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Part and whole face representations in immediate and long-term memory

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ABSTRACT

Although there is empricial support for the old adage that "we never forget a face" (Journal of Experimental Psychology: General 104 (1975) 54–75), the cognitive processes responsible for our long-term face memories are not well understood. By manipulating the upright and inverted orientation of faces during encoding and retrieval, we investigated the influence of holistic processing on our ability to recognize faces stored in long-term memory. In Experiment 1, participants were trained to identify 12 novel upright faces (six male, six female) by name (e.g., "Joe," "Sue") to a criterion of 100% accuracy. Following learning, holistic memory for the upright and inverted faces was tested using the parts/wholes face recognition task. Different groups of participants were tested either immediately, one week, or two weeks after learning. A significant holistic effect was found for faces tested in their original upright orientation that was stable over the immediate, one-week, and two-week testing periods. In contrast, recognition of the same faces when shown inverted was poor and showed no evidence of holistic processing. In Experiment 2, faces were learned in their inverted orientations with 100% accuracy and tested in their upright and inverted orientations. At the immediate, one-week, or two-week intervals, recognition of inverted faces was relatively poor and there was no evidence of holistic processing for faces tested either in inverted or upright orientations. Collectively, these results indicate holistic processing provides an efficient means for the encoding and retrieval of faces in long-term memory that are relatively stable with the passage of time.

1. The encoding, retrieval, and retention of part and whole face representations in long-term memory

Counting friends, family members, celebrities, politicians, and acquaintances, it is estimated that the average adult can recognize approximately 5000 different faces (Jenkins, Dowsett, & Burton, 2018). Although the sheer number of faces that people can remember is remarkable, this number is even more impressive when one considers how perceptually similar all faces are. That is, faces share the same features (i.e., two eyes, a nose, and a mouth) arranged in a similar configuration, and therefore, successful face recognition relies on our ability to perceive and remember the subtle featural and configural differences that distinguishes one facial identity from another (Maurer, Grand, & Mondloch, 2002). Despite the perceptual demands of face recognition, people can identify a familiar face in a single glance without conscious effort or forethought (Tanaka, 2001). It has been argued that faces are encoded, stored and retrieved as a *holistic* representation in which the features of a face (eyes, nose, mouth) and their spatial distances are integrated into a unitary representation. Yet, the connection between holistic processing and long-term face memory has not been directly explored. In the current study, we investigate the contribution of holistic representation for the encoding and retrieval of faces from long-term memory.

1.1. *Long-term memory for faces*

In their classic study "Fifty years of memory for names and faces," Bahrick, Bahrick, and Wittlinger (1975) tested the old adage that "we never forget a face." Applying a cross-sectional study, high school graduates were tested on their ability to associate the names and faces of their classmates over a retention interval ranging from two weeks to 57 years. Participants completed a series of memory tests with old yearbook photos that required free recall, picture recognition, name recognition, perceptual matching, and picture cueing. The results showed that even 34 years after graduation, recognition performance hovered around 90% accuracy for tasks involving name identification and face-name matching. In a similar study, Bruck, Cavanagh, and Ceci (1991) asked participants to match photos of former classmates with a current photo of the same person taken nearly twenty-five years later. To control for the possibility of simply matching the faces based on perceptual cues, a separate group of participants who had no prior experience with any of the faces in the photographs were tested. The

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key finding was that the familiar group were more accurate at the face matching task than the unfamiliar group suggesting that their judgments were aided by their distant memories for the person. Collectively, these studies indicate that humans have an enormous capacity to remember faces over long retention intervals that span years and even decades of time.

1.2. Holistic face processing

Although most objects are recognized at the basic level (e.g., “chair,” “car,” or “dog”; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976), faces are recognized at the level of the individual (e.g., “Johnny Depp”, “Ryan Gosseling”, “Brad Pitt”; Tanaka, 2001). It has been hypothesized that holistic face processes are recruited to support this more specific level of recognition (Diamond & Carey, 1986; Maurer et al., 2002). The holistic face representation is a perceptual gestalt where the features of a face and their configuration form a non-decomposable, unitary representation (Galton, 1879; Sergent, 1984). Over the last several decades of face recognition research, the concept of holistic face representations has been empirically operationalized and validated in three standard experimental paradigms (Piepers & Robbins, 2012; Tanaka & Gordon, 2010): (1) the inversion task, (2) the face composite task, and (3) the parts/whole task.

Evidence for the holistic face representations comes from the classic inversion task in which faces and non-face objects are studied in their upright orientation and then tested in their upright and inverted orientations (Yin, 1969). Using the upright recognition as the baseline for performance, the well-established Face Inversion Effect (FIE) is the finding where the recognition of faces is disproportionately impaired by inversion relative to the recognition of other inverted, non-face objects (for a review see McKone & Yovel, 2009). The interpretation of the FIE is that in their upright orientation, the features of a face and their spatial distances are integrated into a singular holistic representation. When faces are turned upside down, the holistic face processes are disrupted forcing the observer to view the faces in terms of its parts (for an alternative view, see Gold, Mundy & Tjan, 2012).

A direct link between holistic processing and inversion was established in the face composite and the part/whole tasks. In the face composite task, composite faces are condtructed by joining the top half of one face with the bottom half of another face (Young, Hellawell, & Hay, 1987). Participants are instructed to attend only to the top (or bottom) half of the study face and to decide if it is the “same” or “different” as the top (or bottom) half of a test composite face. The main finding was that when the to-be-ignored half of the test face was different from the study face, response times were slower and recognition accuracy poorer. These results indicate that participants cannot restrict their attention to just one half of the face, but are compelled to procees faces holistically. However, when the top and bottom face halves are inverted or misaligned, holistic interference is abolished and recognition performance improves (see Rossion, 2013 for a review).

In the part/whole paradigm, participants learn a set of study faces by name and their memory for the face part (e.g., eyes) are tested in a two-alternative forced choice task in which the target part and its foil are presented either in isolation or in the whole face. The whole-face test items were constructed such that the target and foil faces differed only with respect to the target feature being tested. As shown in Fig. 1, participants are asked to identify “Ann’s eyes” in the isolated part condition and in the whole face condition. Note that the only difference between the “Ann” target and foil in the whole face test is the eyes feature, whereas the hair, external face contour, nose, and mouth features is held constant. The measure of holistic processing is the difference in recognition of the eyes shown in the whole face context versus recognition of the face part shown in isolation. The main result was that accuracy was highest when the features were presented in the context of a whole face as compared to features presented in isolation (Tanaka & Farah, 1993). Critically, the holistic advantage is abolished when the faces are inverted at test, suggesting that inversion disrupts holistic face recognition. Similarly, learning scrambled faces and houses showed no evidence of holistic recognition in the part-whole task (Experiment 2 and 3: Tanaka & Farah, 1993). The parts-whole paradigm has been applied to study holistic processingin young children (Pellicano & Rhodes, 2003; Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998), individuals with autism (Joseph & Tanaka, 2002) and own- a d other-race face recognition in adults (Tanaka, Kiefer, & Bukach, 2004). Collectively, the face inversion, face composite and part/whole findings support the holistic face hypothesis claiming that face memories are encoded, stored, and retrieved as integrated wholes and not individual parts. Although it is controversial whether the three measures tap into a common or distinct holistic face mechanisms (Rezlescu, Susilo, Wilmer & Caramazza, 2017), they have become the de facto standards of holistic face processing in the field.

1.3. What is the connection between holistic processing and long-term memory for faces?

The vast majority of face studies have examined holistic processing when faces are directly perceived or when they are remembered for a relatively short period of time. In the inversion studies, the upright (or inverted) test face is presented either immediately following the study face or after a short retention interval of two or three minutes (e.g., Yin, 1969). In the parts/wholes task, the study and test phases of the experiment occur within the same trial (Tanaka et al., 2004) or after a short retention interval (Tanaka & Farah, 1993). Although the perception and short-term recognition studies have been valuable for understanding holistic face processes, the involvement of holistic mechansims in the learning, retention, and recall of faces from long-term memory is largely unknown. Understanding the contribution of holistic processes to the formation of face represntations might help explain the permanence of our long-time memories for faces.

One approach to studying holistic representation of faces in long-term memory is to examine the recognition of famous faces and personally familiar faces. Employing the composite task with famous faces, Young and colleagues showed that the eye region of famous faces was easier to identify than the faces were shown in their inverted orientation than their upright orientation (Young et al., 1987, Exp. 2). Similarly, a stronger composite inference effect was found for identifying upright personally familiar faces than inverted personally familiar faces (Ramon & Rossion, 2012). The reduced composite effect for inverted faces of celebrities suggests that in their normal upright orientation, celebrity faces are encoded as holistic representations.

A functional link between holistic face processing and long-term face recognition is further demonstrated in studies of patients with prosopagnosia. According to their introspective accounts, patients report that they see a face as separate features and are unable to integrate the features into a coherent whole face representation (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010). To evaluate this claim, prosopagnosic patient (HJA) and age- and IQ-matched control participants were asked to match whole faces or face parts. Whereas the control participants showed better matching performance for the whole faces, the prosopagnosic patient showed an advantage for matching the face parts (Boutsen & Humphreys, 2002). In a test of holistic interference, patient GG and control participants memorized a set of faces and then their memories for separate parts of the learned faces were evaluated. Whereas control participants had difficulty recognizing the isolated parts from the learned faces, patient GG was relatively unaffected by the whole face context suggesting that she encoded faces as separate parts, not as an integrated whole (Busigny et al., 2010). DeGutis and colleagues (DeGutis, Cohan, & Mercado, 2012) found that individuals with developmental prosopagnosia (i.e., the inability to recognize faces without a history of brain impairment, sensory deficit or cognitive dysfunction) also displayed an abnormal pattern of holistic processing. On the parts-wholes task, their participants demonstrated

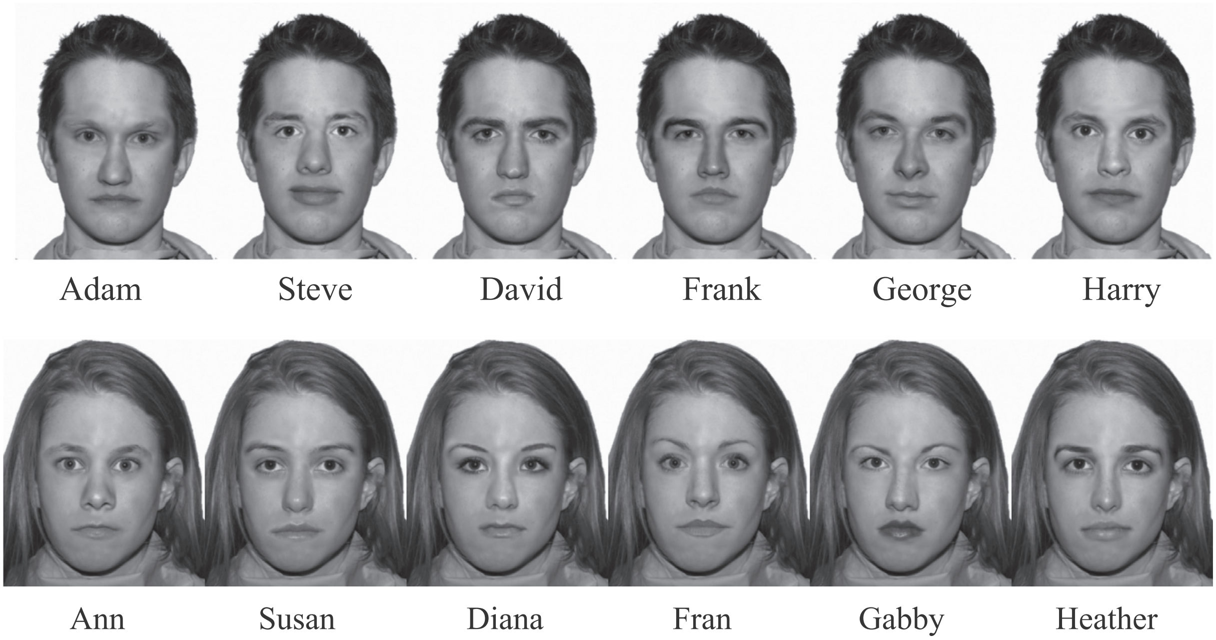

Fig. 1. The six male and six female faces that participants learned to 100% criterion during the study phase of Experiment 1.

an intact holistic advantage for the mouth but a complete absence of the holistic advantage for the eyes. Collectively, these studies suggest that prosopagnosic patients and individuals show deficits in their holistic face processing and these impairments lead to impaired everyday face recognition.

1.4. Current study

In the current study, we examined the impact of holistic and non-holistic processes on the encoding and retrieval of face representations from immediate and long-term memory. For our experiment, we selected the parts/wholes task as our measure of holistic processing. The parts/wholes task has several advantages for testing the holistic representations in long-term memory: (1) it provides an index of both whole face and part recognition, (2) it provides a separate measure of non-holistic and holistic processing for eye, nose, and mouth features, and (3) it correlates well with well established, standardized tests of face recognition (i.e., Cambridge Face Memory Test) with proven construct validity (DeGutis, Wilmer, Mercado, & Cohan, 2013).

2. Experiment 1

The goal of Experiment 1 was to test the effects of orientation on the long-term retention of holistic face memories. Three separate groups of participants were trained to identify 12 upright faces (6 male, 6 female) by name. To discourage participants from using external cues for identification (Ellis, Shepherd, & Davies, 1979), faces of the same gender shared an identical external contour, hairstyles and clothing. Participants were trained until they could identify the faces by name with 100% accuracy. After training, participants were given a two-alternative-forced choice task where they were asked to identify the eye, nose, or mouth part corresponding to a cued name (e.g., Joe's eyes) presented in isolation or in the whole face in their upright or inverted orientation. Participants were tested either: (1) immediately after training, (2) one week after training, or (3) two weeks after training. If holistic processing is necessary for both the encoding and retrieval of face parts, it is predicted that the part-whole advantage would only be observed for faces studied and tested in the upright orientation and not for the faces tested in their inverted orientation. Although performance was expected to decline as a function of the retention interval, holistic recognition of upright faces should be better maintained than the non-holistic recognition of inverted faces. Alternatively, if holistic face processes are only necessary at the encoding stage of a face memory (Richler, Tanaka, Brown, & Gauthier, 2008), a part-whole advantage should be observed at retrieval even when the whole test face is inverted.

2.1. Method

Participants. Sixty University of Victoria undergraduate students (45 female) aged 17–38 (M = 20.4 years, SD = 3.3 years) were recruited to participate in this study. Participants were randomly assigned to one of three test delay groups who were tested either immediately (N = 20), one week (N = 20), or two weeks (N = 20) following training. The experiment was approved by the human ethics committee at the Univeristy of Victoria and participants gave written informed consent prior to their participation.

Stimuli. The face stimuli were composite faces (six males and six females) that were generated by extracting the eyes, nose, mouth features from the neutral faces in the NimStim database (Tottenham et al., 2009). The features were embedded into a male or female face template consisting of a common face contour, hairstyle, and clothing. Twelve target faces (6 male and 6 female), composed of a unique set of eyes, nose and mouth features, were created. For each target face, an eyes, nose, and mouth foil face was constructed by replacing the critical eyes, nose, or mouth feature with the corresponding feature from one of the other five faces of the same gender. To reduce potential practice effects, the foil features from each of the 12 faces were used only once. The images were then converted to grayscale and resized to 251 × 307 pixels.

2.2. Procedure

Face Training. In the training phrase, participants learned to identify 6 male faces and 6 female faces presented in their upright orientation. Training sessions were blocked and counterbalanced by gender such that half of the participants were trained on the six female faces followed by the six males, and half were trained on the male block first, and the female second. At the beginning of each training block, participants viewed a to-be-learned face with its corresponding name

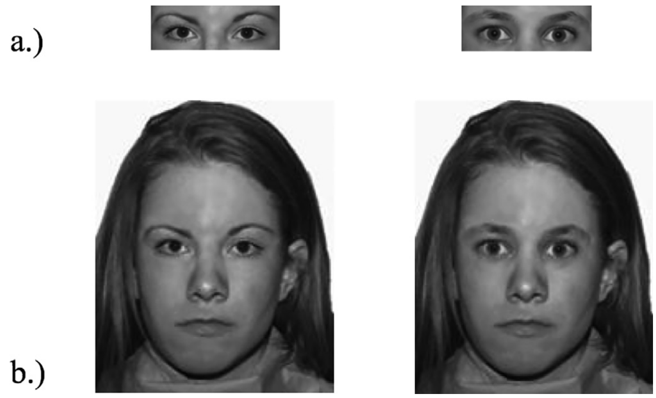

Fig. 2. An example of the part and whole test trials. a.) In the part condition, participants are asked to identify a face part (e.g., Ann's eyes) shown in isolation or b.) in the whole face.

(e.g. "This is Ann", "This is Susan"). Next, the participant saw a face without the name label and was asked to press the keyboard letter key that corresponded to the first initial of the name (e.g., "A" for "Ann", "S" for "Susan", etc.). The face remained on the screen for 5 s or until the participant responded. After their response, the participant received feedback about whether their selection was "correct" or "incorrect". Once the participant was able to identify three repetitions of each of the to-be-learned faces with 100% accuracy, they were introduced to next face and learning continued until all six male (or female) faces were learned with 100% accuracy. The learning procedure was repeated with 6 female (male) faces.

Part and Whole Testing. After participants learned the male and female) faces, their memory for the eyes, nose, and mouth features was assessed immediately following training, one week or two weeks following training in a two-alternative forced choice design (Fig. 2). At the beginning of each trial, a fixation cross appeared for 1000 ms, followed by two face parts shown in isolation or in the whole face. In the isolation condition, participants were asked to identify the target part (e.g., "Which is Ann's nose?"). In the whole face condition, participants

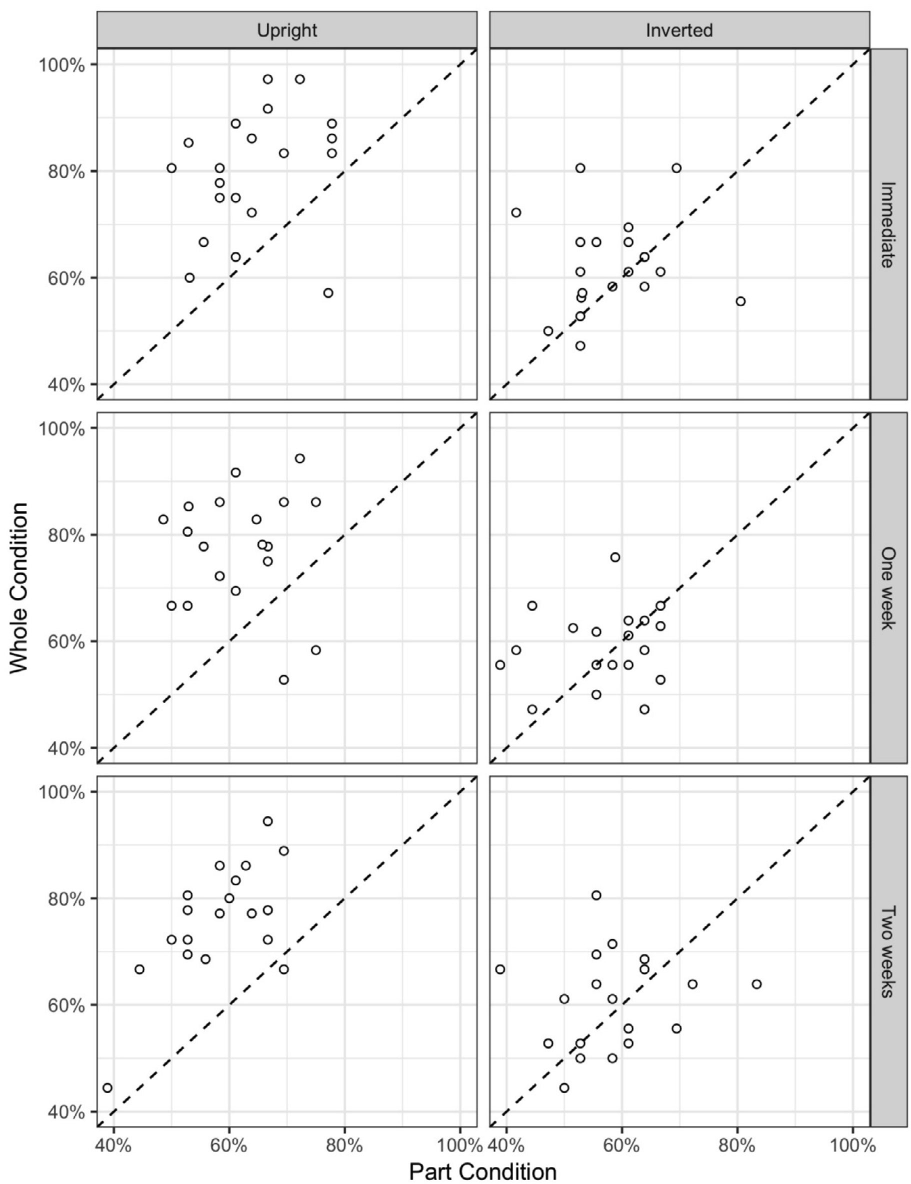

Fig. 3. Experiment 1 results for faces learned in their upright orientation. The data points showed each individual's recognition score for eye and mouth parts tested in the whole face and in isolation presented in their upright and inverted orientations. Note that points above the diagonal line indicate a whole face test advantage whereas points below the diagnonal line indicate an isoltated part test advantage.

were asked to identify the target face (e.g., "Which is Ann?"). In the whole face condition, the target and foil faces differed by the target feature (e.g., eyes) and the non-target features (e.g., nose, mouth) were identical. Participants were instructed to answer as quickly and accurately as possible within a 5 s deadline. The test items were blocked by gender and the presentation order of the male and female test blocks was counterbalanced across participants. Within each male and female block, the upright and inverted faces were pseudo-randomized.

2.3. Results

The training results showed that participants took on average 21.0 training blocks to achieve the 100% accuracy criterion. After successful training, accuracy and response times (RT) were analyzed with three-way ANOVAs with Test Delay (immediate, one week, two weeks) as a between-groups factor and Test Type (part, whole) and Orientation (upright, inverted) as within-subjects factors. The accuracy analysis revealed more accurate performance in upright trials, $F(1, 57) = 97.32$, $p < 0.001$, $\eta_p^2 = 0.63$, and for the whole face trials, $F(1, 57) = 74.32$, $p < 0.001$, $\eta_p^2 = 0.57$. As expected, a significant orientation by test type interaction, $F(1, 57) = 42.39$, $p < 0.001$, $\eta_p^2 = 0.43$, showed that the advantage of whole face trials on recognition accuracy was greater for upright face trials compared to inverted face trials. It is particularly noteworthy that there was no effect of the test delay length on either accuracy or reaction (both $F < 1$), demonstrating that recognition did not diminish across the one- and two-week test intervals even when compared to recognition when tested immediately after training. In an analysis of recognition accuracy by feature type (e.g. eyes, nose, or mouth irrespective of test type condition), a whole-over-part advantage was obtained for all features and in all three test delay groups, but for upright trials only. Fig. 3 shows the whole face and isolated part recognition accuracy scores for individual participants.

Response times for correct trials were analysed and they were submitted to a log transformation before analysis to normalize the typically skewed RT distribution.

Analysis of RT showed that participants took longer to respond to whole trials, $F(1, 57) = 42.39$, $p < 0.001$, $\eta_p^2 = 0.43$, and this effect of test type interacted with orientation, $F(1, 57) = 6.90$, $p = 0.01$, $\eta_p^2 = 0.11$, such that the difference in response time across trial types was greater for inverted trials.

2.4. Discussion

The main finding of Experiment 1 was that participants showed a reliable holistic advantage for faces tested in the upright orientation across the three retrieval intervals (immediate, one week, two weeks). Critically, the whole face advantage remained stable over time and was equally strong for the one- and two-week test group as the immediate test group. The implications of the current results are that the holistic encoding and retrieval of face memories is responsible for the durability of memory for faces (Bahrick et al., 1975; Bruck et al., 1991). For faces tested in the inverted condition, there was no evidence of holistic processing such that feature recognition in the whole upside-down face and in isolation (part) was essentially the same. Whether tested in their upright or inverted orientation, memory for the eyes, nose, mouth features tested in isolation was above chance and remained stable over time.

The response time results showing longer latencies for whole trials than part trials stand in contrast to the findings of DeGutis et al. (2012) who found that control participants were equally fast for whole and part trials. What might explain this discrepancy? In our study, recognition was tested by cueing participants with a name (e.g., Fred) and presenting them with a two-alternative forced choice decision. It is possible that additional processing time was required in the whole face condition so participants could generate a whole face representation to match against the whole face test items. In contrast, participants in the DeGutis et al. (2012) study viewed a study face for 1000 ms that was immediately followed by a part or whole test trial. Arguably, under these conditions, whole test face items have an advantage over part items due to study-test compatibility effects; that is, it is easier to match the whole face test items to the previously whole study face than to match part tests item to whole study face.

Although the results from Experiment 1 suggest that encoding and retrieval of face memories is analytic, the lack of holistic processing for inverted faces could be attributable to other factors. First, the absence of holistic evidence might be an artifact of the mismatch between the encoding condition (upright faces) and the retrieval condition (inverted faces). According to an encoding specificity account (Tulving & Thomson, 1973), inverted faces might show evidence of holistic processing if they were learned and tested in the inverted condition. Compatible with this view, learning to individuate upside-down faces has been shown to ameliorate the Face Inversion Effect. In a training study, participants received 2 weeks (16 h) of practice learning to recognize 30 inverted faces (Laguesse, Dormal, Biervoye, Kuefner, & Rossion, 2012). At the end of training, inverted face training improved the recognition of trained inverted faces (i.e., reduced Face Inversion Effect) and this learning transferred to the recognition of novel upside-down faces. The authors hypothesized that the better inverted face recognition was due to either a more efficient part-based processing of inverted faces or the development of a holistic encoding method applied to the recognition of inverted faces.

Work by Robbins and McKone (2003) suggests that training to recognize inverted faces is aided by efficient part-based encoding and not the adoption of holistic processing. In their study, participants practiced individuating the identities of two pairs of twins displayed in their inverted orientations. After 10 h of training, participants were accurate at recognizing novel pictures of the twins displayed in their inverted orientation, but showed no evidence of holistic processing of these inverted faces as measured by the face composite task. These findings suggest that participants sharpened their parts-based strategy to recognize the upside-down faces. However, as acknowledged by the authors, a specific parts-based might have been optimal in this study because participants needed to learn only a limited number of faces (i.e., four identities).

3. Experiment 2

In Experiment 2, participants were trained to recognize 12 inverted faces with 100% accuracy. After training, participants were administered the parts-wholes test either immediately, one week, or two weeks after training. Faces were tested in both the learned inverted orientation and the novel upright orientation. If inverted faces can be encoded holistically through training, part recognition should be best when tested in the whole inverted face condition relative to the isolated condition and the whole face advantage should persist in participants who are tested one and two weeks after training. No holistic advantage should be found when faces are tested in the novel upright orientation. Alternatively, if inversion disrupts the holistic encoding of faces, part recognition should be equivalent when assessed in the isolated part and whole face test conditions regardless of the test orientation.

3.1. Method

Participants. Sixty University of Victoria undergraduate students (45 female) aged 18–37 (*M* = 21.1 years, *SD* = 3.19 years) were recruited to participate in this study. Participants were randomly assigned to one of three test delay groups who were tested either immediately (N = 20), one week (N = 20), or two weeks (N = 20) following training. The experiment was approved by the human ethics committee at the Univeristy of Victoria and participants gave written informed consent prior to their participation.

Stimuli. The training and test face stimuli were the same faces used

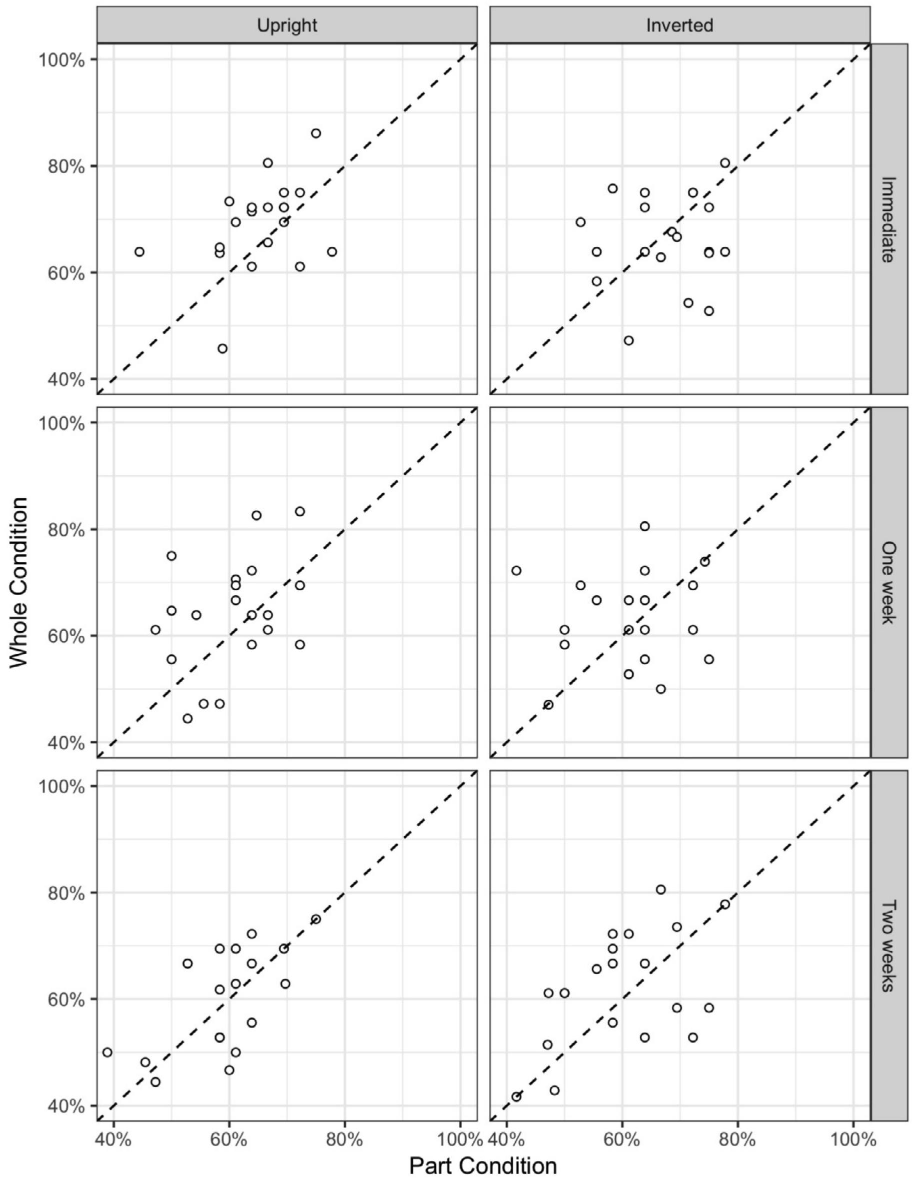

Fig. 4. Experiment 2 results for faces learned in their inverted orientation. The data points showed each individual's recognition score for eye and mouth parts tested in the whole face and in isolation presented in their upright and inverted orientations. Note that points above the diagonal line indicate a whole face test advantage whereas points below the diagnonal line indicate an isoltated part test advantage.

in Experiment 1.

Procedure. We followed the same face training and part and whole test procedures as described for Experiment 1 with the exception that faces were learned in their inverted orientation.

3.2. Results and discussion

The training results showed that participants took on average 30.3 training blocks to achieve the 100% accuracy criterion. The difference in the number of training blocks between the upright training blocks and inverted training blocks to criterion was significant, $p < 0.01$. As in Experiment 1, accuracy and response time (RT) were analyzed with three-way ANOVAs with Test Delay (immediate, one week, two weeks) as a between-groups factor and Test Type (part, whole) and Orientation (upright, inverted) as within-subjects factors. Fig. 4 shows the whole face and isolated part recognition accuracy scores for individual participants.

For accuracy, the analysis showed a main effect of test delay, $F(2, 57) = 6.18$, $p = 0.003$, $\eta_p^2 = 0.17$. Post-hoc comparisons between test delay groups showed that, compared to participants tested immediately after training, recognition accuracy was poorer in participants tested one-week, $t(38) = 2.82$, $p = 0.007$, and two-weeks, $t(38) = 3.25$, $p = 0.002$, after training. No difference was found in recognition accuracy between groups tested one- and two-weeks after training. No other main effects or interactions were significant.

Following the method used in Experiment 1, response times for correct trials were submitted to a log transformation before analysis to normalize the typically skewed RT distribution. As in Experiment 1, participants took longer to respond to the whole face than the isolated trials, $F(1, 57) = 106.02$, $p < 0.001$, $\eta_p^2 = 0.65$.

In summary, the main finding of Experiment 2 was that when the training condition (i.e., whole inverted face) was the same as the test condition (i.e., whole inverted face), part recognition was essentially equivalent (whole face: 62.2%, isolated part: 61.4%). These results indicate that there was no evidence of holistic processing of inverted faces. The absence of a part-whole advantage for inverted faces was consistent with the previous findings (Tanaka & Farah, 1993; Tanaka & Sengco, 1997) and the lack of a composite effect for inverted faces reported by Robbins and McKone (2003). The results from Experiment 2 results rule out a encoding-specificity account (Tulving & Thomson, 1973) for the parts/wholes effect because participants performed no better when the encoding and retrieval conditions were the same (i.e., learning whole inverted faces and testing whole inverted faces) than when they were different (ie., learning whole faces and testing whole upright faces). In contrast to Experiment 1, where recognition performance remained stable across the three test intervals, recognition accuracy of the face parts declined in Experiment 2 at the one and two week testing intervals. These results indicate that part information in an inverted face may be more vulnerable to the passage of time than face information studied in an upright face.

Results from Experiment 2 raise an interesting puzzle about how people remember inverted faces. After learning upside-down faces to 100% accuracy, recognition of face parts was roughly equivalent to part recognition in Experiment 1 where participants learned upright faces. Hence, learning inverted faces does not enhance memory for the individual face parts relative to learning upright faces. Similarly, forcing participants to remember inverted faces does not promote holistic processing as evidenced by the absence of a whole face recognition advantage over isolated part recogniton. Thus, the strategy that people employ to learn and recognize inverted faces remains an open question.

4. General discussion

In two experiments, we examined the effects of orientation on the holistic encoding, retention and retrieval of faces in long-term memory. In Experiment 1, participants learned to identify 12 upright faces (six male and six female faces) presented in their upright orientation with 100% accuracy. After learning, participants were tested for their memories of face features shown in isolation or embedded in the whole face. Participant groups were tested either immediately after learning, one week after learning or two weeks after learning. The main finding was that a holistic processing effect was obtained when faces were tested in their upright orientation immediately after learning, one week and two weeks later. However, when the same faces were tested in their inverted orientation, overall recognition was poor and there was no evidence of holistic processing at any of the three time intervals. In Experiment 2, faces were learned and tested in their inverted orientations. After training, overall recognition of inverted whole faces was relatively poor, there was no evidence of a whole face advantage for upright or inverted faces and recognition declined as the retention interval increased.

The foregoing results suggest that our long-term memories for upright faces are encoded in terms of the individual part (e.g., eyes, nose mouth) and in terms of their instantiation in the whole face context. This hierarchy of parts and wholes is compatible with computational models of high-level vision in which the early layers are dedicated to the representation of basic object features that are connected to more complex, object-level layers (Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Tanaka, Saito, Fukada, & Moriya, 1991). However, it is undetermined whether part representations are mandatory for whole face recognition. In the feed-forward version of the model, object recognition occurs via the initial activation of the part layer that provides input to the whole-object representations. In contrast, the reverse hierarchy version posits that activation of the whole-object representation is primary and activation at the object level trickles down to activation of its local parts (Ahissar & Hochstein, 2004). As evidenced in patients with brain damage, the whole-face representation can be activated in the absence of activation of face parts (Rossion, Dricot, Goebel, & Busigny, 2011). Results from Experiment 1 and 2 (see Figs. 3 and 4) indicate that with the passage of time, memory for the individual features of a face tends to fade whereas memory for the parts shown in the whole face remains robust. Future experiments could test whether increasing retention to even longer delay (e.g., months, years) would further erode memory for the isolated face faces, but preserve their memory in the whole face context.

These findings illustrate a functional link between the level of holistic processing and successful whole face recognition. Specifically, in Experiment 1, faces that were learned and tested in the upright orientation showed an average part-whole face advantage of 16% and were correctly recognized on the 75% of the whole face trials. By comparison, faces learned in the upright orientation and tested in the inverted orientation showed virtually no holistic effect (i.e., a part-whole difference of 2%) and were recognized on only 59% of the inverted whole face trials. Similarly, in Experiment 2, faces learned in their inverted orientation and tested in either their inverted or upright orientation showed virtually no part-whole advantage, 3% and 1%, respectively and were recognized on 65% and 62% of the trials, respectively. Our results demonstrate that face memories include information about the parts and wholes of the to-be-recalled face. That is, in all conditions, participants were performing above chance with respect to their memories for parts of the faces. However, only under conditions when the faces were studied and tested in their upright condition was memory performance boosted by holistic representations.

Is there a connection between holistic face processing and face recognition abilities? In an individual difference study, DeGutis and colleagues (DeGutis et al., 2013) applied regression analysis to show that the Cambridge Face Memory Test (CFMT) of face recogniton (Duchaine & Nakayama, 2006) reliably correlated with parts/wholes(r = 0.46;) and the face composite (r = 0.36) tests. In contrast, a recent study showed that the CMFT demontated a moderate correlation with inversion effect (r = 0.42), a modest correlation with the parts/wholes effect (r = 0.25) and virtually no correlation with the face composite effect (r = 0.04) (Rezlescu et al., 2017) . The authors argued that the inversion, part-whole, and composite effects reflect distinct perceptual mechanisms rather than a unitary holistic face process. Despite the moderate correlations between indepdent tests of face inversion and parts/whole recogntion, the current study establishes a robust *functional* relationship between inversion and holistic face processing. Specifically, when a face is inverted during encoding or retrieval (or both), overall performance declines and holistic face processes are eliminated.

Patients with acquired prosopagnosia provide another line of research linking holistic processing and face recognition. For these patients, damage to temporal lobe structures causes profound deficits in their face processing abilities that are so severe that these individuals have difficulty recognizing the faces of famous celebrities (Henke, Schweinberger, Grigo, Klos, & Sommer, 1998; Schweinberger, Klos, & Sommer, 1995) and even the faces of close friends and family members (Levine & Calvanio, 1989). Neuropsychologists noted in their case reports that problems in face recognition stem from a breakdown in holistic perception where patients have difficulty extracting the overview of the whole face (Levine & Calvanio, 1989) or fail to see the face as an integrated, unitary percept (Spillmann, Laskowski, Lange, Kasper, & Schmidt, 2000). In direct tests of their holistic face processing skills, it has been shown that prosopagnosic patients fail to exhibit the classic face inversion effect (Busigny & Rossion, 2010; Busigny et al., 2010), do not show an interference effects on face composite task (Busigny et al., 2010) and lack a whole face advantage on the part/whole task (Busigny et al., 2010; de Gelder, Frissen, Barton, & Hadjikhani, 2003). Individuals with developmental prosopagnosia (i.e., face recognition deficits in the absence of a brain injury) also show an abnormal whole face advantage eye region on the parts/wholes task (DeGutis et al., 2012). To compensate for their holistic deficit, prosopagnosic patients will resort to a parts-based strategy as demonstrated by a superior recognition for individual parts of the face (Boutsen & Humphreys, 2002) or a paradoxical "reverse" face inversion effect where recognition of upside-down faces is better than recognition of upright faces (Farah, Wilson, Drain, & Tanaka, 1995). In sum, holistic studies with healthy adults and prosopagnosic patients indicate that holistic processes play a central role in everyday face recognition.

Although the holistic explanation provides a viable and testable account of how faces are encoded and retrieved from long-term memory, there are important differences between the current study and real-world face recognition. First, because our experiments focused on recognition of a single face photograph, the present paradigm doesn't capture the richness of everyday face processing where a familiar face is recognizable across changes in lighting, perspective and viewing distance and changes in a person's appearance due to age, expression, hairstyle, clothing factors (Bruce, 1982; Longmore, Liu, & Young, 2008; Jenkins, White, Van Montfort, Burton, & a, 2011). However, it is unlikely that holistic processing reported in our study was an artifact of picture recognition given that holistic operations have been identified in real-world recognition of famous people (Young et al., 1987) and holistic operations are compromised in prosopagnosic patients who have difficulty recognizing publicly familiar (Busigny et al., 2010) and personally familiar faces (Ramon, Busigny, Gosselin, & Rossion, 2015). Second, evidence suggests that a qualitatively different perceptual strategy is used when viewing a familiar versus an unfamiliar face. Whereas recognition unfamiliar faces was dominated by the external features, recognition memory for familiar faces as was more reliant upon the internal features (Ellis et al., 1979; Want, Pascalis, Coleman, & Blades, 2003). In our study, the internal features of each identity were superimposed on the same face outline. Hence, recognition of familiar faces was approximated in our experiment by requiring participants to focus on the invariant facial features and ignore external information.

In conclusion, the current study makes several points regarding the precipitating conditions of holistic face processing. First, holistic processing requires that faces be presented in their upright orientation at the encoding and retrieval stages of recognition. Second, if the upright condition is violated either at the encoding stage, retrieval stage or both stages of processing, holistic processing is disrupted and participants are forced to rely on a parts-based method for encoding and retrieval. Third, holistic processing is not simply a product of individuation or "expert" performance. In this study, participants learned to identify the individual identities of either upright faces (Experiment 1) or inverted faces (Experiment 2) with 100% accuracy. Despite achieving perfect learning performance in both conditions, it was only the faces learned in their upright condition that recruited holistic processes. We speculate that participants employed a non-holistic strategy to learn the identities of the inverted faces during training, but this strategy is less optimum than a holistic approach in terms of overall recognition and resistance to temporal decay. To conclude, these results suggest that holistic processes provide an efficient mechanism by which individual faces can be encoded and retrieved from long-term memory; a process that is remarkably robust and resilient to the passage of time.

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