).

11.3. Acquired prosopagnosia

Acquired prosopagnosia is classically defined as the inability to recognize faces following brain-damage, which cannot be attributed to intellectual or low-level visual defects (Bodamer, 1947). While, it is widely acknowledged that there is a certain amount of variability among the functional impairments of prosopagnosic patients (e.g., Sergent & Signoret, 1992), recent investigations with several cases by Barton and colleagues have shown that acquired prosopagnosics are severely impaired at discriminating faces differing by metric distances between features (Barton, Press, Keenan, & O'Connor, 2002). This prompted the authors to associate acquired prosopagnosia with a particular defect of perceiving configural information. I believe that the most parsimonious account of this last observation is that of a deficit in holistic face perception, causing in turn the increased difficulty at extracting configural relations. Several observations support this view. First, there is a wide evidence in the literature that brain-damaged prosopagnosic patients suffer from an inability to perceive faces holistically (e.g., Barton et al., 2003; Boutsen & Humphreys, 2002; Levine & Calvanio, 1989; Saumier, Arguin, & Lassonde, 2001; Sergent & Signoret, 1992). In line with this, performance of prosopagnosic patients is often less or not at all affected by face inversion (e.g., Boutsen & Humphreys, 2002; Marotta, McKeef, & Behrmann, 2002). Second, as revealed both by accuracy and correct RTs, the deficit of prosopagnosic patients in the study of Barton, Press, Keenan, and O'Connor (2002) is not selective for processing configural relations, but it is relatively larger than for featural manipulations. This is similar to what is observed for face inversion in normal observers, and what is expected if holistic processing impairment affects more the perception of configural than

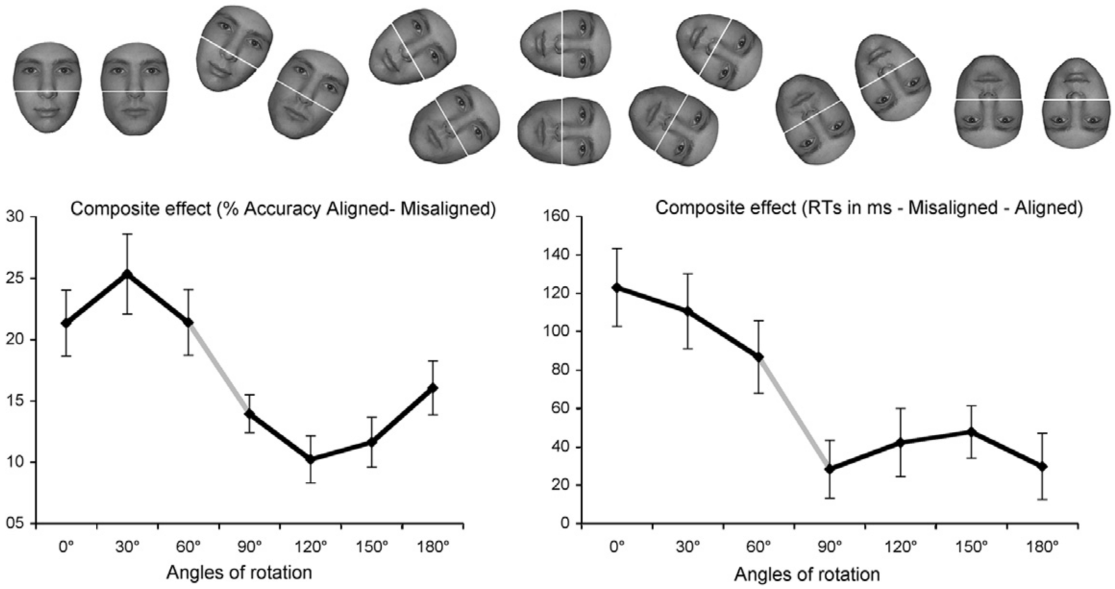

Fig. 4. Adapted from Rossion and Boremanse (in press). When discriminating between two identical top parts of faces presented sequentially, observers are better if they are misaligned with their different bottom parts than when they are aligned. This face composite illusion remains equally strong until at least 60° rotation of the stimulus, and drops down abruptly at 90° orientation. While this observation can be taken as further evidence that rotation of the stimulus affects face perception qualitatively, it is also worth noting the similar tuning function found for processing of configural (i.e., metric) information in individual face discrimination tasks (Schwaninger & Mast, 2005). This suggests that the dramatic disruption of the perception of configural cues with picture-plane rotation is related to the impairment in holistic face perception.

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featural cues. Third, as noted by the authors of that study (Barton, Press, Keenan, & O'Connor, 2002), the prosopagnosic patients' deficit is highly dependent on uncertainty about the location of the diagnostic configural cues, and the deficit is especially manifest when "attention" must be distributed across numerous facial elements (see also Joubert et al., 2003). This is highly indicative of a primary deficit at integrating simultaneously the multiple features of a face stimulus into a single perceptual representation (holistic face perception). In this situation, the prosopagnosic patient has to focus on each and every feature in turn, as separate elements, which makes it particularly difficult to perceive distances between features. Recordings of eye gaze fixations during face identification in acquired prosopagnosia reinforce this view (Orban de Xivry, Ramon, Lefèvre, & Rossion, in press). In summary, despite the variability of functional impairments in prosopagnosia (Sergent & Signoret, 1992), a central aspect of this neurological condition appears to be the loss of holistic face perception. This defect in holistic face perception may lead to both a more severe difficulty at perceiving configural than featural information (Barton, Press, Keenan, & O'Connor, 2002), and an impairment at processing efficiently an area of the face which contains multiple elements of the face, the eyes and eyebrows (Bukach, Bub, Gauthier, & Tarr, 2006; Caldara et al., 2005; Orban de Xivry et al., in press).

12. Conclusions

Altogether, the three sources of evidence briefly reviewed above reinforce the view that the increased difficulties at perceiving configural information on faces following stimulus inversion are merely a *by-product* of an impairment of holistic face perception. It follows that holistic face perception and the extraction of configural information from faces can be dissociated only conceptually (e.g., Maurer et al., 2002), but are inherently confounded empirically. It does not make much sense to suggest that inversion affects both: inversion affects primarily holistic face perception, and the consequence of this is that certain kinds of cues (metric distances) will be more affected than others (local feature changes). Testing how participants in an experiment deal with configural cues relative to featural cues manipulated on faces is in fact a very fine test of their ability to perceive these faces holistically.[4]

The detrimental effect of the perception of configural cues following inversion is a real phenomenon, as we have seen in the main part of this paper, but it should not be taken as evidence that these cues are processed by a specific system. Configural cues are just more dependent on a process that is fundamental for dealing with individual faces. Importantly, this theoretical position should not be misunderstood and associated with claims that holistic perception would be all that matters for processing faces and that local features would not be important, or that the perception of isolated features is not affected by inversion. Faces are extremely rich and complex stimuli, whose perceptual mechanisms are only slowly and gradually revealed and better understood by taking into account both the information measurable on the stimulus, and the human brain as an active perceiver. Fundamentally different paradigms and methods are necessary to tackle this issue of understanding the nature of upright and inverted face perception, and it is unlikely that any simple and strong theoretical position on such a complex issue will prove correct.

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References

Anaki, D., Boyd, J., & Moscovitch, M. (2007). Temporal integration in face perception: Evidence of configural processing of temporally separated face parts. *Journal of Experimental Psychology: Human Perception and Performance, 33*, 1–19.

Bartlett, J. C., & Searcy, J. (1993). Inversion and configuration of faces. *Cognitive Psychology, 25*, 281–316.

Barton, J. J., Keenan, J. P., & Bass, T. (2001). Discrimination of spatial relations and features in faces: Effects of inversion and viewing duration. *British Journal of Psychology, 92*, 527–549.

Barton, J. J., Press, D. Z., Keenan, J. P., & O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology, 58*, 71–78.

Barton, J. J., Radcliffe, N., Cherkasova, M. V., Edelman, J., & Intriligator, J. M. (2006). Information processing during face recognition: The effects of familiarity, inversion, and morphing on scanning fixations. *Perception, 35*, 1089–1105.

Barton, J. J., Zhao, J., & Keenan, J. P. (2003). Perception of global facial geometry in the inversion effect and prosopagnosia. *Neuropsychologia, 41*, 1703–1711.

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

Bodamer, J. (1947). Die-Prosop-agnosie. *Archive für Psychiatrie und Nervenkrankheiten, 179*, 6–54 (English translation by Ellis, H. D., & Florence, M. (1990). *Cognitive Neuropsychology, 7*, 81–105).

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

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[4] One domain in which this association may apparently not hold is the development of face processing: while children perceive faces holistically at least at 4 years old or even earlier as shown by the whole-part advantage or face composite effect (e.g., Pellicano & Rhodes, 2003), some studies have shown that children of that age are less efficient than adults at processing subtle changes of configural cues (Mondloch, Geldart, Maurer, & Le Grand, 2003). However, this view is increasingly disputed (e.g., McKone & Boyer, 2004). It may also be that children do not perceive faces as holistically as adults and that testing for the processing of configural cues may simply be a subtler test of holistic face perception than paradigms leading to very strong effects such as the face composite effect.

Boutsen, L., & Humphreys, G. W. (2003). The effect of inversion on the encoding of normal and "Thatcherized" faces. *The Quarterly Journal of Experimental Psychology, 56A*, 955–975.

Bradshaw, J. L., & Wallace, G. (1971). Models for the processing and identification of faces. *Perception and Psychophysics, 9*, 443–448.

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

Bukach, C. M., Bub, D. N., Gauthier, I., & Tarr, M. J. (2006). Perceptual expertise effects are not all or none: Spatially limited perceptual expertise for faces in a case of prosopagnosia. *Journal of Cognitive Neuroscience, 18*, 48–63.

Cabeza, R., & Kato, T. (2000). Features are also important: Contributions of featural and configural processing to face recognition. *Psychological Science, 11*, 419–433.

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*, 1652–1666.

Carbon, C.-C., Grueter, T., Weber, J. E., & Lueschow, A. (2007). Faces as objects of non-expertise: Processing of Thatcherised faces in congenital prosopagnosia. *Perception, 36*, 1635–1645.

Collishaw, S. M., & Hole, G. J. (2000). Featural and configurational processes in the recognition of faces of different familiarity. *Perception, 29*, 893–909.

Davies, G., Ellis, H., & Shepherd, J. (1977). Cue saliency in faces as assessed by the "photofit" technique. *Perception, 6*, 263–269.

de Heering, A., Rossion, B., Turati, C., & Simion, F. (in press). Holistic face processing can be independent of gaze behavior: Evidence from the composite face illusion. *Journal of Neuropsychology*, *2*, 183–195.

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology General, 115*, 107–117.

Edmonds, A. J., & Lewis, M. B. (2007). The effect of rotation on configural encoding in a face-matching task. *Perception, 36*, 446–460.

Ellis, H. D. (1986). Introduction to aspects of face processing: Ten questions in need of answers. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. W. Young (Eds.), *Aspects of face processing* (pp. 3–13). Dordrecht: Martinus Nijhof.

Endo, M. (1986). Perception of upside-down faces: An analysis from the viewpoint of cue saliency. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. W. Young (Eds.), *Aspects of face processing* (pp. 53–60). Dordrecht: Martinus Nijhof.

Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. (1998). What is "special" about face perception? *Psychological Review, 105*, 482–498.

Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception, 29*, 159–170.

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

Goffaux, V. (in press). The horizontal and vertical relations in upright faces are transmitted by different spatial frequency ranges. *Acta Psychologica*, doi:10.1016/j.actpsy.2007.11.005.

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.

Goffaux, V., & Rossion, B. (2007). Face inversion disproportionately impairs the perception of vertical but not horizontal relations between features. *Journal of Experimental Psychology: Human Perception and Performance, 33*, 995–1002.

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

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology, 35*, 96–111.

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

Haig, N. D. (1986a). Exploring recognition with interchanged facial features. *Perception, 15*, 235–247.

Haig, N. D. (1986b). 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: Martinus Nijhof.

Henderson, J. M., Falk, R., Minut, S., Dyer, F. C., & Mahadevan, S. (2001). Gaze control for face learning and recognition in humans and machines. In T. Shipley & P. Kellman (Eds.), *From fragments to objects: Segmentation processes in vision* (pp. 463–481). New York: Elsevier.

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

Hochberg, J., & Galper, R. R. (1967). Recognition of faces: An explanatory study. *Psychological Science, 9*, 619–620.

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

Homa, D., Haver, B., & Schwartz, T. (1976). Perceptibility of schematic face stimuli: Evidence for a perceptual gestalt. *Memory & Cognition, 4*, 176–185.

Hosie, J. A., Ellis, H. D., & Haig, N. D. (1988). The effect of feature displacement on the perception of well-known faces. *Perception, 17*, 461–474.

Ingvalson, E. M., & Wenger, M. J. (2005). A strong test of the dual-mode hypothesis. *Perception and Psychophysics, 67*, 14–35.

Jacques, C., d'Arripe, O., & Rossion, B. (2007). The time course of the face inversion effect during individual face discrimination. *Journal of Vision, 7*(8), 1–9. http://journalofvision.org/7/8/3/, doi:10.1167/7.8.3.

Jacques, C., & Rossion, B. (2007). Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. *NeuroImage, 36*, 863–876.

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.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Early visual experience and face processing. *Nature, 410*, 890.

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

Leder, H., & Bruce, V. (1998). Local and relational aspects of face distinctiveness. *The Quarterly Journal of Experimental Psychology: Section A, 51*, 449–473.

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

Leder, H., Candrian, G., Huber, O., & Bruce, V. (2001). Configural features in the context of upright and inverted faces. *Perception, 30*, 73–83.

Leder, H., & Carbon, C.-C. (2005). When context hinders! Context superiority versus learn-test-compatibilities in face recognition. *The Quarterly Journal of Experimental Psychology: Section A, 58*, 235–250.

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

Lee, K. J., & Perrett, D. I. (1997). Presentation-time measures of the effects of manipulations in color space discrimination of famous faces. *Perception, 26*, 733–752.

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

Malcom, G. L., Leung, C., & Barton, J. (2005). Regional variation in the inversion effect for faces: Differential effects for feature shape, feature configuration and external contour. *Perception, 34*, 1221–1231.

Marotta, J. J., McKeef, T. J., & Behrmann, M. (2002). The effects of rotation and inversion on face processing in prosopagnosia. *Cognitive Neuropsychology, 19*, 31–47.

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

Mazard, A., Schiltz, C., & Rossion, B. (2006). Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex. *Neuropsychologia, 44*, 912–922.

McKone, E. (2004). Isolating the special component of face recognition: Peripheral identification and a Mooney face. *Journal of Experimental Psychology: Memory and Cognition, 30*, 181–197.

McKone, E., & Boyer, B. L. (2004). Sensitivity of 4-year-olds to featural and second-order relational changes in face distinctiveness. *Journal of Experimental Child Psychology, 94*, 134–162.

McKone, E., Martini, P., & Nakayama, K. (2001). Categorical perception of face identity in noise isolates configural processing. *Journal of Experimental Psychology: Human Perception and Performance, 27*, 573–599.

Mermelstein, R., Banks, W., & Prinzmetal, W. (1979). Figural goodness effects in perception and memory. *Perception and Psychophysics, 26*, 472–480.

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

Mondloch, C. J., Geldart, S., Maurer, D., & Le Grand, R. (2003). Developmental changes in face processing skills. *Journal of Experimental Child Psychology, 86*, 67–84.

Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception, 31*, 553–566.

Murray, J. E., Yong, E., & Rhodes, G. (2000). Revisiting the perception of upside-down faces. *Psychological Science, 11*, 492–496.

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

Pellicano, E., & Rhodes, G. (2003). Holistic processing of faces in preschool children and adults. *Psychological Science, 14*, 618–622.

Rakover, S. S., & Teucher, B. (1997). Facial inversion effects: Parts and whole relationship. *Perception and Psychophysics, 59*, 752–761.

Rhodes, G. (1988). Looking at faces – 1st order and 2nd order features as determinants of facial appearance. *Perception, 17*, 43–63.

Rhodes, G., Brake, S., & Atkinson, A. P. (1993). What's lost in inverted faces? *Cognition, 47*, 25–57.

Rhodes, G., Hayward, W. G., & Winkler, C. (2007). Expert face coding: Configural and component coding of own-race and other-race faces. *Psychonomic Bulletin Review, 13*, 499–505.

Riesenhuber, M., Jarudi, I., Gilad, S., & Sinha, P. (2004). Face processing in humans is compatible with a simple shape-based model of vision. *Proceedings in Biological Sciences, 271 Suppl 6*, S448–S450.

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

Rossion, B., & Gauthier, I. (2002). How does the brain process upright and inverted faces? *Behavioral and Cognitive Neuroscience Reviews, 1*, 63–75.

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.

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

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

Schwaninger, A., & Mast, F. W. (2005). The face-inversion effect can be explained by the capacity limitations of an orientation normalization mechanism. *Japanese Psychological Research, 47*, 216–222.

Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding recognition from the use of visual information. *Psychological Science, 13*, 402–409.

Searcy, J. H., & Bartlett, J. C. (1996). Inversion and processing of component and spatial-relational information in faces. *Journal of Experimental Psychology: Human Perception and Performance, 22*, 904–915.

Sekuler, A. B., Gaspar, C. M., Gold, J. M., & Bennett, P. J. (2004). Inversion leads to quantitative, not qualitative, changes in face processing. *Current Biology, 14*, 391–396.

Sekunova, A., & Barton, J. (2007). Long-range and short-range relations in the perception of the vertical position of the eyes in inverted faces. *Journal of Vision, 7*, 511a (Abstract).

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

Sergent, J., & Signoret, J.-L. (1992). Varieties of functional deficits in prosopagnosia. *Cerebral Cortex, 2*, 375–388.

Sheperd, J., Davies, G., & Ellis, H. (1981). Studies of cue saliency. In G. Davies, H. Ellis, & J. Sheperd (Eds.), *Perceiving and remembering faces* (pp. 105–131). London: Academic Press.

Singer, J. M., & Sheinberg, D. L. (2006). Holistic processing unites face parts across time. *Vision Research, 46*, 1838–1847.

Sjoberg, W., & Windes, J. (1992). Recognition times for rotated normal and "Thatcher" faces. *Perceptual & Motor Skills, 75*, 1176–1178.

Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science, 16*, 184–189.

Stürzel, F., & Spillmann, L. (2000). Thatcher illusion: Dependence on angle of rotation. *Perception, 29*, 937–942.

Suzuki, S., & Cavanagh, P. (1995). Facial organization blocks access to low-level features – An object inferiority effect. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 901–913.

Tanaka, J. W., & Farah, M. J. (1991). Second-order relational properties and the inversion effect: Testing a theory of face perception. *Perception and Psychophysics, 50*, 367–372.

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

Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory and Cognition, 25*, 583–592.

Thompson, P. (1980). Margaret Thatcher: A new illusion. *Perception, 9*, 483–484.

Uttal, W. R. (2001). Are reductive (explanatory) theories of face identification possible? Some speculations and some findings. In M. J. Wenger & J. T. Townsend (Eds.). *Computational, geometric, and process perspectives on facial cognition: Contexts and challenges* (pp. 467–501). Mahwah, NJ: Erlbaum.

Valentine, T. (1988). Upside-down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology, 79*, 471–491.

Valentine, T., & Bruce, V. (1988). Mental rotation of faces. *Memory and Cognition, 16*, 556–566.

Walker-Smith, G. J., Gale, A. G., & Findlay, J. M. (1977). Eye-movement strategies in face perception. *Perception, 6*, 313–326.

Wenger, M. J., & Ingvalson, E. M. (2002). A decisional component of holistic encoding. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28*, 872–892.

Wigan, A. L. (1844). *A new view of insanity: The duality of the mind.* London: Longman.

Williams, C.-C., & Henderson, J. M. (2007). The face inversion effect is not a consequence of aberrant eye movements. *Memory and Cognition, 35*, 1977–1985.

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

Young, A. M., Hellawell, D., & Hay, D. C. (1987). Configural information in face perception. *Perception, 10*, 747–759.

Yovel, G., & Kanwisher, N. (2004). Face perception: Domain specific, not process specific. *Neuron, 44*, 889–898.

Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology, 15*, 2256–2262.

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