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The shape of facial features and the spacing among them generate similar inversion effects: A reply to Rossion (2008)

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ABSTRACT

It is often argued that picture-plane face inversion impairs discrimination of the spacing among face features to a greater extent than the identity of the facial features. However, several recent studies have reported similar inversion effects for both types of face manipulations. In a recent review, Rossion (2008) claimed that similar inversion effects for spacing and features are due to methodological and conceptual shortcomings and that data still support the idea that inversion impairs the discrimination of features less than that of the spacing among them. Here I will claim that when facial features differ primarily in shape, the effect of inversion on features is not smaller than the one on spacing. It is when color/contrast information is added to facial features that the inversion effect on features decreases. This obvious observation accounts for the discrepancy in the literature and suggests that the large inversion effect that was found for features that differ in shape is not a methodological artifact. These findings together with other data that are discussed are consistent with the idea that the shape of facial features and the spacing among them are integrated rather than dissociated in the holistic representation of faces.

It is well accepted that faces have a special status among the myriad of object categories we recognize. In particular, it is commonly argued that faces are processed by *holistic* or *configural* processing mechanisms, whereas non-face objects are processed in a part-based manner (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Le Grand, & Mondloch, 2002). Furthermore, these holistic/configural processing mechanisms are specific for upright faces and do not operate on inverted (up-side down) faces (Maurer et al., 2002; Rossion, 2008; Tanaka & Farah, 1993; Yovel, Paller, & Levy, 2005). Because the definitions of the terms *holistic* and *configural* vary across studies, it is important to clearly state up front to what type of process or representation each of them refers. In a recent review, Rossion (2008) defined the term *holistic* as "an integrative perceptual process". The term *configural* was defined as "a manipulation on a stimulus that consists in increasing or decreasing the metric distances between features." Here I will use the same definition used by Rossion (2008) for the term *holistic*. Because the term *configural* has also been used in reference to holistic processing (Maurer et al., 2002), to avoid confusion I will use the term *spacing* to refer to manipulation of the metric distance among facial features (which is similar to the term "configural" used in Rossion, 2008).

As discussed by Rossion (2008), the processing of the spacing among facial features is often opposed to the processing of the identity of those features (eyes, nose, and mouth) (e.g., Freire, Lee, & Symons, 2000; Goffaux & Rossion, 2007; Rhodes, Hayward, & Winkler, 2006; Yovel & Kanwisher, 2004). A feature manipulation has usually involved either the modification of the color/contrast of facial features (e.g., Barton, Keenan, & Bass, 2001; Leder & Bruce, 2000) the shape of facial features (Malcolm, Leung, & Barton, 2005; Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Yovel & Duchaine, 2006; Yovel & Kanwisher, 2004), or both shape and color/contrast manipulations (e.g., Le Grand, Mondloch, Maurer, & Brent, 2001a; Leder & Bruce, 1998). This variability in feature manipulation across studies is not surprising given that the definition of feature manipulation often includes both shape and color information. According to Rossion (2008), a feature manipulation involves "... changing the shape or surface property of a local feature" (p. 277). A similar definition is proposed in another influential review by Maurer et al. (2002): "To tap featural processing, a set of faces can be created that differ from one another in local information by changing the shape, color or luminance of features" p. 257).

A common procedure that is often used to assess whether spacing and/or features are extracted by the specialized processing mechanism for upright faces involves a comparison between the magnitudes of the inversion effects (i.e., the difference in discrimination abilities for upright and inverted faces) they generate. This

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paradigm presents a discrimination task of upright and inverted faces that differ in the spacing among features but share the same features, and of upright and inverted faces that differ in the features themselves but not in the spacing among them. Many of the studies that compared the inversion effects of such spacing or feature-manipulated faces reported smaller or no inversion effects for faces that differed in features but not in spacing, but the expected face-sized inversion effect for faces that differed in spacing but shared the same features (Freire et al., 2000; Le Grand et al., 2001a; Leder & Bruce, 1998). These findings led to the conclusion that inversion affects discrimination of the spacing among features more than the identity of the features (Freire et al., 2000; Maurer et al., 2002; Rossion, 2008). However, as will be shown later, this conclusion is valid only when facial features differ in contrast information. When features differ primarily in shape, and contrast/color differences are minimized, the magnitude of the inversion effect is similar for features and spacing discrimination tasks.

1. Is the disproportionate effect of inversion smaller for discrimination of features than for the spacing among them?

In contrast to several reports of a larger inversion effect in discrimination of faces that differ in spacing than faces that differ in features, other studies revealed a similar inversion effect for the two types of face manipulations (Rhodes, Brake, & Atkinson, 1993; Rhodes et al., 2006; Riesenhuber et al., 2004; Yovel & Duchaine, 2006; Yovel & Kanwisher, 2004). These findings have been dismissed recently in a review by Rossion (2008), who claimed that they reflect "methodological and conceptual shortcomings" (p. 276). In contrast to this view, I will make the following claims: (1) Feature manipulations of shape or contrast generate substantially different inversion effects and therefore cannot be used interchangeably as the same type of feature manipulation. (2) The discrepancy in the literature with respect to the difference in inversion effects on spacing and features can be fully accounted for by the type of featural manipulation that has been used in each study (for a comprehensive review see, McKone and Yovel (in press)). (3) When contrast/color differences are minimized, the inversion effect for features is similar to the inversion effect for spacing. Importantly, a similar inversion effect for spacing and features is consistent with the definition of holistic processing (Tanaka & Farah, 1993; Tanaka & Sengco, 1997), which suggests that all facial information including features, the spacing among them, face outline and so forth are integrated to a non-decomposable representation (Yovel & Kanwisher, 2008).

1.1. The effect of facial feature manipulation (color/contrast vs. shape)

Whereas the effect of the type of spacing manipulation (i.e., horizontal vs. vertical), which will be addressed here later on, was extensively discussed by Rossion (2008), an important factor that was mostly overlooked (but see, Rossion (2008, p. 279) discussed later) is the effect of feature manipulation on the magnitude of the inversion effect. Yovel and Duchaine (2006) have hypothesized that the reason prior studies have obtained a smaller inversion effect for the feature-manipulated faces than for the spacing-manipulated faces was because the feature differences between the faces included contrast/color information in addition to differences in the shape of the features (e.g., the size of the eyes). Yovel and Duchaine (2006) first compared the inversion effect for the faces used by Yovel and Kanwisher (2004), a study in which the feature manipulation primarily involved differences in shape but not in contrast/brightness, to the face stimuli used by Le Grand et al. (2001a), where the facial features also differed in contrast information (e.g., eye-liner and lipstick). Findings for the feature condition replicated previous reports of a large inversion effect for the face stimuli used by Yovel and Kanwisher (2004), which did not differ from the inversion effect to the spacing condition, and a smaller inversion effect for the feature-manipulated stimuli used by Le Grand et al. (2001a). The magnitude of the inversion effect was similar for the spacing-manipulated faces used in these two studies. These findings confirm the hypothesis that an inversion effect for faces that differ in features may be as large as for faces that differ in spacing when only the shape of features is manipulated. To further examine this idea with a more controlled face set, in a second experiment a new face exemplar was generated - in one set the features differed only in shape, with contrast differences kept to a minimum (see Fig. 1A, top row), similar to the stimuli used by Yovel and Kanwisher (2004) and others (Rhodes et al., 1993; Riesenhuber et al., 2004). In the other set of face stimuli, the features differed in shape and color (see Fig. 1A, bottom row) similar to the stimuli used by Le Grand et al. (2001a) and others (e.g., Freire et al., 2000; Mondloch, Le Grand, & Maurer, 2002). Consistent with the authors' predictions, the magnitude of the inversion effect for faces that differed primarily in the feature shape was similar to the inversion effect for the spacing-manipulated faces. In contrast, the inversion effect for faces that differed in both shape and contrast of their features was significantly smaller (Fig. 1B).

Consistent with the inversion effect findings, developmental prosopagnosic individuals, who suffer from a life-long deficit in face recognition, had difficulty in discriminating between faces that differed in the shape of facial features and the spacing among them, but not between faces that differed in the shape and the contrast of the features (Fig. 1C). These findings suggest that the holistic representation of upright faces incorporates information about the shape of the features and the spacing among them. The absence of an inversion effect for faces that differ in the contrast of their features and the normal discrimination of these stimuli in individuals who suffer from prosopagnosia suggest that a non-face system can be recruited to efficiently discriminate among faces that differ in contrast/color information. However, the fact that prosopagnosics have difficulty in discriminating between faces that differ in the shape of features imply that efficient discrimination of the shape of facial features requires the involvement of the specialized processing mechanism for upright faces, which is impaired in these individuals (Duchaine, Yovel, Butterworth, & Nakayama et al., 2006), just as this mechanism is needed for the extraction of information regarding the spacing among these features.

In a recent comprehensive review of all the studies that examined the effect of feature and spacing manipulation on the magnitude of the inversion effect, McKone and Yovel (in press) clearly showed that the nature of the feature manipulations used in previous reports fully accounts for the variability in the magnitude of the inversion effects reported in the literature. In particular, studies that primarily used faces that differed in contrast information revealed minimal or no inversion effect (e.g., Leder & Bruce, 2000; Searcy & Bartlett, 1996). When shape information combined with color information was used, a intermediate-level inversion effect was found (e.g., McKone & Boyer, 2006; Rhodes et al., 2006). All studies in which the feature manipulation primarily involved a shape change revealed a similar inversion effect for faces that differ in features and those that differ in the spacing among them (Riesenhuber et al., 2004; Yovel & Duchaine, 2006; Yovel & Kanwisher, 2004).

In a recent study, Russell, Biederman, Nederhouser, and Sinha (2007) have shown a significant inversion effect for faces that differ in pigmentation/reflectance of the skin, which did not differ from the inversion effect for faces that differ in shape information. These findings may seem to contradict the suggestion mentioned above that inversion is reduced for faces that differ in color information.

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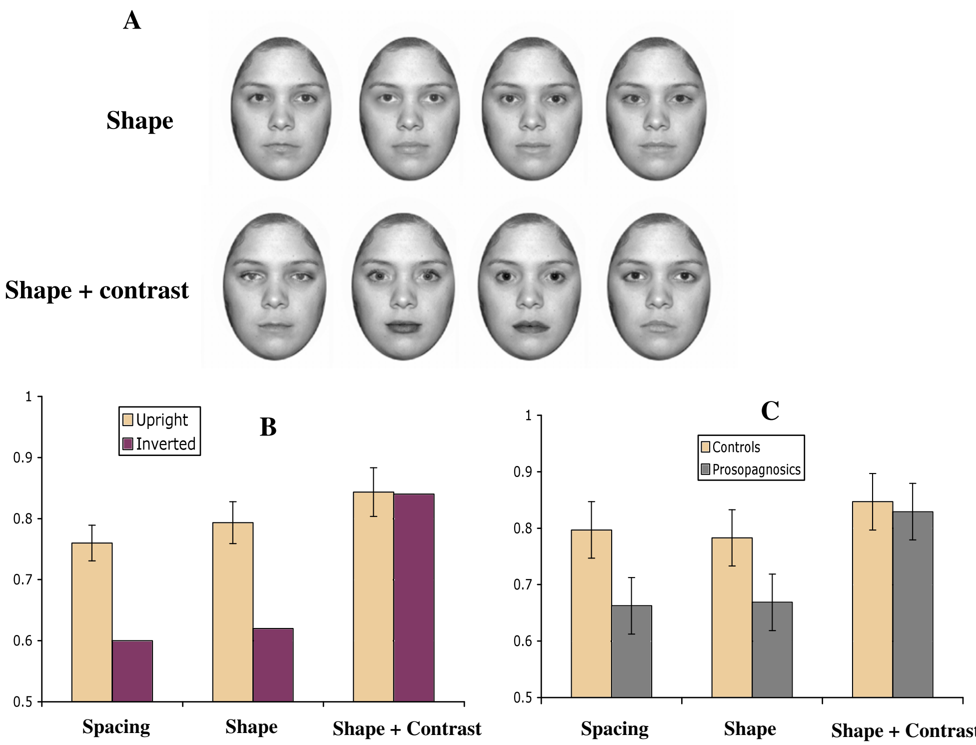

Fig. 1. (A) Face stimuli that differ in features were manipulated in two different ways: either by changing the shape of the features and minimizing the contrast differences (top row), or by adding contrast differences such as make up to the facial features (bottom row). Face stimuli that differed in spacing were also presented to subjects (see Yovel and Duchaine (2006)). (B) Results for normal individuals show no inversion effect for faces that differ in shape and contrast (presented in the top row of Fig. 1A), and a significant inversion effect for faces that differ only in the shape of the features (presented in the bottom row of Fig. 1B). The inversion effect for faces that differ in the shape of the features did not differ from the inversion effect for faces that differ in spacing. (C) Performance level of prosopagnosic individuals for faces that differ in the shape and contrast of the features (presented in the bottom row of Fig. 1A) did not differ from controls, but was much poorer relative to controls for faces that differ only in the shape of the features (presented in the top row of Fig. 1A). Importantly, impairment for faces that differ in the shape of features was similar to the poor performance for the faces that differed in spacing.

However, it is important to make a clear distinction between the pigmentation manipulation of Russell and colleagues, which generates a global change of the tone of the facial skin, and the local color change that has been used in the above-mentioned studies that manipulated featural information. The relative low performance level for upright faces that differ in pigmentation (~70%) suggests that subjects did not simply use color/brightness information per se to discriminate between the faces. In fact, upon debriefing participants were unable to tell that these faces differ in pigmentation (Richard Russell, personal communication). Obviously, discrimination of faces that substantially differ in skin color, such as a Caucasian and an African face, is not expected to generate an inversion effect. Overall, these findings suggest that the subtle pigmentation manipulation used by Russell et al. (2007) and the local color change to a facial feature are not comparable. The inversion effect is not reduced when faces differ in subtle global skin-tone differences, but is reduced when color differences to facial features are local and salient.

1.2. Does a feature shape manipulation involve a spacing manipulation?

A possible explanation for similar inversion effects and a similar effect of prosopagnosia on discrimination of feature shape and the spacing among features is that a change in the shape of the eyes, nose or mouth inherently involves a change in the spacing among the features. In fact, this idea may be consistent with the term "second-order relational information" that was coined in a seminal paper by (Diamond and Carey (1986). Diamond and Carey (1986) suggested that all faces share the same first-order relations (eyes above nose above mouth) but differ in second-order relational information. They defined second-order relational information, which is often used interchangeably with the term "spacing" (Maurer et al., 2002), as the "distinctive relations among the elements that define the shared configuration" (p. 110). This definition refers to the spacing among features but does not exclude the shape of features. However, despite the fact that the Diamond and Carey (1986) paper is cited by most papers that examined the inversion effect on spacing and features, this point was missed or misunderstood by most researchers who defined feature changes as changes in shape and/or color, and contrasted these changes with the spacing/configural differences, which refer only to metric distances among the main face parts (e.g., Maurer et al., 2002; Rossion, 2008). Thus, the shape of features is not necessarily opposed to the spacing among them.

Taken together, given that all studies that primarily manipulated shape information revealed a similar large inversion effect for feature manipulation suggests that these findings cannot be simply dismissed as "methodological and conceptual shortcomings (p. 276)", as was claimed by Rossion (2008). Below I address the various task factors that Rossion has suggested to invalidate similar inversion effects for spacing and parts.

1.3. The similar inversion effect to features and spacing is not due to "methodological and conceptual shortcomings"?

1.3.1. Task difficulty is indeed not a critical factor

The first criticism made by Rossion was that differences in task difficulty for discrimination of spacing and features cannot account for the smaller inversion effect revealed for features compared to spacing, as was suggested by Yovel and Kanwisher (2004). Yovel and Kanwisher (2004), who were the first to claim that spacing- and feature-manipulated faces generate a similar inversion effect, suggested that prior studies have failed to reveal similar inversion effects for spacing- and feature-manipulated faces because they did not equate performance levels for the upright conditions.[1] Equating task difficulty is an essential methodological requirement to allow a valid comparison of the relative drop in performance levels for inverted relative to upright stimuli across two face manipulations as well as when faces are compared to non-face objects (Yovel & Kanwisher, 2004). Ceiling or floor effects may modulate the magnitude of the inversion effect regardless of the specific characteristic of the stimuli. However, consistent with Rossion's (2008) claim, it indeed turned out that this methodological flaw did not account for the discrepancy in the literature. For example, Yovel and Duchaine (2006) compared the inversion effects of two types of feature-manipulated faces that were matched for performance levels and still revealed a significant inversion effect for one type of feature manipulation (shape) but not for another type (shape + contrast) (Fig. 1B). Nevertheless, it is important to emphasize that even though task difficulty was not the main factor that accounted for the dissociation between spacing and features in published studies, a valid comparison between the magnitudes of the inversion effects of any two categories of stimuli requires equating task difficulty of the upright stimuli.

1.3.2. Can we avoid an interaction between feature and spacing manipulations?

Rossion (2008) suggested that similar inversion effects for feature and spacing discrimination may sometimes occur when feature manipulation also involves a spacing manipulation. He further argues that "this effect can be minimized either by carefully selecting the face parts to swap between trials ...., or by using surface changes (eye/mouth brightness, texture, color ...) for the featural condition, as in many studies ...." (p. 279). As mentioned above, the main source for the discrepancy between studies that compared the inversion effect for spacing and features is the type of feature manipulation that was chosen by the authors. Rossion (2008) in fact acknowledged that "... it is important to specify if features of the face are modified according to shape (generally not-orientation variant) or texture/color (generally orientation-invariant) cues in any paradigm given that they may involve distinct processes" (p. 279). However, he does not acknowledge the findings that pure shape manipulation results in a similar inversion effect as the spacing manipulation. A systematic examination of the inversion effects for features across studies showed that the magnitude of the inversion effect does decrease monotonically as a function of the amount of color differences between the features (McKone & Yovel, in press).

We suggest that when low-level visual regions can easily discriminate between sequentially presented images that differ in contrast/color information of specific features, subjects may apply this low-level visual processing strategy and in this way bypass the face system, which unsurprisingly results in the absence of inversion effect. It is plausible that this strategy does not reflect normal, ecological face processing, but an efficient strategy for a sequential matching task used in the laboratory for this specific paradigm.

In summary, whereas the manipulation of feature shape indeed involves subtle changes in spacing, the usage of color to avoid this interaction is not a valid solution, as color discrimination may not necessarily recruit the face processing system. Furthermore, changes in the shape of features should not be opposed to the spacing among features but both may be considered a relational manipulation (Diamond & Carey, 1986).

1.3.3. No differences in reaction times between the effect of inversion on spacing and feature discriminations

Rossion (2008) asserted that it is important to also examine the effect of inversion on reaction times (RTs) for spacing and feature discrimination. The main dependent measure in the task used in Yovel and Kanwisher (2004) was accuracy, which ranged between 75% and 80% correct responses. Reaction time data were reported for the upright conditions in Yovel & Kanwisher, 2004, Supplementary, as an assurance that the two conditions were matched for difficulty. Here I report additional reaction time data from three experiments that we reported in Yovel & Kanwisher (2008), Yovel & Duchaine (2006) and Yovel & Kanwisher (2004) that generated similar inversion effects for spacing and features in accuracy scores, but did not include RT analysis.

In a study reported by Yovel and Kanwisher (2008), which focused on individual differences analyses of accuracy measures, performance levels for spacing- and feature-based discrimination were measured in 77 subjects (to allow principal component analysis). Reaction time analysis revealed faster RTs to inverted faces than to upright faces and faster RT to the features than to the spacing tasks, but the magnitude of the inversion effect on RTs was similar for the spacing (upright 730 ms; inverted 701 ms) and the feature tasks (upright 839 ms; inverted 801 ms). Similar to the accuracy findings, the interaction between Orientation and Face Type (Spacing/Features) was not significant for RTs ($p = .61$).

In Yovel and Duchaine (2006), a female face exemplar was used (see Fig. 1A), which again generated similar inversion effects for spacing and shape-feature manipulations for accuracy measures. Reaction time analysis revealed faster RTs to inverted faces than to upright faces, but the inversion effects were similar for the spacing (upright 632 ms; inverted 554 ms) and the feature tasks (upright 623 ms; inverted 566 ms). The interaction between Orientation and Face Type was not significant ($p = .42$). Thus, spacing- and feature-manipulated faces again generated similar effects on RT measures.

In a third experiment (reported in the supplementary section of Yovel & Kanwisher, 2004, with 18 subjects), upright and inverted conditions were presented in an interleaved manner with a male face exemplar. Reaction time analysis here revealed non-significant slower RTs for inverted than upright faces and no difference in the inversion effect for spacing (upright 798 ms; inverted 829 ms) and features (upright 817 ms; inverted 861 ms). The interaction between Orientation and Face Type was also not significant.

Taken together, data from three studies that used different face exemplars and experimental designs, which showed similar inversion effects in accuracy measures for faces that differ in spacing and the shape of the features, also reveal no difference in RT measures between the effects of inversion on discrimination of spacing and the shape of features.

1.3.4. Horizontal changes vs. vertical changes in spacing

Rossion (2008) claimed regarding the stimuli used in the Yovel and Kanwisher (2004) paper, that "in half of the configural trials ... the difference between faces concerned the inter-ocular distance, a manipulation in the horizontal direction, while in the other half the difference concerned the mouth–nose distance, a vertical manipulation". Because the inversion effect is smaller for inter-ocular distances than for mouth–nose distances (Goffaux & Rossion, 2007), the inversion effect on the spacing task may be moderate and closer in magnitude to the feature task. However, only 20%

[1] The data reported by the influential paper of Le Grand et al. (2001a) did not in fact reveal matched performance for spacing and features as reported in the original paper. An erratum published later in Nature (Le Grand, Mondloch, Maurer, & Brent, 2001b) indicates an error in the data reported in the original publication (Le Grand et al., 2001a). The performance level of the control group for the feature task was 90% rather than 80% correct and therefore it was not matched to the performance of the spacing task.

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of the pairs differed solely in inter-ocular distances, 20% of the pairs differed solely in nose–mouth distances and the remaining 60% of the pairs differed in both inter-ocular distance and mouth–nose distance. Given that horizontal and vertical spacing changes generate inversion effects of different magnitudes, it is indeed important to examine these manipulations separately. However, the combination of both types of manipulation, which is present in 60% of the trials, is not expected to generate a relatively smaller inversion effect and therefore it is not likely that the magnitude of the spacing inversion effect is underestimated in our study. I therefore believe that the similarity between the inversion effects on features and spacing in our studies is not due to the type of spacing manipulation we used. As mentioned above, the inversion effect on spacing discrimination for the stimuli used by Yovel and Kanwisher (2004) was similar in magnitude to the effect for the stimuli used by Le Grand et al. (2001a), a study that is not criticized by Rossion (2008) (see direct comparison in Yovel and Duchaine (2006)) but the data differed substantially in the inversion effect on feature discrimination. It is the type of feature manipulation (contrast vs. shape), which has a much more dramatic effect on the magnitude of the inversion effect relative to the spacing task.

In the context of the discussion regarding horizontal and vertical spacing manipulations, it is important to mention a recent study (Sekunova & Barton, 2008) that was not discussed in Rossion's review (2008). The study examined the effect of horizontal and vertical spacing manipulations on the magnitude of the inversion effect and revealed that the horizontal–vertical dissociation reported by Goffaux and Rossion (2007) actually reflects a difference in long-range spacing manipulations vs. short-range/local spacing manipulations (Goffaux & Rossion, 2007). In particular, the horizontal manipulation in the Goffaux and Rossion (2007) study was a local change (inter-ocular distance) whereas the eye + brow spacing manipulation was a long-range spacing change (the distance between the eyes + brow and the mouth). When a vertical local manipulation was performed (i.e. the distance between the eyes and the eyebrows), the inversion effect was significantly reduced as well (Sekunova & Barton, 2008). These findings suggest that local information may not require the face-system and may be performed by other non-face systems, whereas a face-specific holistic representation may be needed to efficiently estimate long-range spacing differences between faces. These findings interestingly suggest that the terms local vs. configural do not necessarily map to features vs. spacing manipulations, respectively. A spacing manipulation may be either local or global and it is only the latter that is sensitive to inversion and is effectively processed by specialized face processing mechanisms (see also, Goffaux (2008)). A local spacing change may be effectively processed by a non-face system, as evident by the absent or reduced inversion effect. These findings suggest that the magnitude of the inversion effect is not modulated by whether faces differ by spacing vs. feature or by horizontal spacing manipulations vs. vertical spacing manipulations but by global face manipulation vs. local face manipulations of either feature or spacing.

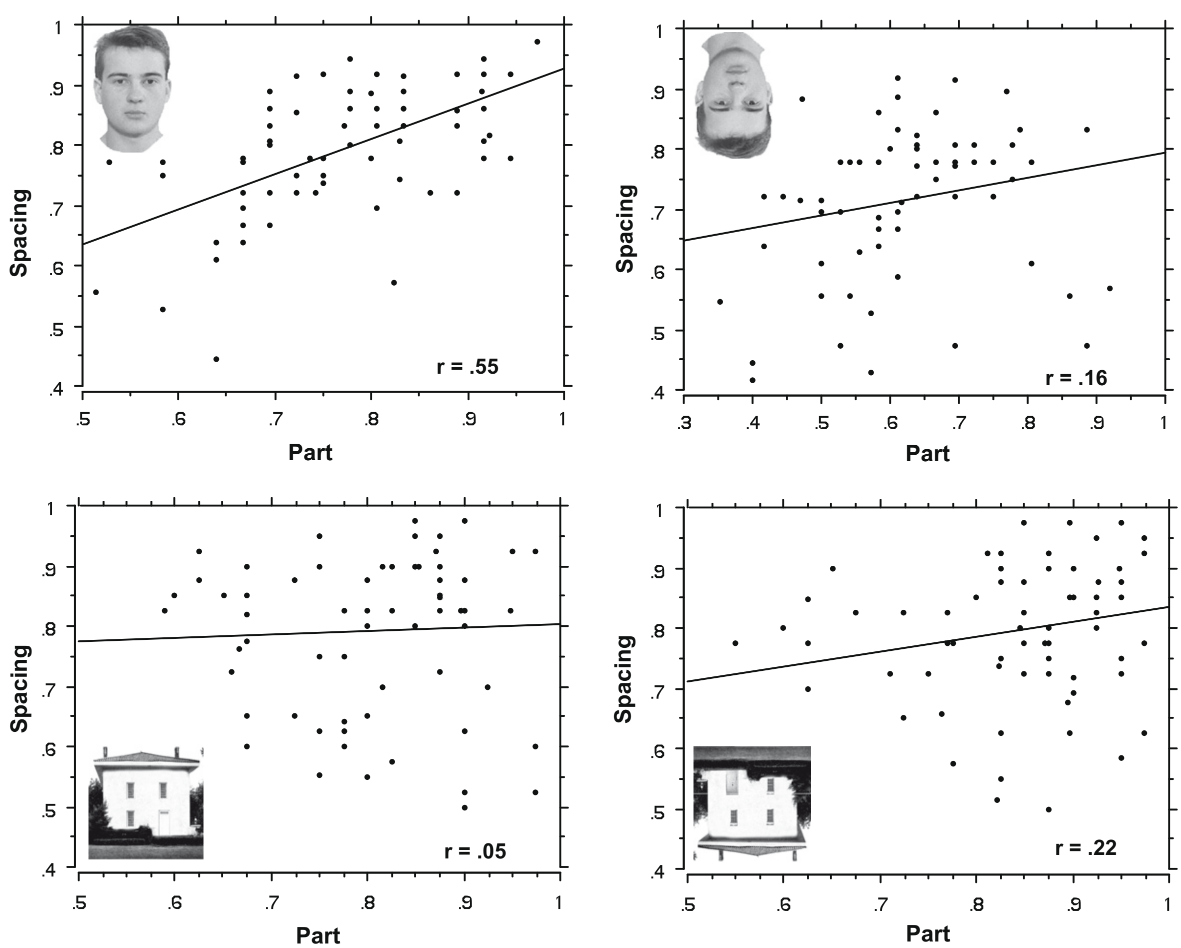

Fig. 2. Scatterplots of performance levels for faces that differ in spacing or in the shape of features reveal a strong significant correlation only for upright faces ($r = .55$, $p < .05$), but not for inverted faces or houses (p's > .16). These findings suggest that information about the features and the spacing among them is dissociated for non-face objects but not for upright faces. (Taken from Yovel and Kanwisher (2008).)

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2. The holistic representation of faces integrates information about the shape of features and the spacing among them

Based on the findings discussed above, I suggest that data are consistent with the idea that the shape of features and the spacing among them are integrated rather than separated. This view is consistent with earlier studies of Tanaka and Farah (for a recent review, see Tanaka and Farah (2003)), which showed that the identification of face features depends on the whole face and that the featural information is integrated with information about the spacing among features (Tanaka & Sengco, 1997). Next I will briefly mention two additional studies that used other methodologies than those reported above, which support this view.

In a recent study, Yovel and Kanwisher (2008) examined the correlations between discrimination levels of faces or houses that differed in their features or in the spacing among them with the same stimuli that were used in the Yovel and Kanwisher (2004) fMRI study. The correlation analyses revealed a high positive correlation between discrimination abilities of spacing and features but only for upright faces. The two tasks were not correlated for inverted faces or houses (Fig. 2). Notably, the spacing and feature trials were presented in an interleaved manner and subjects were not informed about the nature of the face manipulation in advance. Thus, performance on this task was not influenced by strategies that subjects may adapt for discrimination of spacing vs. features, and it therefore reflects the different manners in which individuals process upright faces relative to non-face stimuli. These findings are consistent with the idea that information about the features and the spacing among them is not dissociated for upright faces but is dissociated for non-face stimuli.

A second, functional MRI study also supports the idea that information about facial features and the spacing among them may be dissociated by non-face mechanisms but not by face processing mechanisms (Yovel & Kanwisher, 2004). This study presented the same faces and houses that differed in spacing or features reported above and examined the response of the face-selective area in the fusiform gyrus (fusiform face area – FFA) and the object-general region in the lateral occipital complex (LOC) (Malach et al., 1995), while subjects performed a discrimination task. Findings clearly show that the two regions generate different representations for upright faces. The face-selective area (FFA) was defined independently as voxels in the fusiform gyrus that showed a higher response to faces than to objects. This face-selective area showed a higher response to faces than to houses regardless of the type of stimulus manipulations. In contrast, the object-general region, which was independently defined as voxels in the occipito-temporal cortex that showed a higher response to objects than scrambled objects, revealed no difference between the response to faces and the response to houses, but did reveal a higher response during a feature discrimination task than during a spacing discrimination task (Fig. 3). These findings suggest that object-general brain regions seem to be biased to feature-based information rather than to spacing information, whereas face-selective brain regions equally extract both types of information from faces.

In summary, I suggest that information about both the shape of features and the spacing among them are integral to the holistic representation of faces (Tanaka & Sengco, 1997) and therefore are expected to generate similar inversion effects. The smaller inversion effects to feature manipulation in previous studies resulted from the usage of low-level visual brain regions that are able

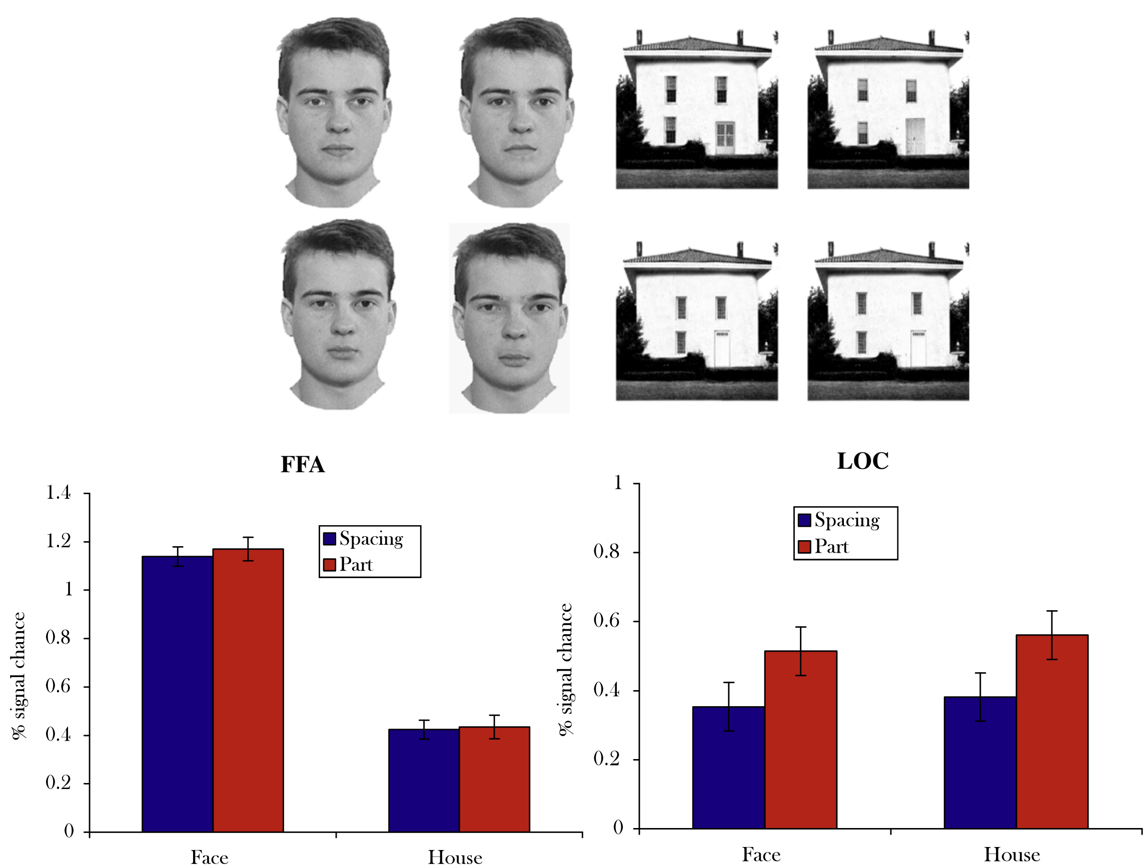

Fig. 3. The response of the face-selective region in the fusiform gyrus (FFA) and the general object region (LOC) to faces and houses that differ in the features or the spacing among them (top). Results show similar responses to stimuli that differ in spacing or features in the FFA (bottom left) but a higher response to stimuli that differ in features than in spacing in object-general regions (bottom right). (Taken from Yovel and Kanwisher (2004).)

to efficiently discriminate between sequentially presented faces that differ in contrast/color of their facial features, particularly in a sequential matching task conducted in the laboratory (McKone & Yovel, in press; Yovel & Duchaine, 2006). These findings suggest that the processing of the shape of features is not necessarily opposed to the processing of spacing and that common mechanisms for the extraction of relational information may underlie the processing of both types of facial information (Diamond & Carey, 1986; McKone & Yovel, in press).

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