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Research report

The nature of upright and inverted face representations: An adaptation-transfer study of configuration

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ABSTRACT

It is considered that whole-face processing of spatial structure may only be possible in upright faces, with only local feature processing in inverted faces. We asked whether this was due to impoverished representations of inverted faces. We performed two experiments. In the first, we divided faces into segments to create 'exploded' faces with disrupted second-order structures, and 'scrambled' faces with altered first-order relations; in the second we shifted features within intact facial outlines to create equivalent disruptions of spatial structure. In both we assessed the transfer of adaptation between faces with altered structure and intact faces. Scrambled adaptors did not adapt upright or inverted intact faces, indicating that a whole-face configuration is required at either orientation. Both upright and inverted faces showed a similar decline in aftereffect magnitude when adapting faces had altered second-order structure, implying that this structure is present in both upright and inverted face representations. We conclude that inverted faces are not represented simply as a collection of features, but have a whole-face configuration with second-order structure, similar to upright faces. Thus the qualitative impairments induced by inversion are not due to degraded inverted facial representations, but may reflect limitations in perceptual mechanisms.

Faces are processed by the human visual system in a manner that is sufficiently precise and efficient to allow us to rapidly identify thousands of individual faces, some at a single glance. This expert processing is orientation-dependent, in that recognition of faces is far better when faces are viewed in the customary upright orientation than when seen inverted, i.e., rotated in the picture plane (Yin, 1969). Because this "inversion effect" is greater for faces than for other objects, it is considered a signature of a type of expert processing used specifically by faces, though perhaps not solely by faces, as there is some evidence that similar inversion effects can emerge for other objects with which subjects have developed an expertise (Diamond and Carey, 1986; Gauthier and Tarr, 1997).

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Many studies have used the face inversion effect to try to clarify the nature of the expert mechanism operating during face processing. The logic has been to identify processes that can operate with upright faces but not with inverted faces, the inference being that such processes may be responsible at least in part for the superiority of recognition for upright as opposed to inverted faces. The different types of processes advanced as candidates have been summarized recently in an ongoing debate (Rossion, 2008, 2009; Yovel, 2009; Riesenhuber and Wolff, 2009). Although there has been some suggestion that there are primarily quantitative differences in efficiency rather than qualitatively differences in mechanism (Valentine, 1988; Sekuler et al., 2004), it is most commonly held that upright faces engage distinct processes (Rossion, 2008). Those studies that have focused on the type of facial information being processed have suggested that it is aspects of facial structure – as opposed to facial texture or color – that are difficult to process in inverted faces (Freire et al., 2000; Leder and Bruce, 2000; Barton et al., 2001, 2003a, 2003b; Yovel and Kanwisher, 2008; McKone and Yovel, 2009). These generally fall under the rubric of the 'configurational hypothesis'. Others have focused on the manner of processing, to suggest that the ability to process information from the entire face rapidly is what is impaired by face inversion – the 'holistic hypothesis' (Tanaka and Farah, 1993; Rossion, 2009). Evidence to support this includes elimination of the composite face effect by inversion (Young et al., 1987; Goffaux and Rossion, 2007; Rossion and Boremanse, 2008), and the superiority of recognizing facial features in their original face context than when they are seen as isolated parts, which is present in upright but not inverted faces (Tanaka and Farah, 1993). Such concepts are not mutually exclusive, however, and there has been some convergence in proposals that the ability to process structural or configurational information across the entire face efficiently and quickly may be the most vulnerable of skills to picture-plane inversion of faces (Barton et al., 2001, 2003b; Sekunova and Barton, 2008).

Studies of facial structure have drawn three distinctions: (a) local feature shape, (b) the precise metrical relationship between features known as 'second-order spatial relations', and (c) the more general categorical position of features relative to each other, such as the fact that the eyes are above the nose which is above the mouth, that define face-like configurations and are known as 'first–order spatial relations' (Diamond and Carey, 1986; Rhodes, 1988). Correct first-order structure clearly is required for determining if a face or face-like object is present, but second-order structure and feature shape play more of a role in determining the identity of a specific face. Inversion effects have been shown for both feature shape and second-order structure (Riesenhuber et al., 2004; Malcolm et al., 2005; Yovel and Duchaine, 2006), though it is thought that second-order structure may be more vulnerable to the effects of inversion because the more spatially constricted or feature-based processing that operates during inverted viewing has more difficulty compensating for the loss of efficient processing of whole-face structure (Sekunova and Barton, 2008; Rossion, 2009).

Most of these studies on processing facial structure have used the strategy of simply showing reduced accuracy and/or increased reaction times for behavioural tasks involving discrimination of stimulus manipulations that probe configural processing. However, the inference that the processes significantly disrupted by inversion are therefore responsible for the difficulty in *recognizing* inverted faces is only an indirect one, and one that is not logically necessary. For example, it is conceivable that several mechanisms are affected by inversion, only some of which may be important for face recognition. To make a more direct link between (1) an observed perceptual failure when faces are turned upside-down and (2) the inversion effect on face recognition, we need to investigate the impact of these stimulus manipulations on tasks that more specifically involve identity processing. Furthermore, a key question remains as to whether the difficulties with processing inverted faces are due to limitations in the way inverted faces are represented in the visual system, or if these difficulties are related to the perceptual mechanisms used to extract information from faces being seen by the observer.

The recent development of face adaptation paradigms offers one such means of evaluating facial representations in the human visual system. It has been shown that even brief viewing of a face for a few seconds can create a perceptual bias in a subsequently viewed ambiguous test face (Leopold et al., 2001), and that this occurs for a variety of facial dimensions, including identity (Fox et al., 2008), expression (Fox and Barton, 2007), gender (Watson and Clifford, 2006), and gaze direction (Jenkins et al., 2006). Types of aftereffects other than perceptual bias can also be shown, including altered contrast thresholds (Guo et al., 2009; Rostamirad et al., 2009) and changes in discrimination accuracy around the adapted face (Oruç and Barton, 2011; Rhodes et al., 2010). All these effects have in common the fact that the aftereffects are stimulus-specific: that is, an aftereffect generated by viewing a certain face does not affect all faces seen in the test phase in the same manner. For example, perceptual bias aftereffects are thought to arise because of asymmetric changes in neural activity for the adapted representation compared to unadapted ones (Coltheart, 1971; Mather and Moulden, 1980). Because of the stimulus-specificity of face adaptation, the study of aftereffects offers a means of exploring the representations corresponding to specific facial identities.

Our goal in this study was to use an adaptation paradigm to ask how alterations in the structural properties of a facial stimulus affected the ability of the stimulus to engage representations of specific facial identities. We focused specifically on second-order and first-order structure. We generated a set of primary hypotheses based on the proposal that second-order structure contributes significantly to face processing when faces are upright but not when they are inverted. First, if both correct second-order structure as well as a face-like configuration based on correct first-order structure are properties critical for engaging upright representations of specific face identities, then altering either first- or second-order structure in an upright adapting face should result in failure of adaptation to transfer to an intact upright test face. Second, if second-order structure is not well perceived in inverted faces because inverted representations are predominantly feature-based, then an inverted face with altered second-order structure should be just as efficient as an intact inverted face in inducing aftereffects in intact inverted test faces. Finally, if inverted faces are processed as merely a set of features divorced and independent of each other, which one might suggest to be the strongest version of the feature-based

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argument, then even a scrambled arrangement with altered first-order structure should be just as effective at inducing aftereffects in inverted faces, despite the lack of a face-like configuration in scrambled stimuli.

1. Experiment 1

Creating faces with altered spatial arrangements can be done in a number of ways, each with their own advantages and disadvantages. One method is to segment faces into pieces and then present the segments in either an exploded arrangement, in which second-order structure is disrupted but the first-order face-like configuration preserved (Moscovitch et al., 1997; Moscovitch and Moscovitch, 2000), or a scrambled arrangement, in which first-order structure is also disrupted, resulting in loss of the face-like configuration. This 'jigsaw-puzzle' technique has the advantage of preserving all information in the original image, but the disadvantage of introducing unavoidable artificial edges and blank gaps into the new image, with disruption of the facial outline. Another common method is to select facial features and move them within the intact facial outline (Barton et al., 2001; Le Grand et al., 2004). While this has the advantage of not creating gaps and edges between facial fragments, it is impossible to preserve all aspects of the original image, as the shifted features will inevitably occlude some relatively feature less regions, and some image processing is necessary to eliminate edges. Given that the advantages and disadvantages of these two techniques are complementary, we performed two experiments, one for each. If the results were replicated, this would strengthen the conclusion that it is the disruption of second-order and/or first-order structure by these manipulations that is responsible for the findings, and not the other consequences of the manipulations upon the altered images. In Experiment 1, we first used the jigsaw puzzle technique to segment faces into pieces that were then separated and rearranged to create altered second-order and altered first-order structure.

1.1. *Methods*

1.1.1. *Participants*

15 subjects participated. One subject was excluded because of extremely poor performance during training, requiring almost 30 tries to reach threshold. Therefore the data used for the analysis are derived from the aftereffect scores of 14 subjects (8 females) with a mean age of 27.7 years (standard deviation – SD = 8.2; range = 20–54 years). All subjects in this and the next experiment were naïve to the purpose and had normal or corrected-to-normal vision. The protocols of both experiments were approved by the institutional review boards of the Vancouver General Hospital and the University of British Columbia. All subjects gave informed consent, and the experiment was conducted in accordance with the principles of the Declaration of Helsinki.

1.1.2. *Stimuli*

Two Versions (A and B) of two male and two female Caucasian faces with neutral expressions were selected from the Karolinska Database of Emotional Faces (Lundqvist and Litton, 1998). The A version of each face was used as an adapting image, while the B version was used to generate the morphed test images, in order to reduce contributions to the measured aftereffects from strictly image-based properties. The face identities were arbitrarily labeled as 'face identity 0' or 'face identity 1'.

The faces were aligned using the pupils as a vertical and the tip of the nose as a horizontal marker. The faces were superimposed on a black background and had a standard width of 7.7° (female) or 7.8° (male) and a height of 9.7° (female) or 10.2° (male) visual angle when viewed from a distance of 57 cm. Using Adobe Photoshop CS2 9.0 (www.adobe.com) we superimposed oval masks that occluded the external contour, including hair and ears. Distinguishing facial features such as moles or scars were removed with the Spot Healing Brush Tool.

To create the test stimuli we used Fantamorph 3.0 (www.fantamorph.com) to generate a series of morphed facial images between the B versions of the two male faces and between the B versions of the two female faces, in steps of 2.5%. The 13 images from the middle of each morph series, ranging from 65/35% to 35/65%, were selected for use as the test stimuli.

All adapting and test face stimuli were then cut in an identical manner into eight pieces (forehead, left eye, right eye, nose, left cheek, right cheek, mouth and chin). To create *exploded* stimuli, we left the nose piece unmoved at the center but moved all other pieces away from this center by unequal amounts (Fig. 1). Thus the forehead piece was moved up by 50 pixels, the eye pieces moved 30 pixels up and 40 pixels laterally, the mouth piece moved down 30 pixels, the chin piece moved down 60 pixels, and the cheek pieces 10 pixels down and 30 pixels laterally (Fig. 1). The resulting "exploded" faces were 9.8° in width and 12.7° in height for female faces, and 9.9° in width and 13.1° in height for male images.

To create *scrambled* stimuli, the same pieces were rearranged further, with all test and adapting images having the identical rearrangement (Fig. 1). These images were 10.2° in width and 11.0° in height for female images and 11.2° in width and 11.4° in height for male images.

1.1.3. *Procedure*

The protocol was designed and conducted with SuperLab 4.0.8 (www.cedrus.com) and images displayed on a Toshiba Tecra A8 notebook with a 15.4F0B2 TFT LCD with a resolution of 1280 × 800 pixels, with a screen refresh rate of 60 Hz. The screen was viewed from a viewing distance of approximately 57 cm. These conditions were also used in Experiment 2.

The experiment consisted of four blocks, two with upright faces, one female and one male, and two with inverted faces, one female and one male, performed in an order that was randomized across subjects. Each block was preceded by its own training session. The duration of a block, including both the training session and the experimental block, was approximately 1 h. The experiment was conducted in 2 sessions on different days, each about 2 h. Participants were permitted and encouraged to take breaks when they felt tired.

1.1.4. *Training sessions*

Each of the 4 blocks was preceded by training sessions intended to familiarize the subjects with the face identities

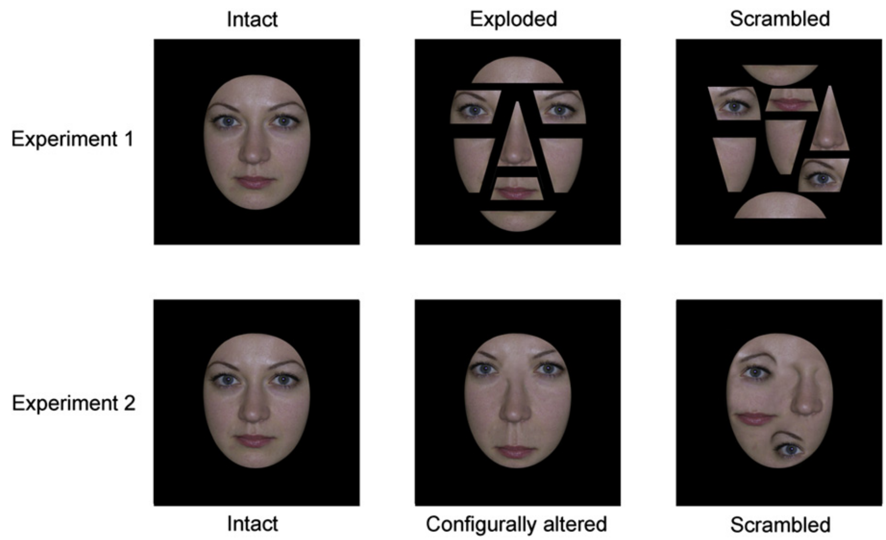

Fig. 1 – Example of face stimuli used as either adaptors or test stimuli in Experiment 1 (top row) and Experiment 2 (bottom row).

they would see in that block, in the orientation that would be used in that block. There were three training sessions for a block, one each for intact, exploded and scrambled faces, with subjects starting with the intact training session. Each training session had four stages that increased in difficulty. In stage 1, one of the two original faces used to create the morphed test stimuli for that gender (the B version of the two identities) was shown for 1000 msec, followed by a blank screen (150 msec) and a choice screen that displayed both of the two original faces. Subjects were to indicate which face they had seen by pressing one of two keypresses. In stage 2 the same images were used but the display time was reduced to 300 msec. In stage 3, we used the 65/35% and 35/65% morphed images rather than the original faces, with a display time of 1000 msec. In stage 4, the images used in stage 3 were displayed for only 300 msec. Each stage consisted of 20 trials, 10 for each the two faces, with the order of the trials randomized, as was the position of the correct face in the choice screen. Feedback on accuracy was provided with words written on the screen. If subjects achieved a score of 19/20 correct in stage 4, they proceeded to the next training session, which was for exploded faces. If not, they repeated stage 4 until they achieved this score. After completing stage 4 of the exploded training session with a score of 19/20 correct, they proceeded to the training session for scrambled faces. Finally, once they had achieved 19/20 correct for all three training sessions, they were allowed to proceed to the experimental block. Thus every subject had to do a minimum of three out of the overall twelve training blocks. The average number of training blocks above this minimum was 1.5 (SD = .65, range = 0–9).

1.1.5. Adaptation experiments

During the adapting period of a trial (Fig. 2), subjects saw the A version of one of the two male faces in a male block (or one of the two female faces in a female block). This was shown for 5000 msec. Subjects were told not to fixate on one particular spot but rather to scan the whole image. After the adapting period there was a Gaussian white noise mask for 50 msec, followed by a white fixation cross on a black screen for 150 msec. The test period was then introduced by a blank (black) screen for 150 msec, followed by the test face stimulus for 300 msec, then a blank screen for 150 msec. The test face stimulus was one of the morphed face images. Finally the choice display appeared, showing both of the A versions of the male faces in a male block (or both A versions of the female faces in the female block), side by side, with the location of face identity 0 relative to face identity 1 randomized, as in the training phase. The choice display remained visible until the subject pressed one of two keypresses to indicate which of the two choice faces the test stimulus most resembled (Fig. 2).

We added two manipulations to minimize the contribution of low-level image properties to the measured aftereffect. First, we increased the size of adapting stimuli further, by 50% more than those reported in the section on stimuli, which are correct dimensions for the test stimuli. Second, while the adapting stimulus was presented at screen center, the test stimulus was displaced horizontally by 1° of visual angle, randomly left or right.

Each block contained seven different adaptor/test combinations, with regards to intact, exploded or scrambled versions. These were intact-adaptor/intact-test, exploded-adaptor/intact-test, scrambled-adaptor/intact-test, intact-adaptor/exploded-test, exploded-adaptor/exploded-test, intact-adaptor/scrambled-test, and scrambled-adaptor/scrambled-test combinations. The first three combinations, which all have intact-test stimuli, allow us to compare the efficacy of the three different adaptors in engaging whole-face representations, and thus address our primary hypotheses.

Among the last four versions, the exploded-adaptor/exploded-test and scrambled-adaptor/scrambled-test combinations allow us to measure the ability of these altered adaptors to adapt their own representations, which would be important to verify if they fail to generate aftereffects in intact-test stimuli. Furthermore, using an intact adaptor with exploded- or scrambled-test stimuli allows us to determine if intact faces engage those exploded or scrambled representations equally well, which would indicate that these representations of altered faces are invariant for the spatial position of their segments.

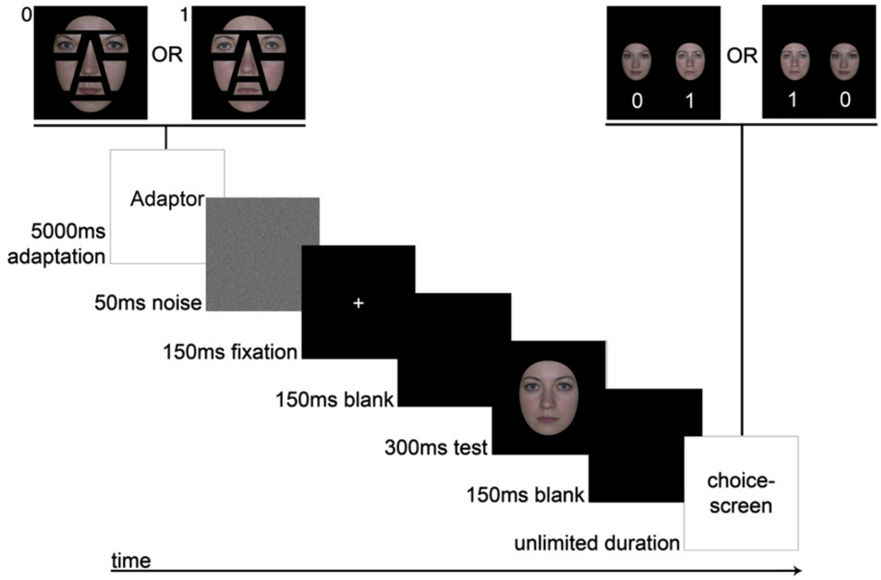

Fig. 2 – Illustration of a trial, for a combination of exploded-adaptor and intact-test stimulus for a female series. The adapting stimulus was the A version of either face identity 0 or face identity 1. The test stimulus is a face that is morphed between the B versions of identity 0 and identity 1. The choice screen shows the A version of identity 0 and identity 1, and subjects must indicate whether the test stimulus most resembled identity 0 or identity 1.

Within each block, the order of the seven adaptor/test combinations and the order of the 13 ambiguous test stimuli used in the test phase were randomized. Each of the 13 test stimuli were shown once for each of the two possible adaptors (face identity 0 *vs*. face identity 1), resulting in 26 trials for each of the 7 adaptor/test combinations in a block, for a total of 182 trials for each of the four blocks, or 728 trials total. In the analysis, because we included data from both genders, this resulted in 52 trials for each adaptor/test combination.

1.1.6. *Analysis*

The aftereffect scores were calculated by assigning a value of 0 when subjects chose face identity 0 as their answer, and 1 when they chose face identity 1, We then averaged their scores over the 13 trials (each with a different test stimulus) when the adaptor had been face identity 0, and likewise when the adaptor had been face identity 1. The difference between these two scores is our index of the magnitude of the face aftereffect. A large index score would indicate a large 'repulsive' aftereffect: that is, subjects had a high frequency of answering that an ambiguous test face looked like face identity 1 after adapting to face identity 0, and a low frequency of answering that it looked like face identity 1 after adapting to face identity 1. Thus, in this scenario 5 sec of viewing one face caused a subsequent morphed stimulus to look more like the other face. We also collapsed scores across the different gender blocks, so that each aftereffect index is derived from the performance from 52 trials per subject.

These aftereffect data were analyzed in two separate repeated-measure ANOVAs, using JMP 8.0.2 (www.jmp.com), to assess the effects of exploded and scrambled versions separately. The first ANOVA examined the impact of exploded stimuli, and hence excluded any adaptor/test combination that included a scrambled version as adaptor or test. It had three factors: orientation (upright, inverted), adaptor type (intact, exploded) and test stimulus (intact, exploded), with subjects included as a random factor. The second ANOVA examined the impact of scrambled stimuli, and hence excluded any adaptor/test combination that included an exploded version as adaptor or test. It had three factors: orientation (upright, inverted), adaptor type (intact, scrambled) and test stimulus (intact, scrambled), with subjects included as a random factor. Significant interactions and *a priori* comparisons of interest were further explored with linear contrasts.

As well, we calculated whether each adaptor/test combination led to an aftereffect that was significantly different from zero, using t-tests aimed at an overall alpha level of .05, with Bonferroni correction adjusted for inter-test correlations (Sankoh et al., 1997).

1.2. Results

1.2.1. *Exploded stimuli*

There was a main effect of adaptor type: intact adaptors induced aftereffects almost twice the size of those induced by exploded adaptors [.168 *vs* .094, $F(1, 13) = 6.08$, $p < .03$]. The main effects of orientation and test stimulus were not significant. There was a significant interaction between test stimulus and orientation [$F(1, 13) = 5.16$, $p < .05$]. This was due to a significant inversion effect for intact-test stimuli [upright: .167, inverted: .098, $F(1, 91) = 4.36$, $p < .0396$], which is evident regardless of whether intact or exploded faces are used as adaptors, but not for exploded-test stimuli [upright: .123, inverted: .133, $F(1, 91) = .08$, $p = .77$] (Fig. 3, top). The three-way interaction between adaptor type, test stimulus, and orientation was not significant [$F(1, 13) = .26$, $p = .62$].

The *a priori* linear contrasts between intact and exploded adaptors showed that for intact-test stimuli, there was a trend

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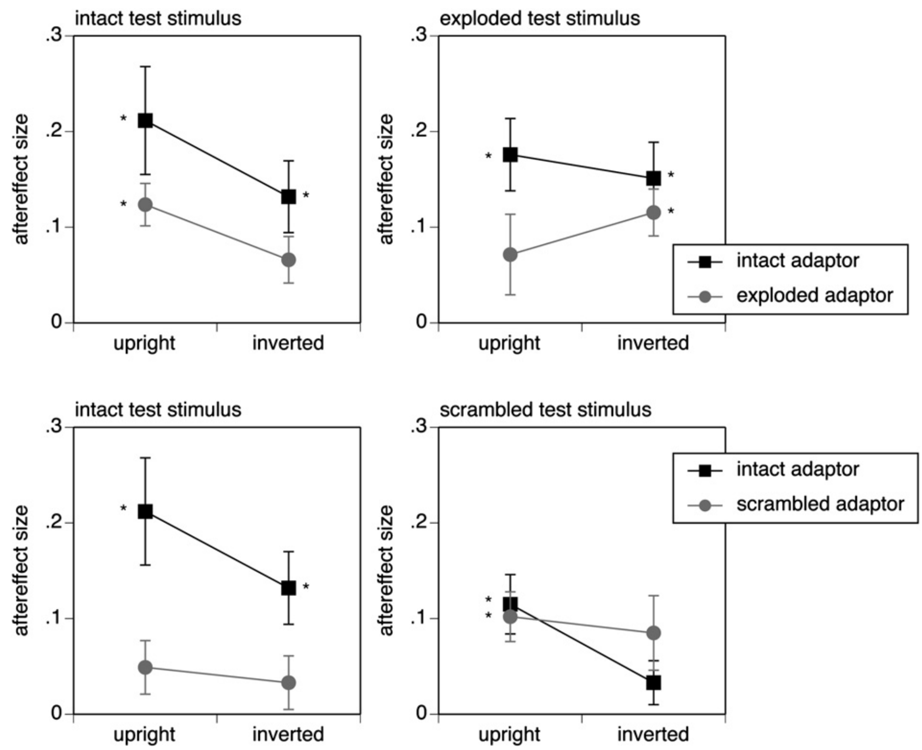

Fig. 3 – Results, Experiment 1. Aftereffect size is the proportion of times they responded identity 1 after adapting to identity 0 minus the proportion of times they responded identity 1 after adapting to identity 1. Top row shows the comparison between intact stimuli and exploded adaptors, for intact-test stimuli in the left graph and for exploded-test stimuli in the right graph. Bottom row shows the comparison between intact stimuli and scrambled adaptors, for intact-test stimuli in the left graph and for scrambled-test stimuli in the right graph. Error bars are one standard error. Asterisks indicate aftereffects that were significantly greater than zero.

to a greater effect from intact adaptors for upright faces [intact: .212, exploded: .124, $F(1, 91) = 3.57$, $p < .062$] but not for inverted faces. Curiously, for exploded-test stimuli, intact adaptors were also more effective at generating an aftereffect than exploded adaptors in the upright orientation [intact: .176, exploded: .071, $F(1, 91) = 5.03$, $p < .027$]. For exploded-test stimuli in the inverted orientation, there was no difference between intact and exploded adaptors.

Regarding which adaptor/test combinations were able to generate a significant aftereffect (Bonferroni correction, $p < .0094$ for alpha $< .05$), we found that intact adaptors induced aftereffects for all test stimuli in all orientations. Exploded adaptors also induced a significant aftereffect for upright intact-test stimuli, and also for inverted but not upright exploded stimuli.

1.2.2. *Scrambled stimuli*

There was a main effect of adaptor type (Fig. 3, bottom), with intact adaptors inducing nearly twice as larger aftereffects as scrambled adaptors [.123 *vs* .067, $F(1, 13) = 5.76$, $p < .04$]. The main effects of test stimulus and orientation were not significant. There was an interaction between adaptor type and test stimulus [$F(1, 13) = 8.03$, $p < .02$]: intact adaptors generated larger aftereffects than scrambled adaptors for intact-test stimuli [.171 *vs* .041, $F(1, 91) = 16.52$, $p < .0002$] but not for scrambled-test stimuli [.074 *vs* .093, $F(1, 91) = .35$, $p = .55$]. Also, intact adaptors generated larger aftereffects in intact-test stimuli than in scrambled-test stimuli [.171 *vs* .074, $F(1, 91) = 9.22$, $p < .0032$], whereas scrambled adaptors did not show this difference between intact and scrambled-test stimuli [.041 *vs* .093, $F(1, 91) = 2.64$, $p = .11$].

The *a priori* linear contrasts between intact and scrambled adaptors showed that for intact-test stimuli, there was a greater effect from intact adaptors for both upright [intact: .212, scrambled: .049, $F(1, 91) = 12.74$, $p < .0005$] and inverted faces [intact: .132, scrambled: .033, $F(1, 91) = 4.74$, $p < .03$]. In contrast, there was no difference between intact and scrambled adaptors for scrambled-test stimuli.

Regarding which adaptor/test combinations were able to generate a significant aftereffect (Bonferroni correction, $p < .0087$ for alpha $< .05$), we found that intact adaptors induced aftereffects for all stimuli in all orientations, with the exception of inverted scrambled-test stimuli. For scrambled adaptors, the key finding was that, unlike the case with exploded adaptors, these were not able to generate an aftereffect in intact-test stimuli, even though they were able to generate an aftereffect in scrambled stimuli when both were presented upright.

1.3. *Comment*

The key findings regarding our primary hypotheses in the introduction related to the conditions with intact-test stimuli. For the effects of second-order structure, intact faces were better than exploded faces as adaptors in both orientations.

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This confirms that second-order structure is a component of face representations, but also shows that this is true of not only upright but also inverted faces. Both types of adaptors showing a significant inversion effect, with a significant aftereffect from exploded adaptors with upright but not inverted faces. Scrambled faces did not generate a significant aftereffect in intact-test faces and hence did not show an orientation effect. Hence this would suggest that an intact first-order structure – a face-like configuration – is mandatory to activate face representations, regardless of orientation.

Before further comment on these data, we proceed to Experiment 2, which was aimed at confirming that the results of Experiment 1 were indeed related to effects on spatial structure and not due to other artificial changes in the stimuli, such as the edges or altered facial contour.

2. Experiment 2

Instead of segmenting the face into pieces that were then spatially shifted, features were selected and moved within faces in the altered stimuli of this experiment. The integrity of the overall face outline is thus preserved, but with the sacrifice of some facial area that is occluded by the shifted features. If the results of Experiment 1 are replicated in Experiment 2, this allows us to exclude the possibility that the effects of Experiment 1 are due to the sharp edges, intervening blank space and disrupted facial outline inherent to the jigsaw puzzle technique. Conversely, replication also implies that the results of Experiment 2 are not due to loss of information secondary to occlusion of feature-less facial regions, since no such loss is present in the stimuli of Experiment 1.

2.1. *Methods*

2.1.1. *Participants*

12 subjects participated, (8 females) with a mean age of 25.6 years (SD = 2.6; range = 21–31 years), none of whom had participated in Experiment 1.

2.1.2. *Stimuli*

We used the same face images for adapting and morphed test stimuli as in Experiment 1. Instead of segmenting the stimuli used as adaptors, we selected features and moved them using Adobe Photoshop CS 8.0 (www.adobe.com). For faces with altered second-order structure (which we will call "*configurally altered*" faces, as the term exploded is not appropriate for this manipulation), we moved the eyes 30 pixels up and 10 pixels laterally and the mouth 30 pixels down in each adapting image (Fig. 1). To create *scrambled* stimuli, we moved the left eye 190 pixels down and 110 pixels to the right, the right eye 20 pixels up and 140 pixels to the left, the mouth 60 pixels up and 60 pixels to the left, and the nose 20 pixels up and 80 pixels to the right (Fig. 1).

2.1.3. *Procedure*

Given the length of Experiment 1, we created a shorter protocol in Experiment 2, by only examining adaptor/test combinations relevant to our primary hypotheses, namely the three with intact-test stimuli, and omitting the four conditions with scrambled or configurally altered test stimuli. The experiment again consisted of four blocks, two with upright faces, one female and one male, and two with inverted faces, one female and one male, performed in an order that was randomized across subjects. The experiment was conducted in 2 sessions. Participants were permitted and encouraged to take breaks when they felt tired. Each block was preceded by a training session identical to that used for the intact stimuli in Experiment 1, intended to familiarize the subjects with the face identities they would see in that block.

Trial parameters were identical to those used in Experiment 1. Again, adapting and test stimuli differed in size and screen position to minimize the impact of low-level image properties. Each block contained three different adaptor/test combinations, with intact, configurally altered or scrambled adaptors, but with test stimuli that were always intact faces. Within each block, the order of the three adaptor/test combinations, and the order of the 13 ambiguous test stimuli used in the test phase were randomized. Each of the 13 test stimuli were shown once for each of the two possible adaptors (face identity 0 *vs.* face identity 1), resulting in 26 trials for each of the 3 adaptor/test combinations in a block, for a total of 78 trials for each of the four blocks, or 312 trials total. In the analysis we included data from both genders, resulting in 52 trials for each adaptor/test combination, as in Experiment 1.

2.1.4. *Analysis*

The aftereffect scores were calculated as in Experiment 1. Maintaining a parallel with Experiment 1, we assessed the effects of configurally altered and scrambled adaptors with separate repeated-measures ANOVAs. The first ANOVA examined the impact of altering second-order structure by using the two factors of orientation (upright, inverted) and adaptor type (intact, configurally altered), with subjects included as a random factor. The second ANOVA examined the impact of altered first-order structure by using the two factors of orientation (upright, inverted) and adaptor type (intact, scrambled), with subjects included as a random factor. Significant interactions and *a priori* comparisons of interest were further explored with linear contrasts. As well, we calculated whether each adaptor/test combination led to an aftereffect that was significantly different from zero, using *t*-tests aimed at an overall alpha level of .05, with Bonferroni correction adjusted for inter-test correlations.

2.2. *Results*

2.2.1. *Second-order configurally altered stimuli*

There was a main effect of adaptor type: intact adaptors induced aftereffects almost twice the size of those induced by second-order configural adaptors [.175 *vs* .063, $F(1, 11) = 12.06$, $p < .002$]. There was also a main effect of orientation [$F(1, 11) = 10.72$, $p < .003$], with larger aftereffects for upright faces, but no interaction between orientation and adaptor type. Thus, as with the exploded stimuli in Experiment 1, adapting faces with altered second-order structure showed inversion effects similar to intact adapting faces (Fig. 4, top). The *a priori* linear contrasts between intact and configurally altered adaptors showed a greater effect from intact adaptors for both upright [intact: .224, configurally altered: .119, $F(1, 33) = 5.36$, $p < .027$] and

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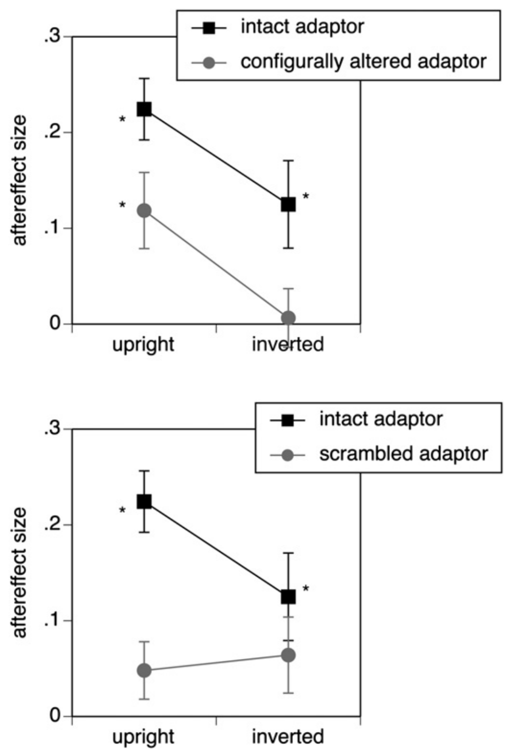

Fig. 4 – Results, Experiment 2. Aftereffect size is the proportion of times they responded identity 1 after adapting to identity 0 minus the proportion of times they responded identity 1 after adapting to identity 1. Top graph shows the comparison between intact stimuli and exploded adaptors. Bottom graph shows the comparison between intact stimuli and scrambled adaptors. Error bars are one standard error. Asterisks indicate aftereffects that were significantly greater than zero.

inverted faces [intact: .125, configurally altered: .006, $F(1, 33) = 6.74$, $p < .014$].

Regarding which adaptor/test combinations were able to generate a significant aftereffect (Bonferroni correction, $p < .024$ for alpha $< .05$), aftereffects were significant for intact-face adaptors, whether upright [$t(11) = 7.00$, $p < .0001$] or inverted [$t(11) = 2.74$, $p = .019$]. Configurally altered adaptors also induced an aftereffect in upright faces [$t(11) = 2.98$, $p = .012$] but not in inverted faces.

2.2.2. *Scrambled stimuli*

There was a main effect of adaptor type (Fig. 4, bottom), with intact adaptors inducing aftereffects about three times larger than scrambled adaptors [.175 *vs* .056, $F(1, 11) = 13.33$, $p < .0009$]. The main effect of orientation was not significant. There was a trend to an interaction between adaptor type and orientation [$F(1, 33) = 8.03$, $p = .085$], due to an effect of orientation on intact faces, but not on scrambled faces. The *a priori* linear contrasts between intact and scrambled adaptors showed that for intact-test stimuli, there was a greater effect from intact adaptors for upright faces [intact: .224, scrambled: .048, $F(1, 33) = 14.73$, $p < .0005$] but not for inverted faces [intact: .125, scrambled: .064, $F(1, 33) = 1.75$, $p = .19$].

The key result was that the examination of whether aftereffects were significant (Bonferroni correction, $p < .026$ for alpha $< .05$) showed that, as in the first experiment, scrambled stimuli were ineffective in either upright or inverted orientations.

2.3. *Comment*

The results of Experiment 2 replicated all the key findings of Experiment 1. Intact faces were better than configurally altered faces as adaptors in both orientations, with both types of adaptors showing a significant inversion effect, and there was a significant aftereffect from configurally altered adaptors with upright but not inverted faces. Scrambled faces did not generate a significant aftereffect in intact-test faces and hence did not show an orientation effect. Given the complementary advantages and disadvantages of the different techniques used to manipulate spatial structure in Experiments 1 and 2, this replication implies that the effects are indeed due to the manipulation of facial structure and not due to other factors related to the way these spatial manipulations were generated.

3. Discussion

Our results first confirm that intact faces can generate significant aftereffects for identity in both inverted and upright orientations, a finding that we and others have observed before (Webster and MacLin, 1999; Zhao and Chubb, 2001; Watson and Clifford, 2003, 2006; Guo et al., 2009; Rhodes et al., 2009a). Although there is the appearance of a decline in aftereffect magnitude with inversion, this was not statistically significant. Most prior studies found no difference in aftereffect magnitude between upright and inverted presentations, across a wide variety of paradigms and facial dimensions tested (Zhao and Chubb, 2001; Webster and MacLin, 1999; Watson and Clifford, 2003, 2006; Guo et al., 2009; Leopold et al., 2001), although one study found larger gender aftereffects with inverted faces (Watson and Clifford, 2006) while another found larger identity aftereffects with upright faces (Rhodes et al., 2009a). We have argued elsewhere that the equivalence of aftereffect magnitude for upright and inverted presentations of intact faces, when both adaptor and test have the same orientation, may simply reflect the fact that a weak adapting stimulus can adapt a weak pattern of activity (inverted faces) as capably as a strong adapting stimulus can adapt a strong pattern of activity (upright faces).

Next, we determined how adaptation was affected by disruption of second-order structure. This was achieved by exploding the images in Experiment 1, and by shifting features within a preserved facial outline in Experiment 2. The results were highly similar in both experiments. Faces with altered second-order structure could still generate an aftereffect in intact upright test faces, though the aftereffect was smaller than that seen when intact faces were used as adaptors. This suggests that despite the disruption in second-order structure between features, faces with altered second-order structure can engage the normal upright face representations, though with reduced efficiency. This reduction in efficiency can be taken as a measure of the contribution of second-order structure within

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these normal upright face representations. On the other hand, the fact that there is still a significant aftereffect from configurally altered adaptors on intact-test stimuli indicates that these upright face representations of identity contain properties other than second-order structure, which could include both local feature shape as well as non-shape properties such as texture and reflectance (O'Toole et al., 1999; Russell et al., 2007).

It is also of interest that the combination of adaptors with altered second-order structure and intact-test stimuli showed an inversion effect similar to that seen with intact adaptors and intact-test stimuli. If second-order structure is an important part of upright representations but less so for inverted representations, then one might expect an interaction stemming from more effective adaptation from intact than configurally altered faces in the upright condition, compared to more similar effects from these two different adaptors in the inverted condition. Instead we find that intact adaptors remain more effective than adaptors with altered second-order structure in the inverted condition, and that in fact configurally altered adaptors do not generate a significant after effect for inverted faces. These two observations suggest that the second-order structure that is disrupted in exploded or configurally altered stimuli also form a significant component of inverted face representations.

While the latter conclusion may sound surprising, it is in fact consistent with observations that not all second-order relations are dramatically affected by inversion. Subjects can still perceive local short-range relations – i.e., spatial distances between adjacent features – in inverted faces, particularly in regions of high-saliency like the eyes (Barton et al., 2001; Malcolm et al., 2005; Goffaux and Rossion, 2007; Sekunova and Barton, 2008), which are the regions that contain the most useful diagnostic information regarding face identity.

Finally, we used scrambled faces to determine the impact on adaptation of altered first-order structure. Such stimuli have the appearance of a collection of facial features rather than a face-like appearance. Scrambled face adaptors did not elicit aftereffects in intact-test faces, in either Experiment 1 or Experiment 2. Therefore, a collection of features that lacks a global face-like structure is unable to engage the normal face representations responsible for face aftereffects.

The fact that scrambled faces also did not generate any aftereffects for inverted intact-test stimuli underscores the point that inverted faces are more than just a collection of independent 'free-floating' features stripped of any spatial relation to each other. This point is further emphasized when contrasted with the data for upright scrambled-test faces, which do have the appearance of free-floating features, being devoid of any face-like organization. The representations of these scrambled stimuli are equally well adapted by both intact and scrambled face adaptors, despite the radically different spatial organizations of these two adapting stimuli. Thus a face-like configuration with correct first-order structure is necessary to generate any aftereffect on intact faces, be they upright or inverted, whereas such a configuration is redundant when the representation is simply a collection of facial features.

All together, the data from the configurally altered adaptors and the scrambled adaptors indicate significant similarities between upright and inverted face representations, in that both require a whole-face configuration for access by adapting stimuli, and both contain second-order structural information. Any failure in perceiving such structural properties in inverted faces, as demonstrated in numerous studies (Rhodes, 1988; Bartlett and Searcy, 1993; Freire et al., 2000; Leder and Bruce, 2000; Barton et al., 2001, 2003a, 2003b; Malcolm et al., 2005), cannot be blamed on their absence in inverted face representations, but rather reflect problems in how inverted faces are processed. That is, the defect lies at a mechanistic rather than a representational level. Consistent with this are observations that deficits in perceiving second-order structure in faces can be mitigated by focusing attention on single changes experimentally or allowing more processing time (Barton et al., 2001).

These and other observations have led to the hypothesis that the critical impairment with inversion of faces is the ability to process multiple aspects of facial structure simultaneously, efficiently and in an integrated manner, over the whole face – essentially a convergence of holistic and configurational views (Malcolm et al., 2005; Sekunova and Barton, 2008; Rossion, 2009). Second-order structure may be more vulnerable than feature information because of the limited spatial range of the local processing that operates with inverted faces. Tellingly, the second-order structure that can be processed relatively well in inverted faces are short-range ones in the highly salient eye region, the region that local processing would tend to target first (Barton et al., 2001, 2003a; Malcolm et al., 2005). Inversion disproportionately impairs the perception of short-range spatial relations in less salient regions like the mouth (Barton et al., 2001), longer-range spatial relations that require referencing across a larger expanse of the face (Goffaux and Rossion, 2007; Sekunova and Barton, 2008), and effects that require integration of spatial relations from different facial regions (Barton et al., 2003b), all of which would logically follow from loss of a whole-face capacity to extract facial structure. Whether whole-face structural processing equates to holistic processing can be debated (Rossion, 2009): the key issue may center on whether non-shape properties of faces are also processed in a manner that is integrated with and indivisible from facial shape. There is some evidence for inversion effects for whole-face reflectance maps that are devoid of shape information, though it has been pointed out that local reflectance variations can create non-shape features that nevertheless also have spatial relations (Russell et al., 2007). On the other hand, reaction time data for upright faces suggest that local feature color is not integrated perceptually with spatial relations in the same manner that two different spatial relations are integrated (Barton et al., 2003b) and, unlike the perception of short-range spatial relations discussed above, the perception of the color of a less salient feature like the mouth does not suffer greatly from inversion (Barton et al., 2003a), which would have been expected if local reflectance were also affected by constriction of the perceptual field from whole face to local regions.

Although ours is not an anatomic study, there are some neuroimaging data on the correlates of the processing of features, spatial relations, and whole-face representations. Some studies suggest a localization of whole-face processing to the right fusiform gyrus, based on a comparison of matching of whole faces versus face parts (Rossion et al., 2000) or on fMRI adaptation of the composite face effect (Schiltz et al., 2010). In

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contrast, feature-based processing may be more typical of either the left fusiform gyrus (Rossion et al., 2000) or other face-network components such as the occipital face area or superior temporal sulcus (Liu et al., 2010). The potential for a common substrate for upright and inverted whole faces in the right fusiform face area is suggested by studies showing comparable activation in the fusiform face area with either upright or inverted faces (Aguirre et al., 1999; Kanwisher et al., 1998; Haxby et al., 1999; Schiltz and Rossion, 2006). Also, others have found that inter-subject differences in the behavioral face inversion effect correlate with activity in the fusiform face area but not in other face-responsive areas (Yovel and Kanwisher, 2005; Goffaux et al., 2009): hence face representations in this region may be key determinants of our perceptual experience of the identity of whole faces. If so, it becomes of interest to ask how fusiform activity is influenced by manipulations of spatial relations. Indeed, fMRI adaptation studies indicate that these relations may be preferentially coded in the fusiform face area (Rhodes et al., 2009b; Goffaux et al., 2009; Liu et al., 2010) – though one task-based analysis suggested that the fusiform sensitivity to spatial relations may not overlap with the fusiform face area (Maurer et al., 2007) – with disagreement as to whether a similar sensitivity is seen in the occipital face area (Rhodes et al., 2009b; Liu et al., 2010). The fact that both upright and inverted faces may be coded in the fusiform face area, and that this area shows sensitivity to the spatial relations of features, could indicate that processing in this region underlies the behavioral effects we have described.

Before closing it is also worth commenting upon the aftereffects generated in exploded and scrambled face representations in Experiment 1. While the adaptation of exploded and scrambled-test stimuli were of secondary interest, the results have relevance to our primary inquiry regarding adaptation of intact-face representations. First, the fact that scrambled face adaptors can induce an aftereffect in upright scrambled-test faces indicates that it is possible to adapt *featural* representations linked to identity, outside of the normal facial context, similar to what we have shown previously for facial expressions (Butler et al., 2008). Furthermore, as we have already mentioned, the fact that both intact and scrambled face adaptors generated equivalent aftereffects on scrambled-test faces implies that these featural representations have a high degree of invariance with regards to their spatial location and relative spatial arrangement. Second, for upright exploded-test stimuli, intact-face adaptors were surprisingly more effective than exploded face adaptors in generating an aftereffect, despite the fact that exploded-test stimuli are more similar to exploded adaptors than to intact adaptors. One possible explanation is that, in addition to being able to activate intact-face representations, as we have seen from the data for intact faces as test stimuli, exploded-test stimuli may *mandatorily* activate these whole-face representations, rather than the spatially independent feature representations adapted by scrambled faces. As we have also seen in the data for intact-test stimuli, whole-face representations are more effectively adapted by intact adaptors than by exploded adaptors, which would thus account for the paradoxical finding that intact adaptors are better than exploded adaptors at creating aftereffects for exploded-test faces.

In summary, our scrambled adaptor data suggest that a face-like configuration is required to adapt intact-face representations, and that this is true for both upright and inverted faces. This is not due to an inability of a non-face-like collection of features to generate aftereffects on features, because scrambled adaptors can adapt scrambled-test faces. Rather, a whole-face configuration may be mandatory to access whole-face representations. These whole-face representations contain both second-order relational and non-relational properties, the latter of which could include properties such as feature shape, surface texture and reflectance. Correct second-order structure is not necessary to partially engage these whole-face representations, but is required for optimal activation. Importantly, these findings concerning second-order structure are true for both upright and inverted faces. Altogether, the data from both scrambled and exploded or configurally altered adaptors suggest that inverted faces are not represented as independent features, but rather as whole faces that also include second-order relations, much like upright faces. These data imply that the evidence showing that the processing of inverted faces emphasizes local features and local spatial relations in high-salience regions, at the expense of efficient whole-face processing and long-range spatial relations, does not reflect limitations inherent to facial representations themselves, but are likely due to reduced spatial range and efficiency of the perceptual processes operating on these complex shape representations.

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