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Holistic Processing of Static and Moving Faces

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Abstract

Humans' face ability develops and matures with extensive experience in perceiving, recognizing, and interacting with faces that move most of the time. However, how facial movements affect one core aspect of face ability—holistic face processing—remains unclear. Here we investigated the influence of rigid facial motion on holistic and part-based face processing by manipulating the presence of facial motion during study and at test in a composite face task. The results showed that rigidly moving faces were processed as holistically as static faces (Experiment 1). Holistic processing of moving faces persisted whether facial motion was presented during study, at test, or both (Experiment 2). Moreover, when faces were inverted to eliminate the contributions of both an upright face template and observers' expertise with upright faces, rigid facial motion facilitated holistic face processing (Experiment 3). Thus, holistic processing represents a general principle of face perception that applies to both static and dynamic faces, rather than being limited to static faces. These results support an emerging view that both perceiver-based and face-based factors contribute to holistic face processing, and they offer new insights on what underlies holistic face processing, how information supporting holistic face processing interacts with each other, and why facial motion may affect face recognition and holistic face processing differently.

Keywords: holistic processing; facial motion; composite face effect; dynamic faces; face perception

Holistic Processing of Static and Moving Faces

Human faces, unlike most objects we see every day, are processed holistically—they tend to be perceived as indecomposable wholes instead of collections of independent facial parts (i.e., eyes, nose, mouth, etc.; Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Le Grand, & Mondloch, 2002; Rossion, 2013). One convincing demonstration of holistic face processing is that the visual system *cannot* selectively process one facial part without any influence from other parts within the face (Cheung, Richler, Palmeri, & Gauthier, 2008; Hole, 1994; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). For example, when a person's top face-half is combined with the bottom half of two different persons' faces (i.e., forming two composite faces), people tend to illusorily perceive the same top-halves as being different from each other (i.e., *composite face effect*, Cheung et al., 2008; Hole, 1994; Young et al., 1987). Such holistic face processing not only applies to perception of facial identity, but also generalizes to the perception of other facial attributes, such as expression (Calder, Young, Keane, & Dean, 2000), gender (Zhao & Hayward, 2010), attractiveness (Abbas & Duchaine, 2008), and trustworthiness (Todorov, Loehr, & Oosterhof, 2010).

Although holistic face processing (and face ability in general) develops with extensive experience in discriminating real-life *moving* faces (O'Toole, Roark, & Abdi, 2002; Yovel & O'Toole, 2016), whether, and, if so, how facial motion affects holistic processing remains poorly understood. Previous studies on holistic face processing—particularly studies using the composite face effect—have almost exclusively focused on *static* faces (see Maurer et al., 2002; Richler & Gauthier, 2014; Rossion, 2013; for comprehensive reviews). While these studies advance our understanding of what may underlie holistic processing of static faces and objects, they are unable to address whether holistic processing applies similarly to dynamic faces, and importantly, whether current theories of holistic processing can be generalized to the perception of moving faces.

How facial motion may influence holistic processing: Theoretical hypotheses

Two influential hypotheses have been proposed to explain what gives rise to holistic face processing and what is required for its generalization. However, neither of them explicitly specifies how facial motion may affect holistic processing. For instance, according to the *domain-specificity hypothesis*, holistic processing results from either an innate face template that the visual system uses to code facial structure holistically or the prioritized face discrimination experience during early infancy (Kanwisher, 2000; McKone, Kanwisher, & Duchaine, 2007; Robbins & McKone, 2007). Two speculations can be made based on this hypothesis. First, if holistic processing is crucially dependent upon the face template (e.g., basic T-shape structure of two eye blobs above a nose blob above a mouth blob; Morton & Johnson, 1991; Tsao & Livingstone, 2008), facial motion may introduce noises into face template matching and therefore hinder holistic processing of moving faces. Second, if holistic face processing is developed due to biased exposure in the sensitive period to faces (which are almost exclusively moving faces), holistic processing may be more pronounced for moving faces than for static faces. Therefore, while the domain-specificity hypothesis predicts that only faces (or things that are sufficiently face-like) can activate holistic processing, it does not clearly specify whether moving and static faces activate holistic processing similarly.

Alternatively, according to the *expertise hypothesis*, holistic processing develops with extensive experience in discriminating homogeneous objects (i.e., expertise), which leads to automatized attention to the whole objects (Diamond & Carey, 1986; Gauthier & Tarr, 1997; Richler, Wong, & Gauthier, 2011). This hypothesis predicts that faces and other objects can be processed holistically via the same mechanism: learned attention to multiple parts that are diagnostic for individuating faces (Chua, Richler, & Gauthier, 2015; Wong, Palmeri, & Gauthier, 2009). One speculation based on this hypothesis is that holistic processing may apply to both static and moving faces, given that people have experience with discriminating both. More experience with moving than static faces may lead to more prominent holistic processing for moving than static faces, and vice versa. Since people interact with moving faces every day, it is very unlikely that holistic processing occurs only for static faces but not for moving faces. Therefore, if expertise with faces drives holistic face processing, moving faces should be

processed holistically, and for most people, holistic processing for moving faces should be equivalent to, if not stronger than that for static faces.

Besides the two influential theories mentioned above, recent studies suggest that both object-based (i.e., bottom-up route) and experience-driven (i.e., top-down route) perceptual grouping contribute to holistic processing (Zhao, Bühlhoff, & Bühlhoff, 2016a, 2016b; see also Curby, Entenman, & Fleming, 2016; Curby, Goldstein, & Blacker, 2013; Zhou, Cheng, Zhang, & Wong, 2012). Consistent with this *dual-route hypothesis*, holistic processing of faces can be reduced or eliminated by disrupting object-based grouping of facial parts, despite humans having life-long experience in individuating faces (Curby et al., 2013; Zhao et al., 2016b). Conversely, even in the absence of expertise, nonface objects with salient object-based grouping cues can be processed holistically like human faces (Wong et al., 2012; Zhao et al., 2016a). Importantly, by highlighting the object-based contribution to holistic processing, the dual-route hypothesis provides one way to explain how facial motion may influence holistic processing. That is, whether or not facial motion modulates holistic face processing is dependent on whether or not it affects perceptual grouping of facial parts (i.e., via bottom-up route to holistic processing, Zhao et al., 2016a). Specifically, in comparison with holistic processing of static faces, facial motion that enhances perceptual grouping of multiple facial parts should enlarge the effect of holistic processing, whereas facial motion that weakens such perceptual grouping should attenuate the magnitude of holistic processing.

Effect of facial motion on holistic processing: Empirical investigations

Several recent studies investigated the influences of facial motion on holistic face processing, but found mixed results and drew opposite conclusions (Cook, Aichelburg, & Johnston, 2015; Favelle, Tobin, Piepers, Burke, & Robbins, 2015; Xiao, Quinn, Ge, & Lee, 2012, 2013). Rigid facial motion (i.e., head rotation and nodding) has been shown to eliminate the composite face effect (Xiao et al., 2012), but non-rigid facial motion (e.g., smiling) often does not (Cook et al., 2015; Favelle et al., 2015; Steede & Hole, 2006; Xiao et al., 2013). Such discrepant results occur not only between studies of rigid and non-rigid facial motion but also between different studies investigating non-rigid facial motion. For instance, while one study showed

that non-rigid facial motion (i.e., simultaneous eye-blinking and mouth chewing) reduced the composite face effect in comparison to static faces (Xiao et al., 2013), other studies found that faces expressing natural facial movements (e.g., happy expression) are processed as holistically as static faces (Cook et al., 2015; Favelle et al., 2015; Steede & Hole, 2006). Thus, how facial motion affects holistic face processing not only remains to be characterized across different theoretical hypotheses, but also remains to be synthesized across different empirical studies.

It has been shown that rigid facial motion *eliminates* holistic processing (measured as the composite face effect, Xiao et al., 2012). However, none of the theories of holistic processing described above predicts that rigid facial motion should remove holistic processing completely. Whether holistic processing is supported by a perceptual gating process based on innate face template (Tsao & Livingstone, 2008), by a domain-specific process that applies to faces or objects that are sufficiently facelike (McKone et al., 2007), by learned attention from expertise training (Chua et al., 2015; Richler, Wong, et al., 2011), or by object-based perceptual grouping (Curby et al., 2013; Zhao et al., 2016a), it should not be eliminated by rigid facial motion. This is because rigid facial motion does not eliminate any of these processes known to support holistic processing. Moreover, since front, quarter, and profile views of static faces are all processed holistically (McKone, 2008), it is not likely that they would no longer elicit holistic processing when they are presented sequentially (i.e., forming rigid motion). On the contrary, by moving all facial parts in a natural and synchronized way, rigid motion may potentially reinforce the perceptual grouping of facial parts via Gestalt principles of common fate and synchrony (Alais, Blake, & Lee, 1998; Lee & Blake, 1999; Piepers & Robbins, 2012; Wagemans et al., 2012). Therefore, according to the dual-route hypothesis, rigidly moving faces, compared to static faces, should elicit a similar or even a stronger holistic processing effect.

There is also a confusing claim that facial motion influences part-based processing but not holistic processing, although in fact the data show that facial motion significantly reduces the composite face effect (Xiao et al., 2012; 2013). Such divergence between the data and the claims may be due to a non-standard way of measuring part-based processing using the composite task. These studies measured part-based processing using either the composite effect

itself (Xiao et al., 2012) or the performance on aligned face conditions (Xiao et al., 2013). However, *neither of these two measures taps exclusively into part-based processing*. According to the design of the composite task (Hole, 1994; Young et al., 1987; Cheung et al., 2008), misaligned faces provide a baseline condition to measure part-based processing (DeGutis, Wilmer, Mercado, & Cohan, 2013; Richler, Cheung, & Gauthier, 2011), whereas aligned faces involve both holistic and part-based processing. Holistic processing is therefore indirectly measured by the difference between the two conditions (i.e., the composite face effect). Therefore, to examine whether facial motion promotes part-based face processing, performance on the misaligned conditions rather than on the aligned conditions should be compared.

Studies that show holistic processing of dynamic faces often employ tasks that involve other aspects of face processing than face perception (e.g., perception of eye-lid motion speed, Cook et al., 2015, or retrieval of learned names of facial parts, Favelle et al., 2015). For instance, Favelle et al. (2015) asked participants to learn the names of top-half faces showing happy expression, and then to perform a naming task for the top face halves embedded in composite faces. The composite faces were made of learned face-tops and novel face-bottoms, with the two halves were either aligned or misaligned. They found that dynamic and static faces showed similar alignment effects in terms of inverse efficiency (i.e., RT divided by accuracy). While this finding suggests that dynamic faces are processed holistically, it remains unclear whether the observed alignment effect reflects holistic perception of faces or interference during retrieving of names. Moreover, the use of emotional faces also makes it hard to differentiate whether holistic processing of dynamic faces is driven by holistic perception of faces regardless of facial motion or is driven by holistic processing of facial expression (Calder et al., 2000). It also remains unclear whether holistic processing of moving faces persists for unfamiliar faces (i.e., without training participants to learn the name/identity of faces). Therefore, to investigate whether holistic processing can be generalized to moving faces, especially during perception of unfamiliar faces, influences of face learning and face recognition (i.e., knowing who the person is) should be minimized.

The present study

Here we investigated the influence of rigid facial motion on holistic and part-based face processing. Specifically, we tested (a) whether rigidly moving faces are processed holistically, and, if so, whether they are processed as holistically as static faces; (b) whether the presence of rigid facial motion enhances part-based processing; and (c) whether perceptual grouping cues associated with rigid facial motion facilitate holistic face processing, and, if so, when. Answers to these questions will not only help reconcile the discrepancies between mixed findings about holistic processing of moving faces, but they will also help address one fundamental question about current theories of holistic processing—whether they can be generalized to moving stimuli or apply only to static faces and objects. Moreover, determining whether holistic and part-based processing are similarly involved between static and rigidly moving faces may also help clarify what is holistic representation of faces (McKone & Yovel, 2009; Piepers & Robbins, 2012; Rossion, 2013) and what type of facial information underlies holistic processing (Rossion, 2013; Zhao et al., 2016b).

We measured holistic processing using a complete-design composite task (Cheung et al., 2008; Richler, Cheung, et al., 2011). This task has been argued to provide a more sensitive and powerful measure of holistic processing than the conventional partial-design composite task (Cheung et al., 2008; Richler, Cheung, et al., 2011; Richler & Gauthier, 2014; but see Rossion, 2013). To fully assess the influence of rigid motion on holistic and part-based face processing, we manipulated the presence of facial motion both during study and at test (Experiments 1 and 2). Our manipulation differs from previous studies that only presented moving faces during study but not at test (Steede & Hole, 2006; Xiao et al., 2012, 2013). Therefore we were able to differentiate whether previously observed elimination of holistic processing by rigid facial motion is a general rule or is only an exception observed under very special testing scenarios. Furthermore, in comparison with a naming task (Favelle et al., 2015), our design could avoid potential influences of perception-irrelevant factors on holistic processing, such as face learning (e.g., training to form name-face associations) and name retrieving (e.g., recall names linked to facial parts). Finally, to assess the influence of rigid facial motion on holistic processing in the

absence of major factors supporting holistic processing (e.g., upright facial information and observers' expertise with them), we also investigated holistic processing of static and moving faces when they are presented upside-down (Experiment 3).

Experiment 1: Are rigidly-moving faces perceived as holistically as static faces?

Experiment 1 investigated whether rigidly moving faces can be processed holistically, and, if so, whether moving faces are processed as holistically as static faces. Participants performed two composite tasks, one using static faces and the other using faces moving rigidly (i.e., turning from left to right). If rigid facial motion reduces holistic face processing, moving faces should be processed less holistically than static faces or no holistic processing at all should be observed. If rigid facial motion promotes part-based processing, performance should be better for moving faces than for static faces when the task taps primarily into part-based processing (i.e., in the misaligned condition, DeGutis et al., 2013; Richler, Cheung, et al., 2011). In contrast, if rigid facial motion mainly provides additional identity-diagnostic information in recognizing faces (i.e., multiple profile views or shape from motion; O'Toole et al., 2002; Yovel & O'Toole, 2016), but does not qualitatively change the way we perceive faces, moving faces should be processed as holistically as, if not stronger than, static faces. Moreover, the presence/absence of rigid facial motion should not affect part-based face processing for misaligned faces.

Methods

Participants

Twenty-four people participated in this experiment (12 females and 12 males, mean age = 23 years old, $SD = 3.5$, ranged between 19 and 33)¹. In accordance with the declaration of

¹ Our sample size is primarily based on previous studies in the literature and our own research using the same paradigm (e.g., Richler & Gauthier, 2014; Zhao et al., 2014; 2016a, 2016b). *A priori* power analysis using G*Power 3 (Faul, Erdfelder, Lang, & Buchner, 2007) indicated that a total number of 48 participants (24 per group) are required to detect an interaction between holistic processing and face type, with a medium effect size $\eta_p^2 = .06$ (or $f = .25$), $\alpha = .025$, power $(1-\beta) = .90$, and correlations among measures $\rho = .30$ (based on a meta-analysis; Richler & Gauthier, 2014).

Helsinki, the procedures used in this and subsequent experiments were approved by Ethical Review Board of the Max Planck Society. Signed consent form was obtained from each participant before the experiment.

Stimuli

Face stimuli were created based on 20 Caucasian faces (10 female and 10 male) from the face database of the Max Planck Institute for Biological Cybernetics (Blanz & Vetter, 1999; Troje & Bühlhoff, 1996). Each face was rendered from 13 views, ranging from left 30° view to right 30° view in steps of 5° (**Figure 1a**). All face images were converted to grayscale, and were placed on a gray background (270 × 270 pixels). For each view of each face, we split the face image into top and bottom halves (270 by 135 pixels each).

We created two types of face stimuli—static and rigidly moving faces, which were either original faces or composite faces. Each face was paired with a same-gender face. For each pair of faces (e.g., male face A and male face B), both original and composite face stimuli were created following the design illustrated in **Figure 1b**. For *static faces* we used only front views. Both original and composite faces could be aligned or misaligned, and their top and bottom halves were clearly separated by a 1-pixel black line (**Figure 1b and 1c**). To create *moving faces*, we first repeated the above procedure for all 13 viewpoints, creating 13 views for both original faces and composite faces. Rigid facial motion was implemented by rapidly presented all these 13 face views in one single sequence (i.e., from left to right 30° view in steps of 5°). Each face view was presented for 34ms, resulting in a total presentation time of 442 ms per moving sequence. To match this presentation time, static faces were also displayed for 442 ms.

----- (Figure 1 about here) -----

Design

We used a complete-design composite task (**Figure 1b**). Participants made same/different judgments about the top parts of two faces presented sequentially with an intervening mask. The first face was always an aligned face and the second face was either

aligned (*aligned condition*) or misaligned (*misaligned condition*). The top parts (i.e., targets) in each trial were either identical (*same condition*) or different from each other (*different condition*). The irrelevant bottom face parts were also manipulated. For the *congruent condition*, they were identical in the *same* condition and different in the *different* condition; whereas for the *incongruent condition*, they were different in the *same* condition and were identical in the *different* condition.

Holistic face processing is indexed by an interaction between congruency and alignment (Richler, Cheung, et al., 2011; Zhao et al., 2016a): Discrimination performance should be better on congruent than on incongruent trials; such congruency effect should be larger in the aligned condition than in the misaligned condition. In contrast, part-based face processing in the composite task is usually indexed by discrimination performance in the misaligned condition (across congruency condition). In the misaligned condition, top and bottom face halves cannot be processed holistically because they are spatially shifted, which encourages part-based processing (DeGutis et al., 2013; Richler, Cheung, et al., 2011). As described in the introduction, a stronger holistic processing effect does not necessarily mean a weaker part-based processing, and vice versa.

Procedure.

Participants performed one composite task with static faces and another with moving faces, with the order counterbalanced across participants. Each task had 160 trials (2 alignment conditions × 2 congruency conditions × 2 same/different conditions × 20 exemplar trials). Trials in each task were presented in random order, with an intertrial interval of 1-second blank screen. In each trial, participants saw a fixation cross (250 ms), a blank screen (500 ms), a study face (442 ms), a mask (500 ms), a test face (442 ms), and finally a response screen, which was displayed until a response was made (**Figure 1c**). We asked participants to focus their attention to the top part and ignore the irrelevant bottom part. They made same/different decisions by pressing corresponding keys on the keyboard. They were instructed to respond as accurately as possible without taking too long for a single judgment (e.g., no more than half a minute).

Results

Participants' performance was measured as response sensitivity (d'), which was calculated based on hit (correct identification) and false alarm rates (mis-identification) in each condition (Stanislaw & Todorov, 1999). The d' scores for each condition are shown in **Figure 2**. Other measures of performance, such as hits, false alarms, and response bias are summarized in Appendix **Table A1**². For this and all subsequent experiments, we report all statistically significant results and report mean values with SEMs.

Rigidly-moving faces are perceived as holistically as static faces. A 2 (Face type: moving vs. static) \times 2 (Alignment: aligned vs. misaligned) \times 2 (Congruency: congruent vs. incongruent) repeated measures ANOVA revealed a significant congruency effect, $F(1,23) = 44.14, p < .001, \eta_p^2 = .66$; performance in the congruent condition ($3.05 \pm .11$) was higher than that in the incongruent condition ($2.58 \pm .12$). The interaction between congruency and alignment was also significant, $F(1,23) = 54.18, p < .001, \eta_p^2 = .70$; a significant congruency effect was only observed in the aligned but not misaligned condition, demonstrating characteristic aspects of holistic face processing. There was also a main effect of alignment, $F(1,23) = 7.34, p = .013, \eta_p^2 = .24$; performance was higher in the misaligned condition ($2.90 \pm .12$) than in the aligned condition ($2.73 \pm .11$). The three-way interaction was not significant, $F(1,23) = 0.17, p = .684, \eta_p^2 < .01$, suggesting that rigidly-moving faces were processed as holistically as static faces.

----- (Figure 2 about here) -----

Separate 2 (Alignment) \times 2 (Congruency) ANOVAs for each face type showed that both moving and static faces are processed holistically. For static faces (**Figure 2, left**), we found a significant congruency effect (congruent condition, 3.06 ± 0.13 ; incongruent condition, $2.60 \pm$

² Holistic processing effect (i.e., interaction between congruency and alignment) observed in terms of response sensitivity cannot be attributed to participants' response bias, because none of our three experiments revealed a significant interaction between alignment and congruency in terms of response bias. Response bias data in Experiment 1 showed only a significant effect of congruency, $F(1,23) = 6.17, p = .021, \eta_p^2 = .21$, whereas response bias data in Experiments 2 and 3 only showed a significant effect of alignment, $F(1,25) = 5.01, p = .034, \eta_p^2 = .17$, and $F(1,27) = 124.678, p < .001, \eta_p^2 = .82$, respectively.

0.14), $F(1,23) = 23.91$, $p < .001$, $\eta_p^2 = .51$, and a significant congruency \times alignment interaction, $F(1,23) = 22.15$, $p < .001$, $\eta_p^2 = .49$. The alignment effect was not significant, $F(1,23) = 1.51$, $p = .232$, $\eta_p^2 = .06$. Planned contrasts showed a significant congruency effect only for aligned trials, $t(23) = 6.93$, $p < .001$, Cohen's $d = 1.41$, but not for misaligned trials, $t(23) = 0.05$, $p = .960$, Cohen's $d = 0.01$. These patterns of results demonstrate holistic face processing.

Moving faces showed the same pattern of results (**Figure 2, right**). Both the congruency effect (congruent condition, 3.04 ± 0.11 ; incongruent condition, 2.56 ± 0.13), $F(1,23) = 19.68$, $p < .001$, $\eta_p^2 = .46$, and the interaction between congruency and alignment, $F(1,23) = 33.22$, $p < .001$, $\eta_p^2 = .59$, were significant. Planned contrasts showed that the congruency effect was significant for aligned trials, $t(23) = 6.19$, $p < .001$, Cohen's $d = 1.26$, but not for misaligned trials, $t(23) = 0.53$, $p = .598$, Cohen's $d = 0.11$. The alignment effect was also significant, $F(1,23) = 9.52$, $p = .005$, $\eta_p^2 = .29$, showing higher performance for misaligned than aligned trials (2.92 ± 0.12 vs. 2.68 ± 0.11).

Rigid facial motion does not promote part-based face processing. To examine whether rigid facial motion enhances part-based processing, we performed a 2 (Face type) \times 2 (Congruency) repeated measures ANOVA on performance in the misaligned condition. This analysis showed that neither facial motion nor congruency manipulation affected performance, all $F(1,23) \leq 0.16$, $p \geq .690$, $\eta_p^2 < .01$. These results indicate that rigid motion does not enhance part-based processing (cf. Xiao et al., 2012).

Bayesian analysis for accepting the null hypothesis (H0). In this and subsequent experiments, part of our conclusions are based on the null effects in the null hypothesis significance testing (i.e., NHST). For instance, moving and static faces show equivalent level of holistic or part-based processing. To seek for evidences that supporting the null hypothesis, we additionally performed Bayesian statistical analysis for three lines of results: (a) similar level of holistic processing between static and moving faces (or tasks); (b) similar level of part-based processing between static and moving faces (or tasks); and (c) neither static nor moving faces are processed holistically. The results are summarized in **Table 1**; they show in general the same pattern of results as obtained by the NHST analysis.

----- (Table 1 about here) -----

Discussion

Experiment 1 demonstrates that rigidly moving faces are perceived as holistically as static faces. Moreover, we found no evidence supporting the view that rigid motion promotes part-based face processing. First, rigid facial motion does not eliminate, or even reduce, holistic face processing. Second, in comparison to the static condition, the presence of rigid facial motion did not improve the processing of facial parts in misaligned faces, which is proposed to primarily recruit part-based face processing (DeGutis et al., 2013; Richler, Cheung, et al., 2011). These results indicate that rigid facial motion neither eliminates holistic processing nor enhances part-based face processing.

It may be argued that rigid motion may eliminate holistic face processing under certain circumstances, such as when participants study moving faces and are tested with static faces (Favelle et al., 2015; Xiao et al., 2012). When facial motion information differs between study and test faces, participants cannot rely merely on image similarity to make same/different judgments. Instead, they need to decide whether two different face stimuli (i.e., one moving and one static) showed the same identity. Such paradigm might be more sensitive to the influence of facial motion on holistic and part-based processing than a perceptual matching task as in Experiment 1. To address this issue, Experiment 2 employed a composite task in which moving faces were presented only during study or only at test.

Experiment 2: Does holistic processing persist across static and moving faces?

Experiment 2 investigated whether holistic processing persists when rigid facial motion is presented only during study or only at test and whether the presence of rigid motion during study or test affects differently part-based face processing. Participants performed two composite tasks. In the *static-to-moving task* they studied static faces and were tested with

rigidly-moving faces; whereas in the *moving-to-static task* they studied rigidly-moving faces and were tested with static faces. Thus, participants had to decide whether the top parts of study and test faces displayed the same person regardless of facial motion. If the presence of rigid facial motion eliminates holistic processing and promotes part-based processing under such circumstance (Xiao et al., 2012, 2013), neither task should exhibit holistic face processing. However, if holistic face processing is supported by perceptual grouping due to either observers' experience with dynamic faces or face-based grouping cues (e.g., 3D facial shape, Zhao et al., 2016a, 2016b), the presence of rigid facial motion should not disrupt holistic processing. The reason is that rigid facial motion should not eliminate such perceptual grouping.

Methods

Participants

Twenty-six people participated in this experiment (15 females and 11 males, mean age = 26 years old, SD = 5.7, ranged between 19 and 38).

Stimuli, design, and procedure

The stimuli, design, and procedure were the same as in Experiment 1 except that one of the two faces in a trial was moving and the other was static. For *static-to-moving* task, the study face was static and the test face was shown with rigid motion. For *moving-to-static* task, the study face was moving rigidly whereas the test face was static. Task order was counterbalanced across participants. Participants were asked to judge whether or not the top parts of the two faces showed the same person while ignoring the irrelevant bottom parts.

Results

Holistic face processing persists whether rigid motion appears during study or at test. The d' scores for each condition are shown in **Figure 3** (performance measured in terms of hits, false

alarms, and response bias is summarized in Appendix **Table A2**). A 2 (Task: static-to-moving task vs. moving-to-static task) \times 2 (Alignment) \times 2 (Congruency) repeated measures ANOVA revealed a significant congruency effect, $F(1,25) = 58.33, p < .001, \eta_p^2 = .70$; performance was better for congruent than for incongruent condition (2.75 ± 0.12 vs. 2.14 ± 0.12). The interaction between congruency and alignment was significant, $F(1,25) = 49.27, p < .001, \eta_p^2 = .66$; the congruency effect was observed in the aligned but not in the misaligned condition, demonstrating holistic processing. The three-way interaction of task, alignment, and congruency was also significant, $F(1,25) = 5.25, p = .031, \eta_p^2 = .17$. Static-to-moving task showed stronger holistic processing effect than moving-to-static task. The main effect of alignment was significant, $F(1,25) = 6.07, p = .021, \eta_p^2 = .20$. Participants showed higher performance on misaligned condition (2.55 ± 0.14) than on aligned condition (2.34 ± 0.11).

----- (Figure 3 about here) -----

Separate 2 (Alignment) \times 2 (Congruency) ANOVAs showed that holistic face processing was evident in both tasks. For static-to-moving task (**Figure 3, left**), both the congruency effect, $F(1,25) = 34.88, p < .001, \eta_p^2 = .58$, and the interaction between congruency and alignment, $F(1,25) = 143.25, p < .001, \eta_p^2 = .85$, were significant. Again, better performance was observed in the congruent condition (2.83 ± 0.14) than the incongruent condition (2.16 ± 0.13). Planned contrasts showed a significant congruency effect for aligned trials, $t(25) = 10.50, p < .001, \text{Cohen's } d = 2.06$, but not for misaligned trials, $t(25) = .65, p = .519, \text{Cohen's } d = 0.13$. There was also a significant alignment effect, $F(1,25) = 4.72, p = .040, \eta_p^2 = .16$, showing higher performance for misaligned than aligned conditions (2.61 ± 0.15 vs. 2.38 ± 0.14).

For moving-to-static task (**Figure 3, right**), we found a significant congruency effect (congruent condition, 2.68 ± 0.12 ; incongruent condition, 2.13 ± 0.13), $F(1,25) = 44.70, p < .001, \eta_p^2 = .64$, and a significant congruency \times alignment interaction, $F(1,25) = 10.87, p = .003, \eta_p^2 = .30$. Planned contrasts showed that the congruency effect was significant for aligned trials, $t(25) = 5.82, p < .001, \text{Cohen's } d = 1.14$, but not for misaligned trials, $t(25) = 0.60, p = .551, \text{Cohen's } d = 0.12$. There was also a trend of higher performance for the misaligned than for the aligned conditions

(2.50 ± 0.14 vs. 2.31 ± 0.12), $F(1,25) = 3.48$, $p = .074$, $\eta_p^2 = .12$. These similar patterns of response across the two composite tasks indicate that holistic processing persists across facial motion.

Presence of rigid facial motion does not enhance part-based processing. As in Experiment 1, we performed a 2 (Task) \times 2 (Congruency) ANOVA on d' data of misaligned conditions. This analysis revealed no significant results, all $F_s < 1.21$, $p \geq .283$, $\eta_p^2 < .05$, suggesting that the presence of facial motion during study or at test does not influence part-based face processing.

To further test whether rigid facial motion enhances part-based face processing, we compared performance obtained in both tasks of Experiment 2 with performance in the static task of Experiment 1. We found numerically higher performance when both study and test faces were static (static-static, 2.89 ± 0.14) than when only one of them moved rigidly (moving-static, 2.50 ± 0.14 ; static-moving, 2.61 ± 0.14), both $F(1,48) \leq 3.70$, $p \geq .060$, $\eta_p^2 \leq .07$. These results provide further evidence that rigid facial motion does not enhance part-based face processing.

Discussion

Experiment 2 shows that holistic processing persists even when study and test faces differ in facial motion, arguing against the view that rigid motion eliminates holistic processing. Holistic processing effect was stronger when participants studied static faces and were tested with moving faces than other way around. This result suggests that facial motion presented during study or at test elicits different levels of holistic processing, although neither condition could eliminate holistic processing. In addition, part-based processing, as measured using performance on misaligned condition, showed no difference between the two composite tasks. These results support the view that rigid facial motion neither eliminates holistic processing nor promotes part-based face processing, whether rigid motion is presented during study, at test, or both (cf. Favelle et al., 2015; Xiao et al., 2012). Note that there are many methodological differences between Xiao et al. (2012) and the present study (e.g., angular differences between successive face views, 26° vs 5° , ranges of face views, 180° vs. 60° , whole faces with hairstyle vs. face only, etc.), exactly which of these differences leads to the elimination of holistic processing remains unclear.

Why rigid motion exerts little or no influence on holistic processing? One possibility is that holistic face processing is completely insensitive to facial motion. Rigid motion changes neither face categorization nor expertise with faces, so it should not disrupt holistic processing whether it is gated by face-template matching (i.e., the domain-specificity hypothesis) or driven by learned attention to whole faces (i.e., the expertise hypothesis). Alternatively, the contribution of rigid motion to holistic processing may be overshadowed by more salient cues supporting holistic face processing. Rigid motion provides additional Gestalt cues for grouping facial parts together (Piepers & Robbins, 2012; Wagemans et al., 2012), which should facilitate holistic processing according to the dual-route hypothesis (Curby et al., 2016; Curby et al., 2013; Zhao et al., 2016a, 2016b). However, such facilitation may be less evident when holistic processing can be activated by more influential factors (e.g., those provided by normal upright faces and expertise with them), which leaves little room for facial motion to further enhance holistic processing. To differentiate between these possibilities, Experiment 3 tested the role of rigid motion on holistic processing using inverted faces, thereby removing the contribution of face template matching and expertise with upright faces to holistic processing.

Experiment 3: Does rigid facial motion facilitate holistic processing of inverted faces?

Experiment 3 investigated whether perceptual grouping cues provided by rigid motion promote holistic processing when faces are inverted. Participants performed the same tasks as in Experiment 1, except that all study and test faces were upside-down. Face inversion should eliminate the contribution of perceiver's expertise and the contribution of upright facial information to holistic processing (McKone et al., 2007; Richler, Mack, Palmeri, & Gauthier, 2011; Rossion, 2008). Therefore, this experiment provides a sensitive way to test potential contribution of facial motion to holistic face processing. Moreover, Experiment 3 also allowed us to test the effect of rigid motion on part-based face processing with little or no influence from holistic face processing, because face inversion is assumed to disrupt holistic face processing (e.g., Maurer et al., 2002; Rossion, 2013).

If rigid motion facilitates perceptual grouping of individual parts within inverted faces (e.g., via object-based Gestalt cues), holistic processing of inverted faces should occur more likely when faces move rigidly than when they do not move. In contrast, if rigid motion does not facilitate holistic face processing or even eliminates it (Xiao et al., 2012, 2013), neither moving nor static *inverted* faces should activate holistic face processing. Without additional assumptions, both the domain-specificity hypothesis and the expertise hypothesis would predict that inverted faces cannot be processed holistically, whether faces are moving or not. This is because the visual system does not have an inverted face template (McKone et al., 2007) and does not develop expertise with inverted faces (Richler, Wong, et al., 2011).

Methods

Participants

Twenty-eight people participated in this experiment (19 females, mean age = 25 years old, SD = 4.5, ranged between 18 and 38).

Stimuli, design, and procedure

The stimuli, design, and procedure were the same as in Experiment 1 except that all composite faces were inverted. Participants were asked to judge whether the bottom parts of the two inverted faces (i.e., the parts including eyes and forehead) were the same while ignoring the irrelevant top parts (i.e., the parts including mouth and chin).

Results

Rigidly-moving, but not static, inverted faces show signature of holistic processing. Mean d' scores in responding to inverted faces are shown in **Figure 4** (performance measured in terms of hits, false alarms, and response bias is summarized in Appendix **Table A3**). A 2 (Face type: moving vs. static) \times 2 (Alignment: aligned vs. misaligned) \times 2 (Congruency: congruent vs. incongruent) repeated measures ANOVA revealed a significant main effect of face type, $F(1,27)$

= 8.87, $p = .006$, $\eta^2 = .25$; the static condition showed higher performance than the moving condition ($2.55 \pm .10$ vs. $2.34 \pm .11$). The interaction between congruency and alignment was not significant, $F(1,27) = 0.88$, $p = .356$, $\eta^2 = .03$. However, the three-way interaction between face type, alignment, and congruency was significant, $F(1,27) = 9.23$, $p = .005$, $\eta^2 = .25$; indicating that when faces were inverted, rigidly-moving faces were processed differently from static faces in terms of holistic processing (i.e., alignment \times congruency interaction).

----- (Figure 4 about here) -----

Separate 2 (Alignment) \times 2 (Congruency) ANOVAs showed that inverted moving faces, but not inverted static faces, exhibited behavioral characteristics of holistic processing. For inverted static faces (**Figure 4, left panel**), neither the main effects nor the interaction between alignment and congruency were significant, all $F(1,27) \leq 1.37$, $p \geq .252$, $\eta^2 \leq .05$. Planned contrasts showed no significant congruency effect for aligned trials, $t(27) = 0.87$, $p = .392$, Cohen's $d = 0.16$, and for misaligned trials, $t(27) = 0.75$, $p = .459$, Cohen's $d = 0.14$. Thus, holistic processing effect observed for upright static faces disappears when faces are inverted.

For inverted moving faces (**Figure 4, right panel**), we found a significant interaction between congruency and alignment, $F(1,27) = 8.77$, $p = .006$, $\eta^2 = .25$. Planned contrasts showed that the congruency effect was significant for aligned trials, $t(27) = 2.27$, $p = .031$, Cohen's $d = 0.43$, but not for misaligned trials, $t(27) = 1.59$, $p = .123$, Cohen's $d = 0.30$. Thus, the key aspects of holistic processing observed with upright moving faces (e.g., significant congruency effect for aligned but not misaligned faces, and significant interaction between congruency and alignment) are preserved for inverted moving faces. These results suggest that rigid motion facilitates holistic processing of inverted faces: face inversion dramatically reduces holistic processing but does not eliminate all behavioral markers of holistic face processing. We also observed a marginally significant effect of alignment (aligned condition, 2.44 ± 0.11 ; misaligned condition, 2.25 ± 0.12), $F(1,27) = 4.15$, $p = .052$, $\eta^2 = .13$.

Rigid motion does not promote part-based processing for inverted faces. To test whether rigid motion enhances part-based processing in inverted faces, we performed a 2 (Face type) \times 2

(Congruency) repeated measures ANOVA on performance for the misaligned condition. This analysis only revealed a significant effect of face type, $F(1,27) = 8.50, p = .007, \eta_p^2 = .24$, showing higher performance for inverted static faces (2.54 ± 0.13) than for inverted moving faces (2.25 ± 0.12). Neither the main effect of congruency nor its interaction with face type were significant, $F(1,27) \leq 2.25, p \geq .145, \eta_p^2 \leq .08$. These results provide further evidence that rigid motion does not enhance part-based face processing, which hold true not only for upright faces but also for inverted faces where part-based processing is predominant.

Face inversion affects holistic processing of static and moving faces differently. To test whether inversion affects holistic processing of static and moving faces differently, we combined data from Experiments 1 and 3 and performed a 2 (Orientation: upright vs. inverted) \times 2 (Face type: moving vs. static) \times 2 (Alignment: aligned vs. misaligned) \times 2 (Congruency: congruent vs. incongruent) mixed ANOVAs, with orientation as between-participants factor and all others as within-participants factors³. The results of this ANOVA are summarized in **Table 1**. Here we focus on the results that illustrate the relationship between face orientation and holistic processing. We found a significant three-way interaction between orientation, alignment, and congruency, $F(1,50) = 20.92, p < .001, \eta_p^2 = .30$, suggesting that face orientation modulates holistic face processing. The four-way interaction between face type, orientation, alignment, and congruency was also significant, $F(1,50) = 5.07, p = .029, \eta_p^2 = .09$, suggesting that face inversion influences holistic processing of static and moving faces differently.

----- (Table 2 about here) -----

To disentangle the four-way interactions, we performed two separate 2 (Orientation: upright vs. inverted) \times 2 (Alignment: aligned vs. misaligned) \times 2 (Congruency: congruent vs. incongruent) mixed ANOVAs for moving and static faces. For static faces, we found a significant congruency effect, $F(1,50) = 12.66, p < .001, \eta_p^2 = .20$, and a significant interaction between congruency and alignment, $F(1,50) = 8.15, p = .006, \eta_p^2 = .14$. These two significant

³ Note that in the cross-orientation comparisons, participants were grouped by experiment but were not randomly assigned to each face orientation condition. The latter would be statistically better to test the influence of face orientation on holistic processing of static and moving faces.

effects were both modulated by face orientation, as revealed by significant interactions between orientation and congruency, $F(1,50) = 11.94, p = .001, \eta_p^2 = .19$, and between orientation, congruency, and alignment, $F(1,50) = 19.16, p < .001, \eta_p^2 = .28$. These results demonstrate that holistic processing involved in upright and inverted static faces are qualitatively different. As reported in previous sections (see also **Figures 2 and 4**, left panel), in comparison with responses to upright faces, face inversion eliminated both the congruency effect and the interaction between congruency and alignment (i.e., holistic processing). This ANOVA also revealed a marginally significant effect of face orientation (d' for upright faces, $2.83 \pm .12$; inverted faces, $2.55 \pm .11$), $F(1,50) = 3.04, p = .087, \eta_p^2 = .06$.

For moving faces, similarly to static faces, we found a significant congruency effect, $F(1,50) = 14.13, p < .001, \eta_p^2 = .22$, and a significant congruency by alignment interaction, $F(1,50) = 38.01, p < .001, \eta_p^2 = .43$. Again, these two significant effects were both modulated by face orientation, as supported by significant interactions between orientation and congruency, $F(1,50) = 11.22, p = .002, \eta_p^2 = .18$, and between orientation, alignment, and congruency, $F(1,50) = 4.17, p = .046, \eta_p^2 = .08$. As reported in previous sections (see also **Figures 2 and 4**, right panel), responses to upright and inverted moving faces both showed characteristics of holistic face processing: A significant congruency effect for the aligned but not the misaligned condition and a significant interaction between congruency and alignment. These results are different from those observed with static faces. Therefore, face inversion appears to quantitatively change holistic processing of moving faces: It significantly reduces—but not completely disrupts—holistic face processing when faces move rigidly. This ANOVA also showed a main effect of face orientation (upright faces, $2.80 \pm .11$; inverted faces, $2.34 \pm .11$), $F(1,50) = 9.04, p = .004, \eta_p^2 = .15$, and a significant interaction between face orientation and alignment, $F(1,50) = 11.83, p = .001, \eta_p^2 = .19$.

Discussion

Experiment 3 shows that rigid facial motion could facilitate holistic processing when more influential factors supporting holistic processing are absent. When faces were inverted,

responses to rigidly moving faces still exhibited key aspects of holistic processing similar to those observed with upright faces (e.g., significant congruency effect for aligned but not misaligned faces). In contrast, face inversion eliminated all behavioral characteristics of holistic processing for static faces. These different response patterns indicate that perceptual grouping cues provided by rigid motion help activate holistic processing for inverted faces. In comparison with holistic processing of upright faces, holistic processing of inverted faces is either eliminated (for static faces) or substantially reduced (for moving faces). These results suggest that upright facial information and participants' expertise with upright faces are more influential factors than facial motion for eliciting holistic processing. These factors, when available, overshadow the contribution of rigid motion to holistic face processing (we will come back to this point in detail in the General Discussion).

Several observations about the influence of inversion on holistic face processing are worth mentioning. First, holistic processing of inverted static faces has been observed previously when faces are presented longer (e.g., 800 ms; Richler, Mack, et al., 2011) and when they are presented with additional grouping cues from the background (e.g., Curby et al., 2013). Consistent with our results, this observation suggests that, under certain circumstances, other object- or observer-based factors can facilitate holistic processing of inverted faces. Second, while rigid motion facilitates holistic processing of inverted faces, it cannot activate holistic processing as upright faces do. We observed a main effect of congruency for upright moving faces but not for inverted moving faces, probably because face inversion significantly reduced overall performance for congruent condition compared to upright faces (see **Figures 2 and 4**, right panel).

General Discussion

Although our face recognition ability develops and matures with extensive experiences in perceiving, recognizing, and interacting with moving faces, how facial motion affects one core aspects of our face recognition ability—holistic processing—has remained unclear. Here we investigated the influence of rigid facial motion on holistic and part-based face processing

by manipulating both the presence of facial motion and face orientation. Our main findings are summarized in **Figure 5**. We found that rigid facial motion does not eliminate holistic processing. Instead, rigidly-moving faces are processed as holistically as, if not more holistically than, static faces when they are shown in normal upright orientation. This finding holds true irrespective of whether rigid motion is shown in study faces only, test faces only, or both. Therefore, holistic processing is not confined to static faces. These findings demonstrate that holistic processing represents a general principle of face perception: both static and dynamic faces are perceived holistically.

----- (Figure 5 about here) -----

Rigid facial motion functions as a minor factor facilitating holistic face processing, but such facilitation effect is only discernable when more influential factors supporting holistic face processing are absent. While inversion eliminates all characteristic effects of holistic processing for static faces, key aspects of holistic processing observed for upright moving faces (e.g., alignment \times congruency interaction) survives inversion manipulation (**Figure 5**, left panel). This result indicates that perceptual grouping cues provided by rigid motion facilitate holistic processing when faces are inverted. However, we observed no such difference between holistic processing of upright static and upright moving faces, indicating that the facilitating role of rigid motion for activating holistic face processing is overshadowed by more influential factors, such as upright facial information and observers' expertise with upright faces. Therefore, the observed holistic processing effect is jointly determined by both object- and observer-based factors, consistent with the dual-route hypothesis (Zhao et al., 2016a, 2016b; see also Curby et al., 2013, 2016).

We observed no evidence supporting the view that rigid motion enhances part-based face processing. Xiao et al. (2012, 2013) argued that facial motion promotes part-based processing based on reduced composite face effect following study of moving faces. However, a reduced composite effect by itself does not necessarily mean that part-based processing is enhanced. For example, a reduced composite effect can be observed when performance drops

on both aligned and misaligned conditions but drops more on the former than the latter. Here we measured part-based processing using discrimination performance in the misaligned condition, because holistic face processing is physically disrupted by misalignment of facial parts (DeGutis et al., 2013; Richler, Cheung, et al., 2011). None of our three experiments showed enhanced part-based processing for moving faces (**Figure 5**, right panel). On the contrary, when faces are inverted—which often encourages part-based processing—discriminating between moving facial parts was even worse than discriminating between static facial parts (Experiment 3). These results clearly favor the view that rigid facial motion does not promote part-based face processing, at least as measured in a composite task.

Generalization of theories of holistic processing to dynamic faces

The finding that holistic processing applies to both static and dynamic faces reshapes some fundamental hypotheses proposed by influential theories. For the domain-specificity hypothesis, if an innate face template primarily supports holistic face processing, such a face template is more likely to take the form of a 3D facial shape (Zhao et al., 2016b) rather than a 2D T-shape structure of front-view faces (McKone et al., 2007; Morton & Johnson, 1991; Tsao & Livingstone, 2008). Indeed, the latter has difficulty in explaining (i) why static and rigidly moving faces are processed equally holistically, (ii) why profile- or quarter-view faces show equivalent holistic processing to front-view faces (McKone, 2008), and (iii) why line-drawing faces that maintain 2D front-view facial structure fail to show holistic processing (Zhao et al., 2016b).

With regard to the expertise hypothesis, if the automatic attention to multiple diagnostic facial parts drives holistic face processing (Richler, Wong, et al., 2011; Chua et al., 2015), both a top-down route (i.e., learned attention) and a bottom-up route (i.e., motion-based perceptual grouping) should be able to activate such holistic attention (Curby et al., 2013, 2016; Wong et al., 2009; Zhao et al., 2016a). Robust holistic processing of moving faces also suggests that expertise helps the visual system to develop integrative models for the spatiotemporal dynamics of natural facial movements, so that correlated movements of facial features (e.g., how eyes and

mouth move during yawn or smiling) will be processed in a perceptually integrative way (Cook et al., 2015; Reinl & Bartels, 2014). Nonetheless, to account for holistic processing of inverted moving faces, the expertise hypothesis has to rely on additional assumptions, such as that expertise underlies the ability to use cues available with faces in motion regardless of orientation or that expertise developed with upright faces can transfer to inverted faces in motion.

The dual-route hypothesis provides a plausible account for why rigid facial motion facilitates holistic processing of inverted faces, which cannot be readily explained by either the domain-specificity hypothesis or the expertise-hypothesis. Curby et al. (2013) also showed that grouping cues provided by background information facilitate holistic processing for inverted faces. Both findings indicate that bottom-up, object-based perceptual grouping contributes to holistic processing (Zhao et al., 2016a, 2016b). Although the dual-route hypothesis highlights that both perceiver- and object-based factors contribute to holistic processing, it does not specify how they interact to elicit holistic processing. The present study shows that upright facial information and the expertise with upright faces can overshadow the role of motion-based grouping in activating holistic face processing. This result suggests that perceiver- and object-based contributions to holistic face processing are not weighted equally (we will get to this point in detail in the next section).

The finding that moving faces are processed holistically also poses new challenges to unravel computational and neural mechanisms underlying holistic face processing. Several recently proposed computational models nicely catch the behavioral markers of holistic face processing (Farzmaahi, Rajaei, Ghodrati, Ebrahimpour, & Khaligh-Razavi, 2016; Tan & Poggio, 2016; Xu, Biederman, & Shah, 2014), but they are only applied to static faces. It remains unclear whether these models can be generalized to dynamic faces and how they may account for the effects of various facial motions on holistic processing (e.g., the present study; Favelle et al., 2015; Xiao et al., 2012, 2013). Similarly, previous neuroimaging studies have suggested that the fusiform face area primarily supports holistic perception of static faces (Liu, Harris, & Kanwisher, 2010; Renzi et al., 2015; Schiltz & Rossion, 2006; Zhao, Cheung, et al., 2014). In

comparison with static faces, dynamic facial information often elicit stronger neural responses in the distributed brain network for face perception (O'Toole, Natu, An, Rice, Ryland, & Phillips, 2014; Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011; Schultz & Pilz, 2009). It remains unknown whether holistic processing of moving and static faces is supported by the same neural mechanisms.

Nonlinear contribution of object- and perceiver-based factors to holistic processing

The facilitation effect of rigid motion on holistic face processing was observed for inverted faces but not upright faces. This result suggests that object-based factors (e.g., motion-based perceptual grouping) and perceiver-related factors (e.g., expertise in processing upright faces) may contribute to holistic processing in a nonlinear way. That is, the magnitude of holistic face processing is not linearly related to the number or strength of factors supporting holistic processing (**Figure 6**). Several lines of research support this idea. First, holistic processing of upright faces is not further enhanced by adding perceptual grouping cues such as rigid facial motion (the present study), homogeneous color frame (Curby et al., 2013), or extended real-life experience (Crookes & McKone, 2009). Second, increasing encoding time does not further enlarge holistic processing effect for upright faces as long as it is sufficient for above-chance performance (Richler, Mack, Gauthier, & Palmeri, 2009). Third, adding emotional facial expression to static faces does not enhance the composite face effect (Calder et al., 2000). Therefore, when influential factors are available to activate holistic processing, adding additional cues does not necessarily enhance holistic processing.

----- (Figure 6 about here) -----

This nonlinearity also occurs when holistic processing is disrupted (**Figure 6**). When normal upright faces are gradually rotated away from upright orientation, holistic processing effect shows a nonlinear relationship with increasing angles of rotation (Rossion & Boremanse, 2008). Similar nonlinear relationship also occurs between holistic processing effect and the

amplitude of the misalignment. Gradually increasing the lateral shift between top and bottom face halves did not lead to a gradual reduction of holistic processing effect—the magnitudes of holistic processing dropped rapidly when face halves were shifted by 8.3% or 16.7% of face width, but showed no further drop for larger shifts up to 100% face width (Laguesse & Rossion, 2013). Furthermore, combining inversion and misalignment—two independent manipulations to disrupt holistic processing—does not disrupt holistic processing more strongly than using each separately (Esins, Schultz, Stemper, Kennerknecht, & Bühlhoff, 2016). Therefore, whether removing or weakening one cue further reduces holistic processing is contingent upon whether preexisting cues support or disrupt holistic processing.

Different effects of facial motion on recognition and holistic processing tasks

While moving faces are often better recognized than static faces (Esins et al., 2016; Lander & Bruce, 2003; Lander & Chuang, 2005; O'Toole et al., 2011; O'Toole et al., 2002), we observed no such motion-advantage in terms of holistic face processing (see also Favelle et al., 2015; Xiao et al., 2013). Why does facial motion enhance face recognition performance but not strengthen holistic processing effect? One possibility is that the influence of facial motion on face recognition is dissociated from that on holistic processing. Visual information that improves recognition of moving faces does not necessarily promote holistic face perception and vice versa. Consistent with this view, while people with congenital prosopagnosia are unable to use facial motion information to improve face recognition performance, they can still process faces holistically (Esins et al., 2016; Longmore & Tree, 2013). Alternatively, the composite task used to measure holistic processing might not be sufficiently sensitive to facial motion information. That is, while the composite task offers the most convincing demonstration of holistic processing for static faces (Maurer et al., 2012; Richler & Gauthier, 2014; Rossion, 2013), it might be less capable of catching the contribution of facial motion to holistic processing.

Note that facial motion is not the only factor that differently affects face recognition and holistic processing measured with a composite task. Facial race and photograph negation (i.e., contrast reversal) also show a dissociable influence on face recognition and holistic face

processing. For instance, while recognition of own-race faces is better than recognition of other-race faces (e.g., Meissner & Brigham, 2001), no such own-race advantage is consistently observed for holistic processing (Harrison, Gauthier, Hayward, & Richler, 2014; Mondloch et al., 2010; Zhao, Cheung, et al., 2014; Zhao et al., 2016b; Zhao & Hayward, 2010; Zhao, Hayward, & Bühlhoff, 2014a, 2014b). Similarly, although negation of photographs dramatically reduces people's ability to recognize faces (e.g., Galper, 1970), it does not break down holistic face processing (Hole, George, & Dunsmore, 1999; Taubert & Alais, 2011). These results suggest that facial information used for recognition is dissociable from that underlying holistic face processing, at least when holistic processing is indexed by the composite face effect.

Influence of different types of facial movements on holistic face processing

Faces can move in various ways, raising the question of whether different types of facial movements affect holistic processing similarly. One conventional classification of facial movements differentiates rigid motion (e.g., head rotation) from non-rigid motion (e.g., smile; Christie & Bruce, 1998; Lander & Bruce, 2003; O'Toole et al., 2002). The present study shows that rigid facial motion neither eliminates holistic processing nor promotes part-based processing in comparison to static faces (but see Xiao et al., 2012). This finding also holds true for dynamic faces animated by natural, non-rigid facial motion. Faces displaying dynamic happy expression are processed as holistically as static happy faces (Favelle et al., 2015). However, holistic processing seems to be less prevalent for faces moving non-rigidly but unnaturally than for static faces (e.g., faces exhibiting eye-blinking and mouth-chewing simultaneously, Xiao et al., 2013). That is, depending on the task or context, rigid and non-rigid facial motion may affect holistic processing similarly and different examples of non-rigid facial motion may affect holistic processing differently. These results suggest that a simple differentiation between rigid and non-rigid facial motion is unable to consistently characterize how facial movements influence holistic processing.

We speculate that the influence of facial motion on holistic processing is not determined by whether faces moving rigidly or non-rigidly, but determined by whether or not facial

movements affect perceptual grouping of facial parts (i.e., the bottom-up route to holistic processing, Zhao et al., 2016a, see also Curby et al., 2013). When faces move in a natural and synchronized way (e.g., rigid facial motion as used in the present study, or dynamic facial expressions as used in Favelle et al., 2015), then facial motion should facilitate holistic face processing (see also Piepers & Robbins, 2012). Such motion encourages the grouping of facial parts together based on Gestalt principles of common fate and synchrony (Alais et al., 1998; Lee & Blake, 1999; Wagemans et al., 2012) or based on learned attention to whole faces in discriminating facial expressions (Calder et al., 2000; Chua et al., 2015). When facial movements are unnatural (e.g., simultaneous eye-blinking and mouth chewing as used in Xiao et al., 2013), facial motion should weaken holistic face processing. This type of facial motion may attract attention to the moving parts and hinders object-based perceptual grouping (Abrams & Christ, 2003; Franconeri & Simons, 2005; Howard & Holcombe, 2010).

Conclusions

Our study demonstrates that holistic processing represents a general principle of face perception that applies to both static and moving faces. Rigid facial motion neither eliminates holistic face processing nor promotes part-based face processing, regardless of whether it is presented during encoding, at test, or both. These results not only place fundamental constraints on the generalization of current theories holistic processing, but also offer new insights in theoretically framing what underlies holistic face processing, how various types of information supporting holistic processing interact with each other, and why facial motion influences differently face recognition and holistic processing. While the dual-route hypothesis provides a plausible cognitive account for these results, the exact computational and neural mechanisms underlying holistic perception of static and dynamic faces remain to be determined.

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Tables (2 Tables)

Table 1. Summary of Bayesian factors (BF_{01}) from Bayesian analyses and corresponding p values from NHST in testing the key null hypotheses in Experiments 1-3.

Null hypotheses	<i>Static and moving faces show equivalent holistic processing</i>		<i>Static and moving faces show equivalent part-based processing</i>		<i>No holistic processing for static faces</i>		<i>No holistic processing for moving faces</i>	
	<i>Type×Alignment</i>	<i>×Congruency</i>	<i>Main effect of Face type/task</i>		<i>Alignment×Congruency</i>			
Effect	BF_{01}	p	BF_{01}	p	BF_{01}	p	BF_{01}	p
Experiment 1	4.31	.684	4.46	.761	<.001	<.001	<.001	<.001
Experiment 2	0.54	.031	3.20	.350	<.001	<.001	0.004	.003
Experiment 3	0.13	.005	0.16	.007	2.55	.252	0.29	.006

Note. Bayesian analysis was performed using JASP software (Rouder, Morey, Verhagen, Swagman, Wagenmakers, 2016). The Bayes factor, BF_{01} , indicates how many times more likely the null hypothesis (H_0) is true than the alternative hypothesis (H_1) given the observed data. A custom cutoff value of BF_{01} is 3 and 1/3, with BF_{01} values greater than 3 providing moderate to strong evidence for H_0 and BF_{01} values smaller than 1/3 providing moderate to strong evidence for H_1 . BF_{01} values between 1 and 3 and between 1/3 and 1 provide anecdotal evidence for H_0 and H_1 respectively.

Table 2. Statistical results of 2 (Orientation) × 2 (Motion) × 2 (Alignment) × 2 (Congruency) ANOVAs performed on the combined data from Experiments 1 and 3.

Source	<i>F</i> (1,50)	<i>p</i>	η_p^2
<i>Main effects</i>			
Orientation	6.28	.015	.112
Motion	5.03	.029	.091
Alignment	0.43	.514	.009
Congruency	32.16	.000	.391
<i>Interactions</i>			
Orientation × Motion	3.02	.088	.057
Orientation × Alignment	8.24	.006	.142
Orientation × Congruency	27.79	.000	.357
Motion × Alignment	0.07	.789	.001
Motion × Congruency	0.03	.859	.001
Alignment × Congruency	34.61	.000	.409
Orientation × Motion × Alignment	2.37	.130	.045
Orientation × Motion × Congruency	.001	.980	.000
Orientation × Alignment × Congruency	20.92	.000	.295
Motion × Alignment × Congruency	2.57	.115	.049
Orientation × Motion × Alignment × Congruency	5.07	.029	.092

Note. Significant *F* statistics related to face orientation appear in boldface.

Figures (6 figures)

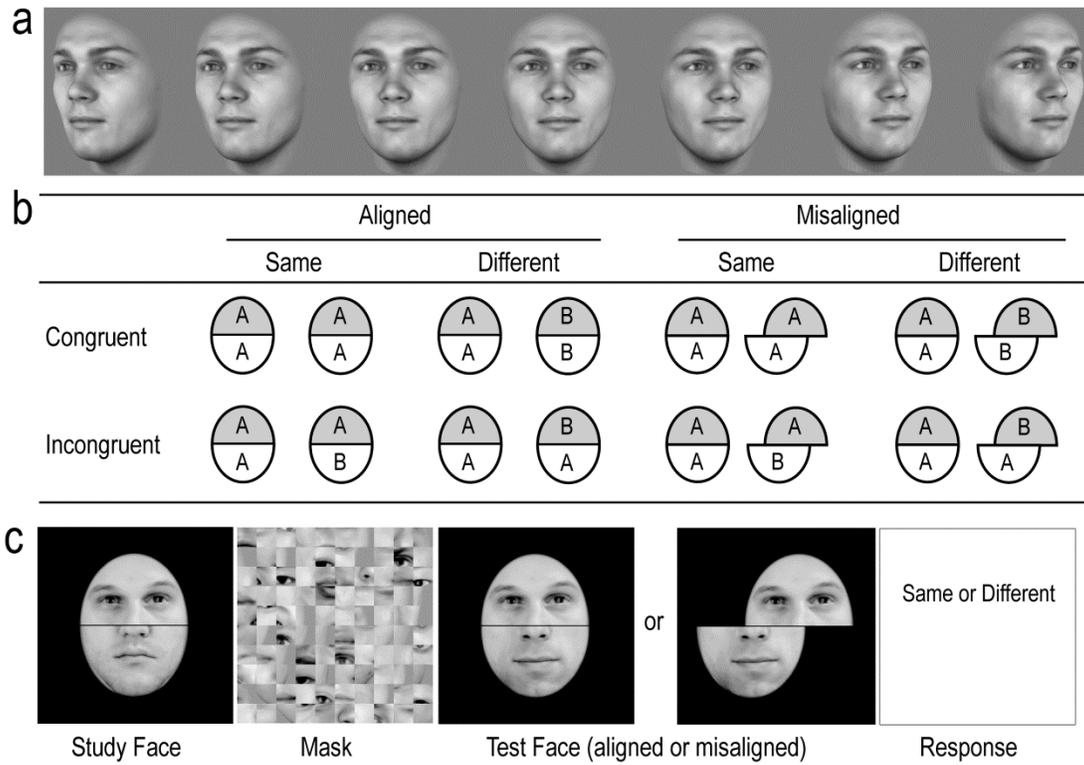


Figure 1. Stimuli, trial sequence, and design used in Experiments 1 to 3. (a) Each face was rendered from 13 viewpoints; here we show seven of them. (b) Design of a composite task. This figure also illustrates how composite faces are formed. Letters represent identities of face parts. (c) In each trial, participants saw a study and a test face separated by an intervening mask, and made same/different judgment about their top parts.

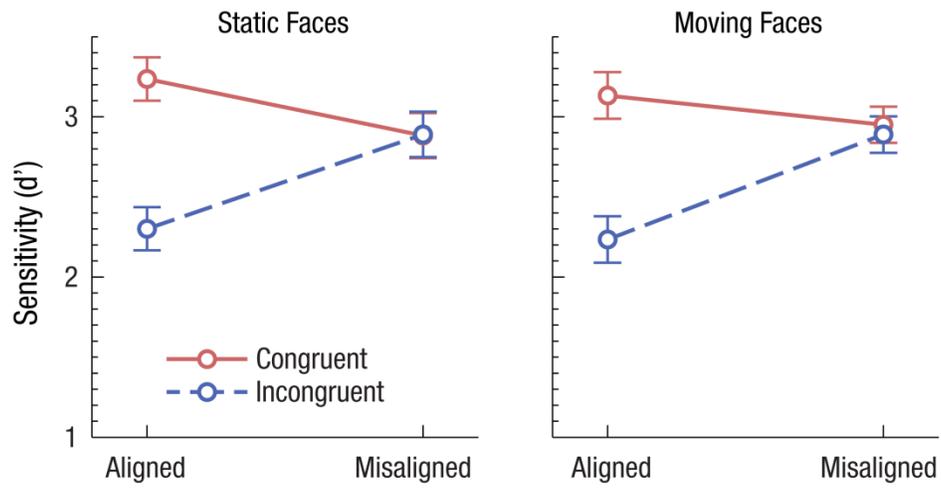


Figure 2. Response sensitivity to upright composite faces as a function of face type, alignment, and congruency in Experiment 1. Error bars represent ± 1 SEM.

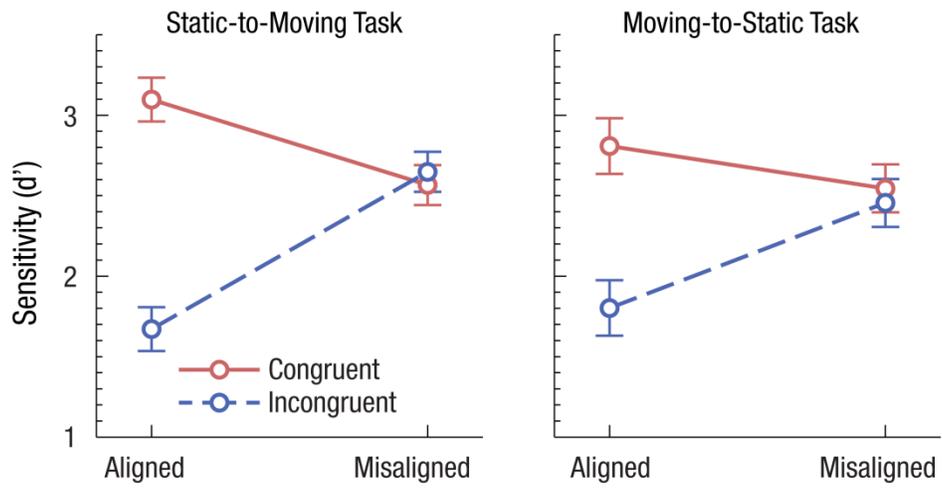


Figure 3. Response sensitivity to upright composite faces as a function of task, alignment, and congruency in Experiment 2. Error bars represent ± 1 SEM.

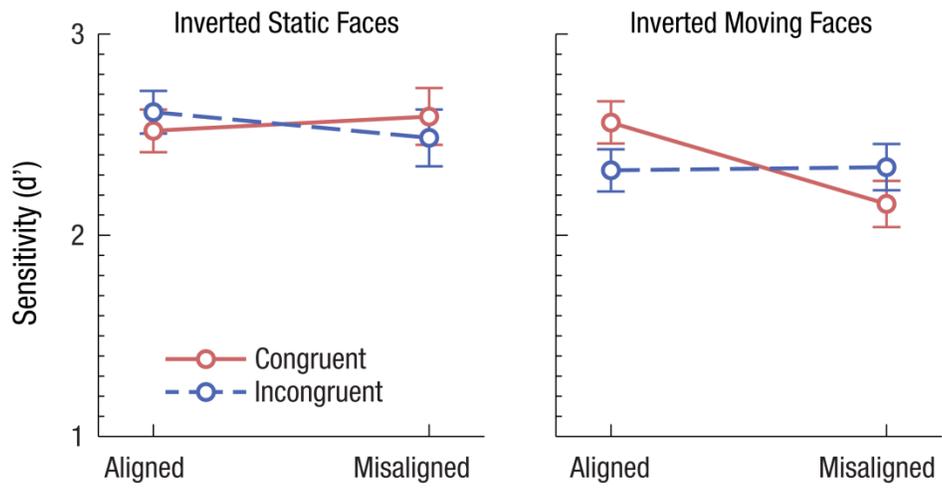


Figure 4. Response sensitivity to inverted composite faces as a function of face type, alignment, and congruency in Experiment 3. Error bars represent ± 1 SEM.

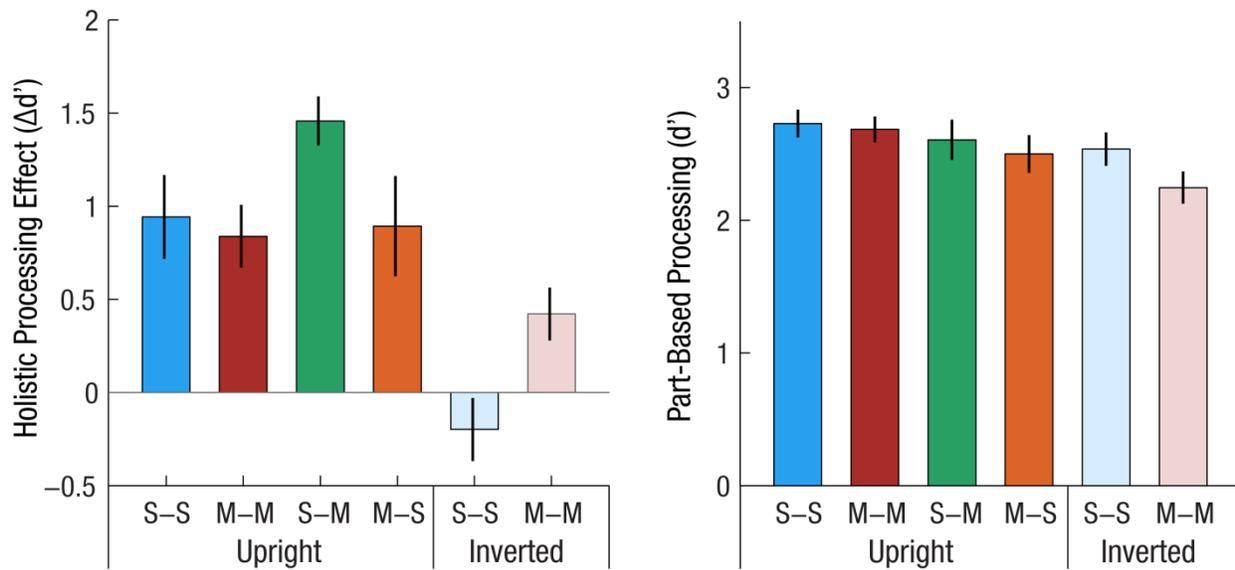


Figure 5. Magnitudes of holistic processing effect (left) and part-based processing (right) as a function of facial motion and face orientation. Holistic processing was calculated by subtracting the congruency effect observed in the misaligned condition from that in the aligned condition; whereas part-based processing was indexed by discrimination performance on misaligned conditions. Larger values indicate stronger evidence of holistic processing or part-based processing, respectively. Note that the magnitudes of holistic processing does not always covary with the magnitudes of part-based processing. S = static faces; M = rigidly moving faces; S-S, study static and test static faces; M-S, study moving and test static faces, and so on. Error bars represent ± 1 SEM.

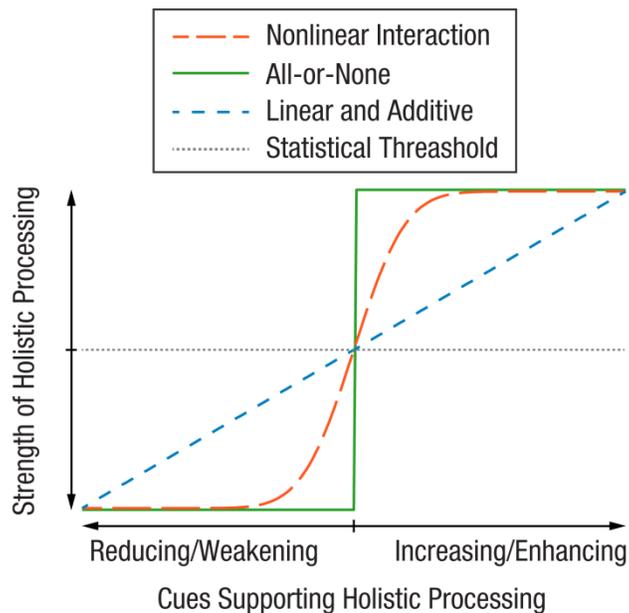


Figure 6. Hypothetical relations between the number and/or strength of factors supporting holistic processing and the observed holistic processing effect. Note that while the observed holistic processing effect is all-or-none in terms of statistical significance, the magnitudes of holistic processing effect is not all-or-none (i.e., zero versus maximum) but often varies depend on available cues.

Appendixes (3 Tables)

Table A1. Mean (and standard error) of hits, false alarms (FA), d' , and response bias (C) observed in Experiment 1.

	Aligned		Misaligned	
	Congruent	Incongruent	Congruent	Incongruent
<i>Study and Test Static Upright Faces</i>				
Hit	.95/.01	.83/.02	.91/.02	.91/.02
FA	.09/.02	.17/.03	.12/.02	.10/.02
d'	3.24/.12	2.30/.16	2.88/.18	2.89/.14
C	-.12/.06	.05/.10	-.08/.06	-.04/.07
<i>Study and Test Moving Upright Faces</i>				
Hit	.95/.01	.86/.03	.94/.01	.92/.02
FA	.12/.02	.20/.04	.13/.02	.11/.02
d'	3.13/.13	2.13/.14	2.95/.12	2.89/.14
C	-.23/.08	-.12/.10	-.18/.07	-.08/.07

Table A2. Mean (and standard error) of hits, false alarms (FA), d' , and response bias (C) observed in Experiment 2.

	Aligned		Misaligned	
	Congruent	Incongruent	Congruent	Incongruent
<i>Study Static Test Moving Upright Faces</i>				
Hit	.94/.02	.77/.03	.86/.03	.86/.03
FA	.10/.02	.24/.03	.13/.02	.13/.02
d'	3.10/.14	1.67/.14	2.57/.17	2.65/.16
C	-.14/.05	-.01/.09	.02/.08	-.01/.09
<i>Study Moving Test Static Upright Faces</i>				
Hit	.94/.01	.84/.02	.88/.02	.86/.03
FA	.15/.03	.27/.03	.14/.03	.14/.02
d'	2.81/.14	1.80/.15	2.55/.16	2.46/.16
C	-.22/.06	-.23/.06	-.05/.07	-.04/.07

Table A3. Mean (and standard error) of hits, false alarms (FA), d' , and response bias (C) observed in Experiment 3.

	Aligned		Misaligned	
	Congruent	Incongruent	Congruent	Incongruent
<i>Study and Test Inverted Static Faces</i>				
Hit	.92/.01	.93/.01	.85/.03	.85/.02
FA	.19/.02	.18/.03	.11/.02	.13/.02
d'	2.52/.12	2.61/.11	2.59/.15	2.48/.14
C	-.28/.06	-.28/.06	.06/.07	.03/.07
<i>Study and Test Inverted Moving Faces</i>				
Hit	.93/.01	.91/.02	.83/.02	.86/.02
FA	.19/.02	.24/.03	.16/.02	.16/.02
d'	2.56/.12	2.32/.13	2.16/.13	2.34/.14
C	-.34/.06	-.37/.08	-.02/.06	-.06/.06