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Inverted faces benefit from whole-face processing

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Abstract

Upright faces are thought to engage holistic processing whereby local regions are integrated into a unified whole for the purposes of rapid, efficient analysis. In contrast, inverted faces are thought to recruit a slower, less-accurate serial analysis of local features. Aperture paradigms, whereby a target face is revealed by a dynamic viewing window that shifts over the stimulus image, offer a compelling test of this view. If upright faces are processed holistically, perceptual judgements ought to be substantially disrupted when stimuli are viewed through apertures. In contrast, aperture viewing should produce little or no decrement in perceptual decisions when judging inverted faces, as they are thought to be subjected to serial feature-based analysis. Here we present four experiments that elucidate the effects of aperture viewing on the perception of upright and inverted faces. In our first two experiments, we find evidence of disproportionate aperture effects for upright faces relative to inverted faces. However, these findings are qualified by the fact that observers found it harder to discriminate inverted faces presented in the 'baseline' whole-face condition. When observers' ability to discriminate faces in the whole-face condition was matched for difficulty (Experiments 3 and 4), we show that upright and inverted faces produce very similar aperture effects. These findings indicate that both upright and inverted faces benefit from whole-face processing and accord with other lines of evidence that faces engage qualitatively similar types of processing in both orientations.

Key words: Aperture viewing; face perception; face inversion effect; holistic face processing.

Introduction

Although orientation inversion impairs perceptual judgements about many classes of visual stimulus, the magnitude of the decrement seen with faces is particularly large (Rossion, 2008; Yin, 1969). In their strongest form[1], theories of "holistic" or "whole-face" processing argue that this *face inversion effect* reflects the fact that upright and inverted faces are processed in qualitatively different ways: Upright faces are thought to engage holistic processing, whereby distal features are processed in parallel, and integrated into a unified perceptual whole. When judging inverted faces, however, observers are unable to process stimuli holistically and are therefore forced to base perceptual decisions on a slower, less-accurate serial analysis of local features (Farah, Wilson, Drain, & Tanaka, 1998; McKone, Kanwisher, & Duchaine, 2007; Robbins & McKone, 2003; Rossion, 2008; Tsao & Livingstone, 2008; Yovel, 2016; Yovel & Kanwisher, 2008).

Theories of holistic processing have been strongly influenced by findings from the composite face illusion (Hole, 1994; Young, Hellawell, & Hay, 1987). When face halves taken from different individuals are aligned, they appear to fuse together perceptually. The illusion appears to reveal the integration of information from distal facial regions (Murphy, Gray, & Cook, 2017; Rossion, 2013), and manifests more strongly when composite arrangements are presented upright than when inverted (McKone et al., 2013; Susilo, Rezlescu, & Duchaine, 2013). Evidence of putative feature integration processes that operate when faces are shown upright, but not when inverted, accord well with theories of holistic face processing (Farah et al., 1998; McKone et al., 2007; Richler, Wong, & Gauthier, 2011; Robbins & McKone, 2003; Rossion, 2008; Tsao & Livingstone, 2008; Yovel, 2016; Yovel & Kanwisher, 2008).

There is, however, increasing uncertainty about the functional significance of the composite face illusion. In particular, several authors have found no association between illusion susceptibility and face recognition ability in the typical population (Konar, Bennett, & Sekuler, 2010; Rezlescu, Susilo, Wilmer, & Caramazza, 2017) and have found that individuals with severe lifelong face-recognition difficulties – developmental prosopagnosics – exhibit normal susceptibility to the illusion (Biotti et al., 2017; Le Grand et al., 2006; Susilo et al., 2010; Ulrich et al., 2017). There has also been considerable debate about the perceptual, attentional, and decisional components of the effect (Fitousi, 2015, 2016; Richler & Gauthier, 2014; Rossion, 2013), and it has been noted that the

illusion can be seen with abstract cartoon faces (Murphy et al., 2017). Given the uncertainty surrounding the composite face illusion, it is important that we develop new complementary ways to test theories of holistic face processing.

Aperture paradigms – whereby observers judge stimuli inspected through a dynamic viewing window – represent a promising new approach. In the context of face perception research, authors have employed aperture techniques to address two questions. First, aperture methods, including 'Bubbles' (Gosselin & Schyns, 2001) and reverse correlation methods (e.g., Sekuler, Gaspar, Gold, & Bennett, 2004), have been used to reveal which facial regions are informative when making particular judgments. Studies in this tradition have repeatedly highlighted the value of the information contained within the eye-region (Gosselin & Schyns, 2001; Haig, 1985; Sekuler et al., 2004). Second, aperture techniques have been used to investigate holistic face processing (Evers, Van Belle, Steyaert, Noens, & Wagemans, 2018; Murphy & Cook, 2017; Van Belle, De Graef, Verfaillie, Busigny, & Rossion, 2010; Van Belle, De Graef, Verfaillie, Rossion, & Lefèvre, 2010). It is this application of the aperture paradigm that we are concerned with in the present article.

By forcing observers to inspect faces through a viewing window, aperture paradigms block or reduce holistic face processing. While participants still have the opportunity to inspect each local feature, they are unable to process distal regions in parallel. Instead, observers must process faces in a serial region-by-region way similar to the piecemeal analysis thought to be engaged when viewing inverted faces. The results from aperture paradigms are important because they allow vision scientists to directly assess the causal contribution of holistic processing to perceptual judgements about faces – researchers can block holistic processing and examine the consequences (Tanaka & Farah, 1993; Van Belle, De Graef, Verfaillie, Rossion, et al., 2010).

Strong versions of holistic face processing theory (Farah et al., 1998; McKone et al., 2007; Robbins & McKone, 2003; Rossion, 2008; Tsao & Livingstone, 2008; Yovel, 2016; Yovel & Kanwisher, 2008) predict disproportionate aperture effects when viewing upright faces, relative to inverted faces. Because they are thought to engage holistic processing, perceptual judgements about upright faces briefly viewed in their entirety ought to be more accurate than when the same stimulus is viewed through a dynamic aperture. Conversely, if inverted faces are subject to serial feature-based analysis, aperture viewing should produce

little or no decrement in perceptual decisions, relative to whole-face presentation. To date, however, studies using aperture paradigms have produced mixed support for these predictions.

Van Belle, De Graef, Verfaillie, Rossion, et al. (2010) described results from an aperture viewing experiment (N = 16) that appear to support the predictions made by holistic face processing theories. Having first seen a target face in full-view (1 second), participants were required to judge which of two simultaneously presented faces matched the target (unlimited). The two test faces were either viewed in full, or inspected through a gaze-contingent aperture window that revealed local facial regions as they were fixated by the observer. When the target and test faces were viewed in their entirety, Van Belle, De Graef, Verfaillie, Rossion, et al. (2010) found that matching accuracy (% correct) was reduced substantially by orientation inversion. When the test faces were inspected through the aperture, however, face matching accuracy was largely unaffected by the orientation manipulation – the face inversion effect did not reach significance.

Murphy and Cook (2017) published contradictory results that appear to challenge some of the prevailing assumptions made about holistic face processing. In a series of twelve experiments (all N = 16), Murphy and Cook (2017) compared perceptual judgements made about faces either viewed in their entirety, or inspected through a fixed-trajectory dynamic aperture that gradually moved across a single target image. Participants were required to make simple binary decisions about morphed facial images, including classifications of identity, facial sex, and expression. The degree of decision noise seen in the different viewing conditions was inferred from the slope of participants' psychometric functions. Murphy and Cook (2017) failed to find evidence for disproportionate aperture effects when viewing upright faces in any of the twelve experiments. Instead, they found that the aperture-induced decrements seen when judging inverted faces were similar – or sometimes greater – than those seen for upright faces.

Here we present four experiments that sought to elucidate the effects of aperture viewing on the perception of upright and inverted faces. In our first two experiments, we found evidence of disproportionate aperture effects for upright faces relative to inverted faces, replicating the findings of Van Belle, De Graef, Verfaillie, Rossion, et al. (2010). However, these findings were qualified by the fact that observers found it harder to discriminate

inverted faces presented in the whole-face condition; i.e., they were closer to floor in the 'baseline' condition. When observers' ability to discriminate faces in the whole-face condition was matched (Experiments 3 and 4), we show that upright and inverted faces produce comparable aperture effects, consistent with the findings of Murphy and Cook (2017).

Experiment 1

In the study reported by Murphy and Cook (2017) participants made binary classification judgements about stimuli drawn from morph continua. Levels of decision noise were inferred from the slope of the resulting psychometric functions; a measure that describes the change in response likelihood as a function of the strength of the signal present in the stimulus. In the present study we switched to a complementary facial sex categorisation paradigm. Observers judged the sex of faces briefly viewed in their entirety, or inspected through a fixed-trajectory dynamic aperture that moved across the image. The rationale for this change was two-fold: First, the new approach allowed us to derive a reliable measure of perceptual sensitivity (*d´*) from fewer trials and was therefore expected to be easier for naïve observers. Second, we were keen to establish whether the findings of Murphy and Cook (2017) could be replicated using a different psychophysical paradigm.

Methods

Twenty typical adults completed Experiment 1 (M_{age} = 27.2 years; SD_{age} = 7.0; 6 males). Three participants were replacements for observers who performed at chance levels.
In all four experiments, sample size was determined *a-priori* through reference to previous aperture studies (Murphy & Cook, 2017; Van Belle, De Graef, Verfaillie, Rossion, et al., 2010). Ethical clearance was granted by the local ethics committee and the experiment was conducted in line with the ethical guidelines laid down in the 6th (2008) Declaration of Helsinki. All participants gave informed consent and were fully debriefed upon task completion.

Video stimuli presented a single static facial image (Figure 1a) either upright or inverted. Each image was a morph containing 20% of a particular facial identity (16 females, 16 males), and 80% of an androgynous average face created by combining all 32 faces (Figure 1b). The strong weighting of the androgynous average was intended to dilute sexually dimorphic signals present in each facial identity, and thereby make the sex categorisation

task challenging. All faces were taken from the Chicago Face Database (Ma, Correll, & Wittenbrink, 2015). Morphing was completed using the procedure developed by Adams, Gray, Garner, and Graf (2010). All faces were presented in greyscale. The external features (e.g., hairline) were occluded by an oval mask.

Figure-1

Each video sequence was constructed from a series of bitmap images. These sequences were compiled in Matlab (The MathWorks, Natick, MA) and saved as uncompressed .avi files. Whole-face sequences presented a single static face in its entirety for 480ms (Figure 1c). Faces were presented briefly in this condition to prevent observers employing a protracted serial analysis of the local features; for example observers who are thought be reliant on trivial local cues (e.g., developmental prosopagnosics) find this kind of presentation duration particularly challenging (Biotti & Cook, 2016; Biotti, Gray, & Cook, 2019; Cenac, Biotti, Gray, & Cook, 2019). Aperture sequences depicted a viewing window moving over the facial image with a vertical directionality (Figure 1d), either starting at the top and moving downwards, or starting at the bottom and moving upwards. The aperture was 12% the height of the face (~4.8° of visual arc when viewed at 58cm) and took 7.2 secs to move across the face. The timing of the sequence ensured that the aperture motion was smooth and gave participants ample time to inspect local features.

Each trial started with a cue indicating whether a whole-face or an aperture stimulus would be presented. On aperture trials, the cue also indicated the directionality of the aperture transition[2]. Next, participants were presented with a single video stimulus and were required to make a binary categorization judgement about the facial image presented ("Female or Male?"). Following stimulus offset, a response screen was visible until a keypress response was registered. Facial Orientation (upright, inverted) and Viewing Condition (whole-face, aperture) were manipulated in a factorial design. Each of the 32 target faces were presented 4 times in the whole-face condition (twice upright, twice inverted), 4 times through an aperture that moved upwards (twice upright, twice inverted), and 4 times through an aperture that moved downwards (twice upright, twice inverted), yielding 384 experimental trials in total. Trial type was randomly interleaved within four mini-blocks of 96 trials. All experiments were programmed in Matlab using the

Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a LCD display at 60 Hz refresh rate.

Signal Detection Theory (Macmillan & Creelman, 1991) was employed to estimate observers' perceptual sensitivity (*d´*) in each viewing condition. A 'female' response in the presence of a female stimulus was deemed to be a hit. A 'female' response in the presence of a male stimulus was deemed to be a false alarm. Where participants achieved the maximum number of hits possible in a given condition, the raw frequency was adjusted downwards by 0.5; similarly, where participants made no false alarms, the raw frequency was adjusted upwards by 0.5, in order to estimate *d´*. We also collected response time (RT) data for all experiments, analyses of which are provided as supplementary online material.

Results

Sensitivity estimates (Figure 2a) were analyzed using ANOVA with Viewing Condition (whole-face, aperture) and Facial Orientation (upright, inverted) as within-subjects factors. We observed main effects of Viewing Condition [$F(1,19) = 104.163$, $p < .001$, $\eta^2 = .846$] and Facial Orientation [$F(1,19) = 49.036$, $p < .001$, $\eta^2 = .721$], whereby whole-face presentation and upright orientation, were associated with superior discrimination sensitivity, respectively. The analysis also revealed a Viewing Condition × Orientation interaction [$F(1,19) = 12.756$, $p = .002$, $\eta^2 = .402$], whereby whole-face presentation was associated with greater benefit when viewing upright faces, than inverted faces. Nevertheless, we observed significant aperture effects for both upright [$t(19) = 8.120$, $p < .001$, Cohen's $d = 1.816$] and inverted faces [$t(19) = 3.846$, $p = .001$, Cohen's $d = .860$]. Significant effects of orientation inversion were seen in both the whole-face [$t(19) = 6.649$, $p < .001$, Cohen's $d = 1.487$] and aperture [$t(19) = 4.437$, $p = .003$, Cohen's $d = .768$] viewing conditions.

When judging upright faces, both the downwards [$t(19) = 7.283$, $p < .001$, Cohen's $d = 1.626$] and upwards [$t(19) = 7.100$, $p < .001$, Cohen's $d = 1.590$] aperture conditions produced significant performance decrements relative to the whole face condition. The aperture effects produced by downwards ($M = .730$, $SD = .449$) and upwards transitions ($M = .879$, $SD = .553$) did not differ significantly [$t(19) = 1.376$, $p = .185$, Cohen's $d = .308$]. Similarly, when judging inverted faces, both the downwards [$t(19) = 3.436$, $p = .003$, Cohen's $d = .767$] and upwards [$t(19) = 2.770$, $p = .012$, Cohen's $d = .618$] aperture

conditions produced significant performance decrements relative to the whole face condition. Once again, the aperture effects produced by downwards (M = .353, SD = .460) and upwards transitions (M = .249, SD = .403) did not differ significantly [$t(19) = 1.021$, p = .320, Cohen's d = .228].

Figure-2

Experiment 2

Our first experiment employed an aperture with a short-wide aspect-ratio that made a vertical transition, from top-to-bottom, or *vice-versa*. Our second experiment was identical to the first, except that an aperture with a tall-thin aspect-ratio made a horizontal transition, from left to right, or *vice versa*. Different aperture shapes might conceivably induce different patterns of aperture decrement (Murphy & Cook, 2017). For example, short-wide viewing windows such as that employed in the first experiment may allow observers to view the eye-region – known to be particularly informative when judging faces (Gosselin & Schyns, 2001; Sekuler et al., 2004) – in its entirety. Alternatively, tall-thin viewing windows may help observers extract the horizontal information structure (the facial 'bar-code') thought to be important for the recognition of faces (Dakin & Watt, 2009; Goffaux & Rossion, 2007). We therefore sought to replicate the results of Experiment 1 using an aperture window with a different aspect-ratio.

Twenty typical adults completed Experiment 2 (M_{age} = 28.2 years; SD_{age} = 7.7; 1 male). One participant was a replacement for an observer who performed at chance levels. Experiment 2 was identical to the first, except that in the aperture condition, a tall-thin viewing window made a horizontal transition across the image. The viewing window could start at the left and move rightwards, or start at the right and move leftwards. The aperture was 12% the width of the face (~4.5° of visual arc when viewed at 58cm) and took 7.2 secs to move across the face. Once again, whole-face sequences presented a single static face in its entirety for 480ms.

Results

Sensitivity estimates (Figure 2b) were analyzed using ANOVA with Viewing Condition (whole-face, aperture) and Facial Orientation (upright, inverted) as within-subjects factors. We observed main effects of Viewing Condition [$F(1,19) = 17.506$, $p < .001$, $\eta_2 = .480$]

and Facial Orientation [$F(1,19) = 92.693$, $p < .001$, $\eta^2 = .830$], whereby whole-face presentation and upright orientation, were associated with superior discrimination sensitivity, respectively. The analysis also revealed a Viewing Condition × Orientation interaction [$F(1,19) = 8.218$, $p = .010$, $\eta^2 = .302$], whereby whole-face presentation was associated with greater benefit when viewing upright faces, than inverted faces. We observed significant aperture effects for upright faces [$t(19) = 5.153$, $p < .001$, Cohen's $d = 1.152$], but not for inverted faces [$t(19) = 1.525$, $p = .144$, Cohen's $d = .341$]. Significant effects of orientation inversion were seen in both the whole face [$t(19) = 7.466$, $p < .001$, Cohen's $d = 1.669$] and aperture [$t(19) = 6.640$, $p < .001$, Cohen's $d = 1.485$] viewing conditions.

When judging upright faces, both the rightwards [$t(19) = 4.056$, $p = .001$, Cohen's $d = .907$] and leftwards [$t(19) = 4.812$, $p < .001$, Cohen's $d = 1.076$] aperture conditions produced significant performance decrements relative to the whole face condition. The aperture effects produced by rightwards ($M = .640$, $SD = .706$) and leftwards transitions ($M = .635$, $SD = .590$) did not differ significantly [$t(19) = .047$, $p = .963$, Cohen's $d = .011$]. When judging inverted faces, however, neither the rightwards [$t(19) = 1.710$, $p = .104$, Cohen's $d = .382$], nor the leftwards [$t(19) = .772$, $p = .450$, Cohen's $d = .173$] aperture conditions produced significant performance decrements relative to the whole face condition. The aperture effects produced by rightwards ($M = .196$, $SD = .513$) and leftwards transitions ($M = .128$, $SD = .740$) did not differ significantly [$t(19) = .690$, $p = .498$, Cohen's $d = .154$].

Experiment 3

Despite using different aperture windows with different shapes and transition-directionalities, the results of our first two experiments were very similar. Observers in both experiments exhibited less perceptual sensitivity when they inspected faces through apertures, than when they were permitted to briefly view target faces in their entirety. Importantly, perceptual decrements induced by aperture viewing were greater when faces were viewed upright, than when presented upside-down, replicating the findings of Van Belle, De Graef, Verfaillie, Rossion, et al. (2010).

At first glance, these results accord with strong theories of holistic face processing (Farah et al., 1998; McKone et al., 2007; Robbins & McKone, 2003; Rossion, 2008; Tsao & Livingstone, 2008; Yovel, 2016; Yovel & Kanwisher, 2008). These accounts predict larger

aperture effects when viewing upright faces because the dynamic viewing window blocks holistic processing. In contrast, the piecemeal or parts-based processing thought to be recruited by inverted faces ought to be disrupted less by aperture viewing. It is possible, however, that inverted faces produce smaller aperture decrements simply because this condition is harder. When categorising the sex of items presented in the whole-face condition, participants were able to achieve far better levels of performance in the upright conditions (mean *d´*s of ~ 1.8) than in the inverted conditions (mean *d´*s of ~ 0.8). As a result, there may have been less scope to detect decrements in performance arising from aperture viewing in the inverted conditions. We sought to distinguish these possibilities in Experiments 3 and 4.

In the first two experiments the facial stimuli presented in the upright and inverted conditions were identical; i.e., the signal present in the 32 to-be-judged faces was always 20%. In Experiments 3 and 4, we sought a fairer comparison of the aperture effects observed for upright and inverted faces by matching the difficulty of the baseline whole-face conditions. To this end, we increased the signal strength in the to-be-judged faces in the inverted condition. In Experiment 3, the aperture made a vertical transition from top to bottom, or *vice-versa*. In Experiment 4, the aperture made a horizontal transition, from left to right, or *vice versa*.

Method

Twenty typical adults completed Experiment 3 (M_{age} = 27.3 years; SD_{age} = 6.7; 1 male). Two participants were replacements for observers who performed at chance levels. The stimuli used in the upright condition were identical to those employed in Experiment 1 (the male and female identities were presented at 20% strength). However, in order to make the sex discriminations in the inverted condition a little easier, the male and female identities were presented at 40% strength. Informal piloting suggested this would equate baseline levels of discrimination ability in the upright and inverted whole-face conditions. In all other respects, Experiment 3 was identical to Experiment 1.

Results

Sensitivity estimates (Figure 2c) were analyzed using ANOVA with Viewing Condition (whole-face, aperture) and Facial Orientation (upright, inverted) as within-subjects factors. We observed main effects of Viewing Condition [$F(1,19) = 35.771$, $p < .001$, $\eta_2 = .653$]

and Facial Orientation [$F(1,19) = 5.790$, $p = .026$, $\eta_2 = .234$] whereby whole-face presentation and *inverted* orientation, were associated with superior discrimination sensitivity, respectively. The Viewing Condition × Facial Orientation interaction failed to reach significance [$F(1,19) = 3.832$, $p = .065$, $\eta_2 = .168$]. We observed significant aperture effects for both upright [$t(19) = 5.252$, $p < .001$, Cohen's $d = 1.174$] and inverted faces [$t(19) = 4.946$, $p < .001$, Cohen's $d = 1.106$]. A significant effect of orientation (inverted > upright) was seen in the aperture condition [$t(19) = 3.437$, $p = .003$, Cohen's $d = .736$], but not in the whole-face condition [$t(19) = .861$, $p = .400$, Cohen's $d = .193$].

When judging upright faces, both the downwards [$t(19) = 4.292$, $p < .001$, Cohen's $d = .960$] and upwards [$t(19) = 5.117$, $p < .001$, Cohen's $d = 1.144$] aperture conditions produced significant performance decrements relative to the whole face condition. Upwards transitions ($M = 1.025$, $SD = .896$) produced greater decrements than downwards transitions ($M = .696$, $SD = .725$) [$t(19) = 2.793$, $p = .012$, Cohen's $d = .625$], suggestive of a perceptual advantage when the aperture window reveals the eyes before the nose and mouth[3]. When judging inverted faces, both the downwards [$t(19) = 4.481$, $p < .001$, Cohen's $d = 1.002$] and upwards [$t(19) = 4.451$, $p < .001$, Cohen's $d = .995$] aperture conditions produced significant performance decrements relative to the whole face condition. The aperture effects produced by downwards ($M = .628$, $SD = .626$) and upwards transitions ($M = .513$, $SD = .515$) did not differ significantly [$t(19) = .802$, $p = .432$, Cohen's $d = .175$].

Experiment 4

Twenty typical adults completed our fourth experiment ($M_{age} = 26.8$ years; $SD_{age} = 9.5$; 2 male). Three participants were replacements for observers who performed at chance levels. Experiment 4 was identical to Experiment 3, except that in the aperture condition, the viewing window made a horizontal transition across the image, either from right-to-left, or *vice-versa*. The shape of the aperture window and the duration of the horizontal transitions were the same as in Experiment 2.

Results

Sensitivity estimates (Figure 2d) were analyzed using ANOVA with Viewing Condition (whole-face, aperture) and Facial Orientation (upright, inverted) as within-subjects factors. We observed a main effect of Viewing Condition [$F(1,19) = 64.797$, $p < .001$, $\eta_2 = .773$]

whereby whole-face presentation was associated with superior discrimination sensitivity. However, we saw no effect of Facial Orientation [$F(1,19) = 0.049$, $p = .828$, $\eta^2 = .003$], and no Viewing Condition × Facial Orientation interaction [$F(1,19) = .553$, $p = .466$, $\eta^2 = .028$]. We observed significant aperture effects for both upright [$t(19) = 6.686$, $p < .001$, Cohen's $d = 1.496$] and inverted faces [$t(19) = 5.567$, $p < .001$, Cohen's $d = 1.245$]. We saw no effect of orientation in either the whole-face [$t(19) = .498$, $p = .624$, Cohen's $d = .112$] or the aperture [$t(19) = .249$, $p = .806$, Cohen's $d = .056$] conditions.

When judging upright faces, both the rightwards [$t(19) = 6.997$, $p < .001$, Cohen's $d = 1.565$] and leftwards [$t(19) = 5.212$, $p < .001$, Cohen's $d = 1.165$] aperture conditions produced significant performance decrements relative to the whole face condition. The aperture effects produced by rightwards ($M = .919$, $SD = .588$) and leftwards transitions ($M = .798$, $SD = .685$) did not differ significantly [$t(19) = 1.000$, $p = .330$, Cohen's $d = .224$]. Similarly, when judging inverted faces, both the rightwards [$t(19) = 5.110$, $p < .001$, Cohen's $d = 1.143$] and the leftwards [$t(19) = 5.087$, $p < .001$, Cohen's $d = 1.137$] aperture conditions produced significant performance decrements relative to the whole face condition. The aperture effects produced by rightwards ($M = .720$, $SD = .630$) and leftwards transitions ($M = .717$, $SD = .631$) did not differ significantly [$t(19) = .023$, $p = .982$, Cohen's $d = .005$].

Discussion

In their strongest form, theories of holistic processing argue that upright and inverted faces recruit qualitatively different perceptual mechanisms: Upright faces are thought to engage holistic processing whereby local regions are integrated into a unified whole. In contrast, inverted faces are thought to recruit a serial parts-based analysis of local features (Farah et al., 1998; McKone et al., 2007; Richler, Wong, et al., 2011; Robbins & McKone, 2003; Rossion, 2008; Tsao & Livingstone, 2008; Yovel, 2016; Yovel & Kanwisher, 2008). Aperture paradigms offer a compelling test of this view (Evers et al., 2018; Murphy & Cook, 2017; Van Belle, De Graef, Verfaillie, Busigny, et al., 2010; Van Belle, De Graef, Verfaillie, Rossion, et al., 2010). If upright faces are processed holistically, perceptual judgements ought to be substantially disrupted when observers are forced to view stimuli through apertures. In contrast, aperture viewing should produce little or no decrement in perceptual decisions when judging inverted faces, as they are thought to be subjected to serial feature-based analysis.

Our findings do not accord with these predictions. When upright and inverted faces were matched for discriminability in the baseline whole-face condition, we found that aperture viewing produced substantial performance decrements in both orientation conditions, consistent with the results described by Murphy and Cook (2017). Together, these findings imply that both upright and inverted faces benefit from whole-face processing. We find evidence that aperture viewing disproportionately impairs judgements about upright faces – replicating the results of Van Belle, De Graef, Verfaillie, Rossion, et al. (2010) – only when performance in the baseline whole-face condition was significantly better in the upright condition, than in the inverted condition. Where observed (Experiments 1 and 2; Van Belle, De Graef, Verfaillie, Rossion, et al., 2010), disproportionate aperture effects for upright faces may therefore be caused by the limited scope to detect performance decrements in the inverted condition; i.e., evidence of whole-face processing of inverted faces may be obscured by restricted range or floor effects.

In the present study we employed a fixed-trajectory aperture manipulation in which a viewing window moved across the image in a predetermined direction, at a predetermined rate. In contrast, Van Belle, De Graef, Verfaillie, Rossion, et al. (2010) employed a gaze-contingent aperture paradigm whereby the region of the target face revealed by the viewing window was determined by the gaze fixations of the participant (see also: Evers et al., 2018; Van Belle, De Graef, Verfaillie, Busigny, et al., 2010). Under the gaze-contingent aperture paradigm employed by Van Belle, De Graef, Verfaillie, Rossion, et al. (2010), the participant determines which parts of the stimulus are visible, how long they are visible, and in which order the regions are revealed.

We prefer the fixed-trajectory approach because control over stimulus presentation resides with the experimenter. By using a fixed-trajectory approach we were able to ensure that all observers were exposed to the same visual information, irrespective of stimulus orientation (Murphy & Cook, 2017). Moreover, this approach lets researchers systematically manipulate the order in which regions are revealed. This may well be an interesting avenue for future research; for example, the fact that better perceptual decisions were made when the eye region of the target face was revealed early in aperture sequences (Experiment 3), suggests that information extracted from different local regions is combined in a non-arbitrary way. It might occur to some readers that the gaze-contingent approach allows

participants to sample facial information 'naturally'. Contrary to this intuition, however, it appears that observers do not inspect the target face as they would typically; rather, there is a tendency to fixate a region at the top of the nose (Van Belle, De Graef, Verfaillie, Rossion, et al., 2010), possibly because participants *try* to view both eye regions simultaneously (even where the size of the aperture window does not permit this).

In the present study we used facial sex judgements and image morphing to derive our facial stimuli. In contrast, Van Belle and colleagues used an identity matching procedure and unmodified images. We would be surprised if these factors explained the discrepant pattern of results seen in Experiments 3 and 4. Judgements about facial sex and facial identity are thought to depend on a common structural representation formed early in the face processing stream (Bruce & Young, 1986). Both types of judgements also exhibit markers of holistic processing including inversion and aperture effects (e.g., Murphy & Cook, 2017), and the composite face illusion (Baudouin & Humphreys, 2006). Similarly, morphed facial images produce substantial inversion effects; for example, typical observers find the Cambridge Face Perception Test extremely challenging when to-be-sorted faces are shown upside-down (e.g., Biotti et al., 2019). Morphed target faces also produce aperture effects (Murphy & Cook, 2017) and the composite face illusion (Gray et al., in press).

Importantly, we were able to replicate the results of Van Belle, De Graef, Verfaillie, Rossion, et al. (2010) in Experiments 1 and 2. This suggests that the different pattern of results seen in Experiments 3 and 4 is not attributable to our use of a fixed-trajectory aperture paradigm, facial sex judgements, or face morphing. We cannot say for certain what Van Belle and colleagues would have found if their upright and inverted conditions had been matched for difficulty. In light of the present results, however, we speculate that they would have found similar aperture effects in both orientation conditions.

Target-face ambiguity and holistic processing

We sought to match performance in the upright and inverted whole-face conditions in order to provide a fair test of the view that aperture viewing disproportionately disrupts the processing of upright faces. This was achieved by employing faces in the upright and inverted conditions with weaker (20%) and stronger (40%) sexually dimorphic signals, respectively. We have argued that the comparable aperture effects seen for upright and inverted faces in Experiments 3 and 4 reflect the fact that we had equal scope to detect

performance decrements associated with aperture viewing; i.e., that we eliminated potential floor effects in the inverted face conditions.

During peer-review, it was suggested that we have *not* provided a fair comparison of the whole-face processing engaged by upright and inverted faces; that we only find comparable aperture effects for upright and inverted faces because we have unfairly constrained the holistic processing seen for upright faces. Because the sexually dimorphic signals present within the 20% faces were relatively weak, observers may have consciously sought diagnostic local features to augment their perceptual decisions. As a result, the 20% faces may have engaged weaker holistic processing and produced relatively small aperture effects. Consistent with this interpretation, it is clear that i) sex categorisation judgements can be based on trivial local features (e.g., eye-lashes, specular highlights on the lips), and ii) observers sometimes search for trivial details or distinctive features when confronted with challenging face discrimination tasks (Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006; de Xivry, Ramon, Lefevre, & Rossion, 2008; Duchaine & Weidenfeld, 2003; Ramon & Van Belle, 2016).

Taken to its extreme, this account might argue that the 20% faces used in the upright conditions engaged so little holistic processing, as to render our key result – comparable aperture effects for upright and inverted faces – meaningless. This is demonstrably not the case. In our first two experiments the 20% faces produced striking effects of inversion and aperture viewing – both thought to be markers of holistic processing (Murphy & Cook, 2017; Van Belle, De Graef, Verfaillie, Rossion, et al., 2010). As predicted by theories of holistic processing, we also observed Orientation × Viewing Condition interactions in Experiments 1 and 2, whereby aperture viewing produced greater perceptual decrements when observers judged upright faces. In both experiments, these effects were as strong (or even stronger) than those reported by Van Belle and colleagues (2010). In short, observers' judgements of the 20% faces behaved precisely as proponents of holistic processing theories would expect (Experiments 1 and 2), until the comparison inverted conditions were matched for difficulty (Experiments 3 and 4).

There are other aspects of this alternative interpretation that we also find questionable. First, several features of the 20% stimuli are likely to *increase* – not discourage – holistic processing. In order to dilute the sexually dimorphic signals present in the target faces, we

blended each facial image with an androgynous average face created by combing 32 individual faces. Because of the heavy weighting of this average, the 20% faces contained little high-spatial frequency information and depicted relatively average non-descript features. Trivial details present in unmodified natural images (eye-lashes, specular highlights) were therefore unlikely to appear in the 20% faces. Moreover, previous findings indicate that composite-face arrangements that preserve low-spatial frequency information, but eliminate high-spatial frequency information, produce larger illusions than full-spectrum faces (Goffaux & Rossion, 2006). Using a feature-context congruency paradigm, Goffaux (2012) also found that context-induced interference increased – suggestive of stronger holistic processing – as local feature discriminability *decreased*.

Second, the presentation durations of 480ms employed in the whole-face conditions permit little, if any, controlled processing of local facial regions. It is certainly the case that observers sometimes look for trivial details or distinctive features to perform challenging perceptual discrimination tasks. However, the characteristic feature of this processing is that it tends to be slow and effortful; for example, it typically takes prosopagnosics several seconds to find distinguishing details that let them identify faces. Observers who are reliant on this kind of analysis (e.g. cases of developmental or acquired prosopagnosia) therefore find brief presentation durations extremely challenging (Biotti & Cook, 2016; Biotti et al., 2019; Cenac et al., 2019). The fact that typical observers exhibit good discrimination and categorisation of briefly presented (upright) faces has been widely attributed to rapid, efficient holistic processing (Farah et al., 1998; McKone & Yovel, 2009; Richler, Wong, et al., 2011; Rossion, 2008, 2013).

Third, holistic processing appears to be automatic and obligatory, not something that observers can consciously inhibit (Jacques & Rossion, 2009, 2010; Kuefner, Jacques, Prieto, & Rossion, 2010; Murphy et al., 2017; Rossion, 2013). For example, when composite face arrangements are presented aligned and upright, typical observers cannot inhibit the manifestation of the resulting illusion, even where it hinders the speed and accuracy of their responding (Murphy et al., 2017; Rossion, 2013). Further evidence obtained using EEG suggests that holistic processing influences the structural encoding of faces within 200 ms of stimulus onset, as one would expect of an obligatory perceptual process (Jacques & Rossion, 2009, 2010; Kuefner et al., 2010).

Finally, it has been argued by some that the emergence of holistic processing is driven by the need to make challenging within-category discriminations between exemplars that share common first-order feature relations. In contrast, easier between-category discriminations are thought to be insufficient to trigger the emergence of automatic holistic processing (e.g., Richler, Wong, et al., 2011). A closely-related view is that typical observers have exquisite ability to encode and distinguish faces *because* they process faces holistically (DeGutis, Cohan, & Nakayama, 2014; Michel, Rossion, Han, Chung, & Caldara, 2006; Richler, Wong, et al., 2011; Tanaka, Kiefer, & Bukach, 2004). These views are hard to reconcile with the claim that easy-to-identify faces are processed holistically, but hard-to-identify faces are not.

What causes the face inversion effect?

Our results argue against the view that marked performance decrements when judging upside-down faces are caused by a shift from holistic to parts-based processing. So what is responsible for the face-inversion effect? In our first two experiments we saw striking inversion effects not only in the whole-face condition, but also in the aperture condition. A similar finding was also described by Murphy and Cook (2017). These inversion effects – seen in conditions where decisions are based on a serial analysis of local features – suggest that inverted faces may be harder to perceive because we are less able to encode the local regions. This conclusion accords with previously reported inversion effects for isolated facial features (Leder & Bruce, 2000; Leder, Candrian, Huber, & Bruce, 2001; Rakover & Teucher, 1997).

The suggestion that inverted faces benefit from whole-face processing appears inconsistent with the orientation sensitivity of the composite face illusion (e.g., McKone et al., 2013), widely regarded as a key measure of holistic face processing (Murphy et al., 2017; Rossion, 2013). Although the composite face illusion manifests more strongly when arrangements are shown upright, we note that significant illusory effects are still seen for inverted arrangements (Richler, Mack, Palmeri, & Gauthier, 2011; Susilo et al., 2013). We speculate that inverted composite face arrangements may induce weaker illusions, not because integration mechanisms are 'turned-off', but rather because inversion impairs the accuracy with which the constituent regions are encoded. Noisy local descriptions may induce weaker perceptual predictions; for example, a poor representation of the mouth region may

afford a weak prediction about the nature and likely content of the eye-region (Gray et al., in press).

We have examined the effects of aperture viewing on faces only. We therefore make no claims about the domain-specificity of our findings. Future studies, however, could use aperture paradigms to test the view that holistic processing also underlies orientation-specific perceptual expertise for non-face objects. Some authors have argued that other classes of object that comprise numerous exemplars, that share consistent first-order feature relations, and that have a canonical orientation, may also come to recruit orientation-specific holistic processing (Diamond & Carey, 1986; Gauthier & Tarr, 1997; Richler, Wong, et al., 2011). Consistent with this view, several studies have reported that so-called 'objects-of-expertise' produce substantial inversion effects, including dogs (Diamond & Carey, 1986), bodies (Reed, Stone, Bozova, & Tanaka, 2003), and budgerigars (Campbell & Tanaka, 2018). It would be interesting to see whether or not these objects-of-expertise also produce substantial inversion effects when viewed through apertures. In light of the present findings, we speculate that orientation-specific perceptual expertise may owe more to the accurate encoding of local features than currently appreciated.

It is beyond doubt that orientation inversion greatly hinders the processing of faces (Rossion, 2008; Valentine, 1988; Yin, 1969). However, evidence that both upright and inverted faces benefit from whole-face processing, accords with previous findings that suggest that upright and inverted faces engage similar neuro-cognitive mechanisms. For example, people tend to use the same facial regions to discriminate upright and inverted faces (Sekuler et al., 2004). Individual differences in upright and inverted face matching correlate strongly (Biotti et al., 2019; Klargaard, Starrfelt, & Gerlach, 2018) and perceptual learning about upright faces appears to generalise – at least in part – to inverted faces (Kramer, Jenkins, Young, & Burton, 2017). Neuroimaging studies indicate that upright and inverted faces both engage the fusiform face area (e.g., Haxby et al., 1999; Kanwisher, Tong, & Nakayama, 1998; Yovel & Kanwisher, 2005), although some authors have found that upright faces elicit greater signal change (e.g., Yovel & Kanwisher, 2005). Similarly, inverted faces elicit the N170 ERP component – a measure of structural encoding (Eimer, 2000) – albeit delayed and amplified relative to the ERPs seen for upright faces (Rossion et al., 2000). The foregoing findings provide convergent evidence for the view that the

processing of upright and inverted faces differs quantitatively, not qualitatively (Sekuler et al., 2004).

Footnotes

[1]Many authors use "holistic processing" as short-hand for "whole-face" processing. We follow this convention here. We note, however, that some authors have advanced an alternative view, arguing that isolated local regions may recruit some form of orientation-specific holistic or 'configural' processing in the absence of the wider face context (e.g., Leder & Bruce, 2000; Leder et al., 2001; Rossion, 2008, 2013).

[2]We elected to inform observers about the type of stimulus at the start of each trial to ensure that observers could orient to the window and anticipate its direction of travel as easily as possible. If this were not the case, aperture decrements might have arisen for theoretically uninteresting reasons.

[3]Where observed, feature-order effects (e.g., superior perceptual performance when eye-regions are revealed early in a sequence) are consistent with the serial accumulation of evidence from local regions.

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Figure 1

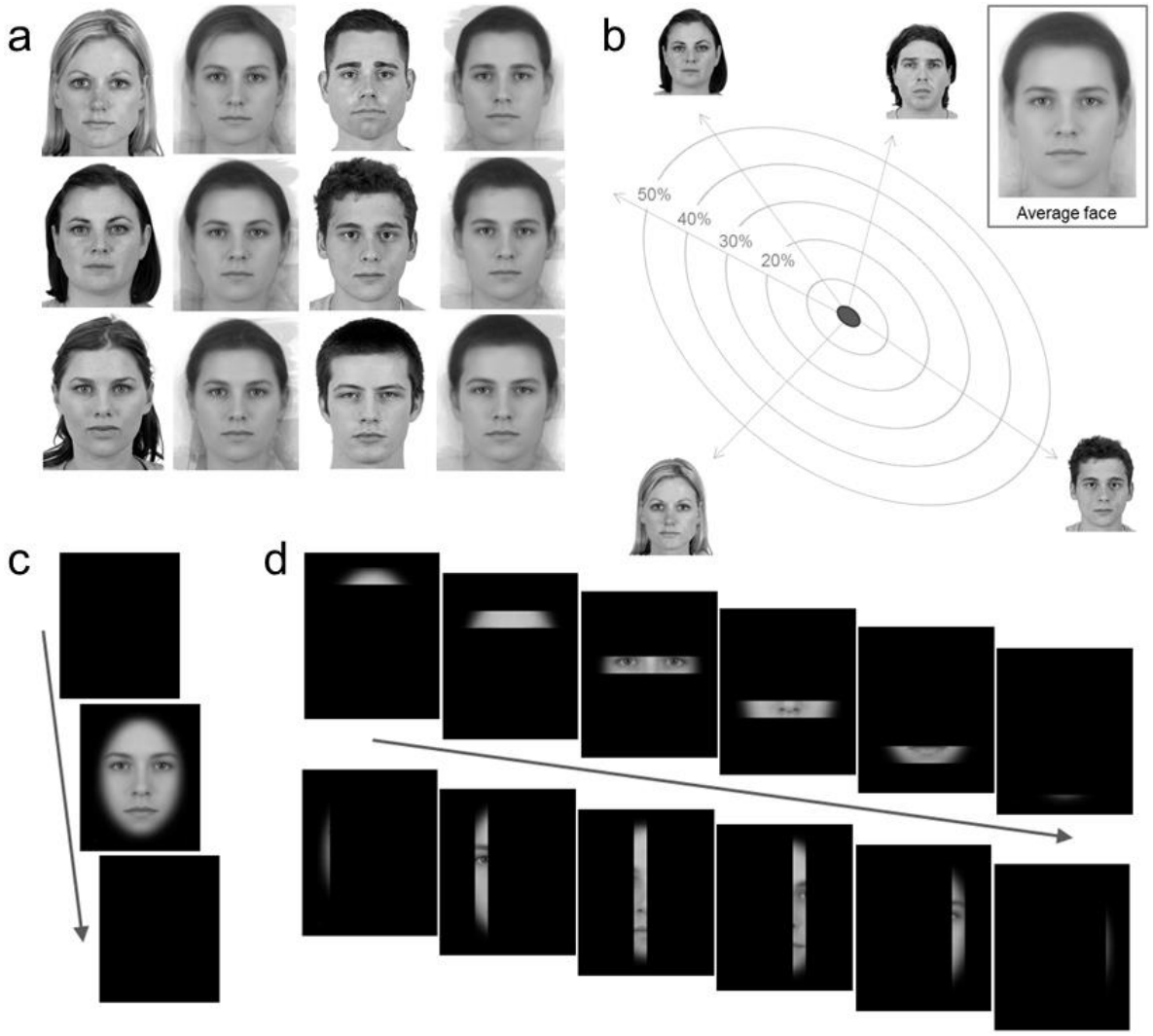

Figure 1: (a) Examples of the stimulus images judged by participants shown alongside the original facial image used to create each morph. (b) The stimulus images were weighted blends of an androgynous average face (80%) and the raw facial image (20%). (c) In the whole-face condition, trials presented a single stimulus image in its entirety for 480ms. (d) In the aperture conditions, a viewing window revealed the image incrementally over a period of 7.2 seconds, moving with a vertical (Experiments 1 & 3) or horizontal (Experiments 2 & 4) directionality.

Figure 2

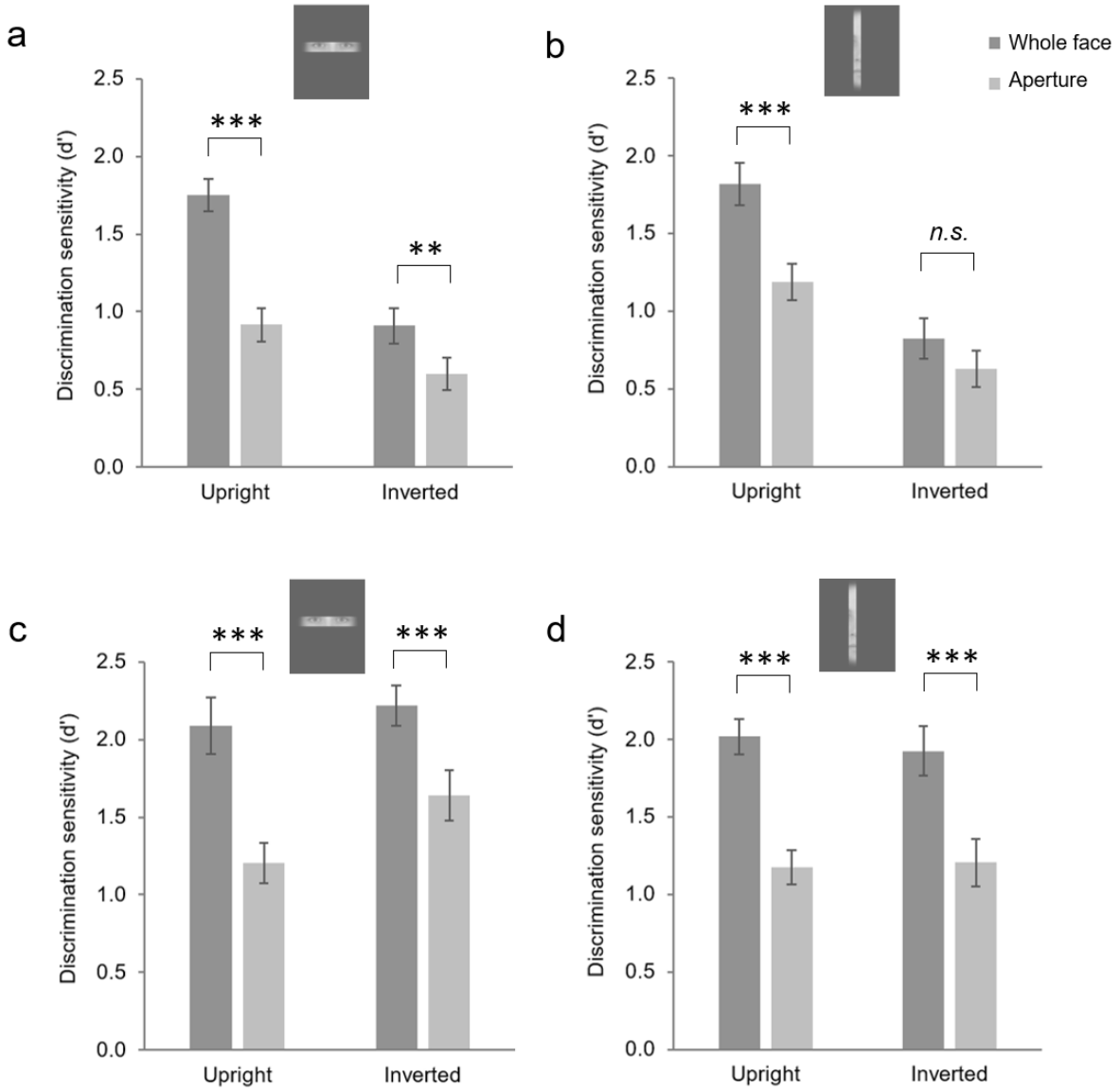

Figure 2: Results from Experiments 1-4 (a-d, respectively). Error bars denote ±1 SEM. ** denotes $p < .01$; *** denotes $p < .001$.

Supplementary analyses of response times

Experiment 1

Having excluded outlying values (> 3 *SD*s of each participant's mean RT), response times for correct responses (Figure S1a) were analyzed using ANOVA with Viewing Condition (whole-face, aperture) and Facial Orientation (upright, inverted) as within-subjects factors. We observed a main effect of Facial Orientation [$F(1,19) = 5.757$, $p = .027$, $\eta^2 = .233$], whereby responses tended to be slightly slower in the inverted condition. Responses were significantly slower in the inverted aperture ($M = 513$, $SD = 204$) condition than in the upright aperture condition ($M = 479$, $SD = 160$) [$t(19) = 2.118$, $p = .048$]. Responses in the upright whole-face condition ($M = 466$, $SD = 174$) and the inverted whole-face condition ($M = 489$, $SD = 155$) did not differ [$t(19) = .754$, $p = .460$]. We observed no main effect of Viewing condition [$F(1,19) = .578$, $p = .456$, $\eta^2 = .030$] nor a Viewing-Condition × Facial Orientation interaction [$F(1,19) = .073$, $p = .789$, $\eta^2 = .004$].

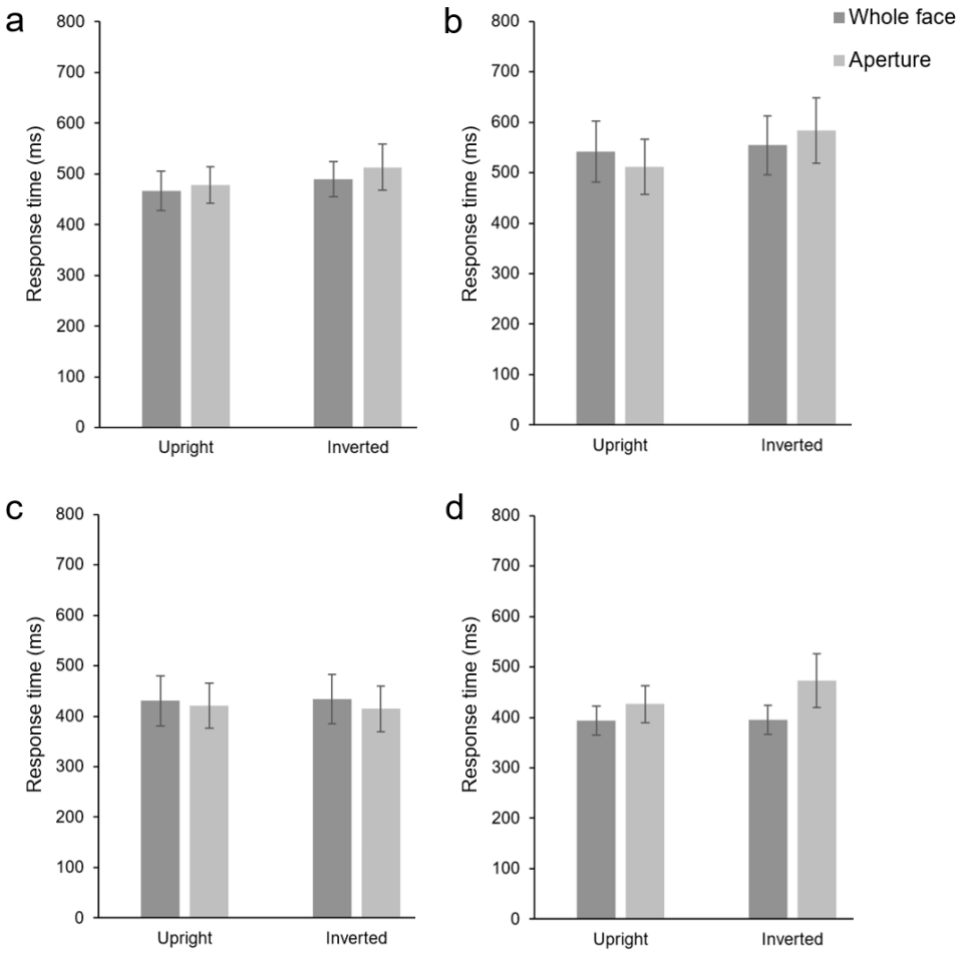

Figure S1: Mean response times seen in each condition for Experiment 1-4 (panels a-d, respectively). Error bars indicate ± 1 SEM.

Experiment 2

Having excluded outlying values (> 3 *SD*s of each participant's mean RT), response times for correct responses (Figure S1b) were analyzed using ANOVA with Viewing Condition (whole-face, aperture) and Facial Orientation (upright, inverted) as within-subjects factors. We observed a main effect of Facial Orientation [$F(1,19) = 4.558$, $p = .046$, $\eta^2 = .193$], whereby responses tended to be slightly slower in the inverted condition. Responses were significantly slower in the inverted aperture ($M = 583$, $SD = 288$) condition than in the upright aperture condition ($M = 512$, $SD = 243$) [$t(19) = 5.783$, $p < .001$]. Responses in the upright whole-face condition ($M = 542$, $SD = 270$) and the inverted whole-face condition ($M = 554$, $SD = 261$) did not differ [$t(19) = .339$, $p = .738$]. We observed no main effect of Viewing condition [$F(1,19) = .002$, $p = .964$, $\eta^2 = .000$] nor a Viewing-Condition × Facial Orientation interaction [$F(1,19) = 2.782$, $p = .112$, $\eta^2 = .128$].

Experiment 3

Having excluded outlying values (> 3 *SD*s of each participant's mean RT), response times for correct responses (Figure S1c) were analyzed using ANOVA with Viewing Condition (whole-face, aperture) and Facial Orientation (upright, inverted) as within-subjects factors. We observed no main effect of Viewing condition [$F(1,19) = .464$, $p = .504$, $\eta^2 = .024$], no main effect of Facial Orientation [$F(1,19) = .016$, $p = .902$, $\eta^2 = .001$], nor a Viewing-Condition × Facial Orientation interaction [$F(1,19) = .463$, $p = .504$, $\eta^2 = .024$].

Experiment 4

Having excluded outlying values (> 3 *SD*s of each participant's mean RT), response times for correct responses (Figure S1d) were analyzed using ANOVA with Viewing Condition (whole-face, aperture) and Facial Orientation (upright, inverted) as within-subjects factors. We observed no main effect of Viewing condition [$F(1,19) = 3.771$, $p = .067$, $\eta^2 = .166$] and no main effect of Facial Orientation [$F(1,19) = 3.298$, $p = .085$, $\eta^2 = .148$]. However, the analysis revealed a significant Viewing-Condition × Orientation interaction [$F(1,19) = 6.067$, $p = .023$, $\eta^2 = .242$], whereby aperture viewing slowed down responding more in the inverted condition, than in the upright condition.