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# Greater reliance on the eye region predicts better face recognition ability

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ABSTRACT

Interest in using individual differences in face recognition ability to better understand the perceptual and cognitive mechanisms supporting face processing has grown substantially in recent years. The goal of this study was to determine how varying levels of face recognition ability are linked to changes in visual information extraction strategies in an identity recognition task. To address this question, fifty participants completed six tasks measuring face and object processing abilities. Using the Bubbles method (Gosselin & Schyns, 2001), we also measured each individual's use of visual information in face recognition. At the group level, our results replicate previous findings demonstrating the importance of the eye region for face identification. More importantly, we show that face processing ability is related to a systematic increase in the use of the eye area, especially the left eye from the observer's perspective. Indeed, our results suggest that the use of this region accounts for approximately 20% of the variance in face processing ability. These results support the idea that individual differences in face processing are at least partially related to the perceptual extraction strategy used during face identification.

## 1. Introduction

Face identification is a great challenge for the visual system, as human faces consist of a small set of facial features (e.g. the eyes, the nose, the mouth) with only subtle variations in inter-attribute distances (Dupuis-Roy, Fiset, Dufresne, Caplette, & Gosselin, 2014; Taschereau-Dumouchel, Rossion, Schyns, & Gosselin, 2010; see also Burton, Schweinberger, Jenkins, & Kaufmann 2015; Sandford & Burton, 2014). In the last few decades, the processes supporting face identification have been extensively investigated using group-based approaches where interindividual variations were typically regarded as uninformative noise. However, significant variations in face identification ability have been observed within the healthy population (Bate, Parris, Haslam, & Kay, 2010; Bowles et al., 2009; Duchaine & Nakayama, 2006; Royer, Blais, Gosselin, Duncan, & Fiset, 2015; Wilmer et al., 2010), and many authors now highlight the importance of individual differences to gain a better understanding of face processing mechanisms (e.g. Yovel, Wilmer, & Duchaine, 2014; see also Richler, Cheung, & Gauthier, 2011 for a discussion).

An example of this growing interest for individual differences is found in recent papers studying holistic processing, i.e. the extent to which individuals integrate facial parts into a unified whole or "gestalt" (Farah, Wilson, Drain, & Tanaka, 1998; see Richler, Palmeri, & Gauthier, 2012 for precisions regarding the measures and subtypes of holistic processing). The experimental effects thought to measure holistic processing (e.g. composite effect, Young, Hellawell, & Hay, 1987; part-whole task, Tanaka & Farah, 1993) have been replicated numerous times at the group-average level (see Richler et al., 2012). However, if holistic processing is indeed important for face processing and identification, individual differences in the ability to discriminate and recognize faces might be expected to at least partly depend on this mechanism. Results addressing this question are mixed: While some have obtained a significant correlation between face recognition ability and the magnitude of certain experimental effects thought to reflect holistic processing (DeGutis, Wilmer, Mercado, & Cohan, 2013; Richler et al., 2011; Wang, Li, Fang, Tian, & Liu, 2012), others have not (Konar, Bennett, & Sekuler, 2010; Richler, Floyd, & Gauthier, 2014). Moreover, studies finding a link indicate differences in holistic face perception only account for a limited proportion of differences in face recognition ability. We thus believe it is important to investigate other perceptual

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and cognitive mechanisms known to be involved, on average, in face recognition using an individual differences based approach.

Here, we explore the hypothesis that the visual information extracted during face recognition is systematically related to face processing abilities. In line with this proposition, Pachai, Sekuler, & Bennett (2013) demonstrated that tuning for horizontal information is significantly correlated with upright face identification accuracy as measured within the same recognition task (see also Pachai, Sekuler, Bennett, Schyns, & Ramon, 2017). To our knowledge, this is the first study to show a clear link between the use of specific low-level visual information (i.e. perceptual strategies) and face recognition ability. However, based on these results, we cannot disentangle whether the best face recognizers are especially sensitive to horizontal information itself or to certain features that contain greater amounts of this type of information, for instance the eye area. Indeed, past research investigating visual information extraction strategies in face identification using group-average approaches have repeatedly demonstrated that the eye region is crucial for the correct identification of facial stimuli (Bentin, Allison, Puce, Perez, & McCarthy 1996; Butler, Blais, Gosselin, Bub & Fiset, 2010; Caldara et al., 2005; Gosselin & Schyns, 2001; Itier, Alain, Sedore, & McIntosh, 2007; Sekuler, Gaspar, Gold & Bennett, 2004; Vinette, Gosselin & Schyns, 2004; Xivry, Ramon, Lefevre & Rossion, 2008). Although this result sheds light on the nature of the most diagnostic facial feature in the healthy population, it may hide important individual differences in the visual strategies used to process faces. Indeed, the average perceptual strategy used by a group of observers may not necessarily predict the use of information in the most skilled individuals in a given task. For instance, previous results show that the mouth region (Blais, Roy, Fiset, Arguin, & Gosselin, 2012; Calvo, Fernández-Martín, & Nummenmaa, 2014) and tuning for horizontal information (Balas & Huynh, 2015; Duncan et al., 2017; Huynh & Balas, 2014) are particularly diagnostic for the task of facial expression categorization. However, recent evidence suggests that individual differences in utilization of horizontal information were predicted by the diagnosticity of the eye area, and not the mouth (Duncan et al., 2017). In the case of face recognition, if the eye area is indeed important (or diagnostic) for face recognition in human observers, we should expect that the individual observers that are especially skilled in face processing rely on this strategy to a greater extent than individuals with weaker face processing ability. Other types of information such as spatial frequencies (SFs) may also be associated with face processing ability. Although low SF information is not used, on average, by human observers, ideal observers are able to make use of this information (see for example Gold, Bennett, & Sekuler, 1999; Näsänen, 1999). On the other hand, the use of horizontal orientations in face recognition appears to be subtended by mid-to-high SFs (Goffaux, Van Zon, & Schiltz, 2011), which may suggest a link between this band of SFs and face processing abilities.

Eye-tracking studies also provide some insight into the potential importance of the eye region of the face for predicting individual differences in face processing ability. For instance, Sekiguchi (2011) showed that participants with higher face memory abilities tend to fixate the eyes more than individuals with lower face memory abilities. However, a more recent study using a different task to measure eye movements obtained a correlation between time spent fixating the nose region and face recognition ability in control observers (Bobak, Parris, Gregory, Bennetts, & Bate, 2017). Nevertheless, the features that are fixated foveally by an observer are not necessarily *used* for a given task (Arizpe, Kravitz, Yovel, & Baker, 2012; Blais, Fiset, Roy, Saumure Régimbald, & Gosselin, 2017; Jonides, 1981; Posner, 1980). This potential link between individual differences in face processing abilities and use of facial information can be directly investigated using psychophysical methods such as Bubbles (Gosselin & Schyns, 2001).

The current study explores how variations in the ability to recognize faces in healthy observers are linked to the visual strategies used in face identification, i.e. the diagnostic facial regions and SFs for accurate face recognition. Fifty participants first completed three tasks measuring face processing abilities. A principal component analysis carried out on the results from these tests yielded a single score to assess general face processing ability (see Furl, Garrido, Dolan, Driver, & Duchaine, 2011 for a similar procedure). The participants also completed three non-face object recognition tasks to take into account the role of general recognition ability in the observers' use of facial information. Next, to pinpoint the features in which SFs are associated with face identification, we designed a 10-choice identification task using the Bubbles method (Gosselin & Schyns, 2001; see Caldara et al., 2005 for a very similar task). The general idea behind Bubbles is that by randomly sampling specific visual information on a trial-by-trial basis, we will be able to precisely determine, after many trials, what information is significantly correlated with performance in any given visual categorization task (e.g. Smith, Cottrell, Gosselin, & Schyns, 2005; Thurman & Grossman, 2008; Willenbockel, Fiset, et al., 2010; Robinson, Blais, Duncan, Forget, & Fiset, 2014; Royer et al., 2016). In this case, we combined the Bubbles results and the face identity factor scores derived from a principal component analysis to reveal which facial regions at which spatial frequency ranges are significantly correlated with face recognition accuracy.

## 2. Materials and method

### 2.1. Participants

Fifty (28 women) Caucasian, right-handed participants provided informed consent to complete several tests for this study: three face recognition tasks and three object recognition tasks completed in a counterbalanced order. Participants also completed a 10-choice identification task using Bubbles. All participants were between 18 and 40 years of age (mean age of 23.9, S.D. = 4.4). The study was approved by the Université du Québec en Outaouais's Research Ethics Committee and was conducted in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). The number of participants was set at fifty to include individuals with a wide range of face and object recognition ability in our sample. All participants had normal vision as indicated by their score on the Snellen Chart and Pelli-Robson Contrast Sensitivity Chart (Pelli, Robson, & Wilkins, 1988).

### 2.2. Apparatus

The experiments were conducted on MacPro QuadCore computers. Stimuli were displayed on a 22-inch 120 Hz Samsung LCD monitor. The monitor's resolution was set to 1680 × 1050 pixels. Minimum and maximum luminance values were 0.4 cd/$m^2$ and 101.7 cd/$m^2$, respectively. The participants were seated in a dark room and viewing distance was maintained constant with a chinrest. Relation between luminance and RGB values was set to linear.

### 2.3. Face and object tasks

Each participant completed a total of six face and object recognition ability tests: the Cambridge Face Memory Test + (CFMT+; Duchaine & Nakayama, 2006; Russell, Duchaine, & Nakayama, 2009; see also Cho et al., 2015), the Cambridge Face Perception Test (CFPT; Duchaine, Germine & Nakayama, 2007), the Glasgow Face Matching Test short version (GFMT; Burton, White, & McNeil, 2010), the Horse Memory Test (HMT; Duchaine & Nakayama, 2005), the Cambridge Car Memory Test (CCMT; Dennett et al., 2012), and the Cambridge Hair Memory Test (CHMT; Garrido et al., 2009). All Cambridge tests were programmed in Java; the others (GFMT and HMT) were programmed in Matlab (Natick, MA) using functions from the Psychophysics toolbox (Brainard, 1997; Pelli, 1997).

**Fig. 1.** 10 faces used in the bubbles experiment.

### 2.4. Bubbles task

We selected ten faces (five women) from a small database of faces (twenty faces; ten women) presented in a previous study (Royer et al., 2017; Willenbockel, Fiset, et al., 2010). The grayscale stimuli were shown through an elliptical aperture, which masked their external facial features. Image resolution was 256 × 256 pixels, and the face width was six degrees of visual angle. The spatial frequency spectrum of each face stimulus was set to the average spectrum of all faces using SHINE (Willenbockel, Sadr, et al., 2010) and the stimuli were spatially aligned on the average positions of the main internal facial features (eyes, mouth, and nose) using translation, rotation, and scaling. It is important to note that the relative distances between features are not affected by the alignment procedure. The stimuli used in the bubbles experiment are shown in Fig. 1.

To create a *bubblized* stimulus, a face (Fig. 2A) was first decomposed into five different spatial frequency (SF) bands (Fig. 2B; 103.50–51.75, 51.75–25.88, 25.88–12.94, 12.94–6.47, and 6.47–3.23 cycles per face, the remaining low-frequency band serving as a constant background) using the Laplacian pyramid transform implemented in the pyramid toolbox for Matlab (Simoncelli, 1999; 128–64, 64–32, 32–16, 16–8 and 8–4 cycles per image). The entire range of SFs were used and successive scales were one octave apart, mirroring natural energy statistics and the sensitivity of the human visual system. Each SF band was then independently and randomly sampled with Gaussian apertures (i.e. bubbles) of different standard deviations (FWHM for bands 1 to 5: 14.1; 28.3; 56.5; 113.0; 226.1). The size of the bubbles was adjusted in accordance with the frequency band to only reveal three cycles (corresponding to a size of 6, 12, 24, 48 and 96 pixels in pixels; Fig. 2C). Since the size of the bubbles is much larger for lower SF bands, the number of bubbles was adjusted at each scale to maintain a constant probability of a given pixel being revealed across the five SF bandwidths. A point-wise multiplication was then performed between the bubbles' masks and the filtered images to obtain one bubblized face for each SF band (Fig. 2D). Finally, these five randomly sampled images plus the constant background were summed to produce the bubblized stimulus, i.e. what is shown to the participant on a given trial (Fig. 2E).

The participants learned to associate the faces with common French Canadian names (e.g. Caroline, Cynthia, Vincent, etc.) from printed grayscale pictures displayed along with these names. Each of the numerals (0–9) on a regular computer keyboard was associated with a particular face name. The practice session began once the participants

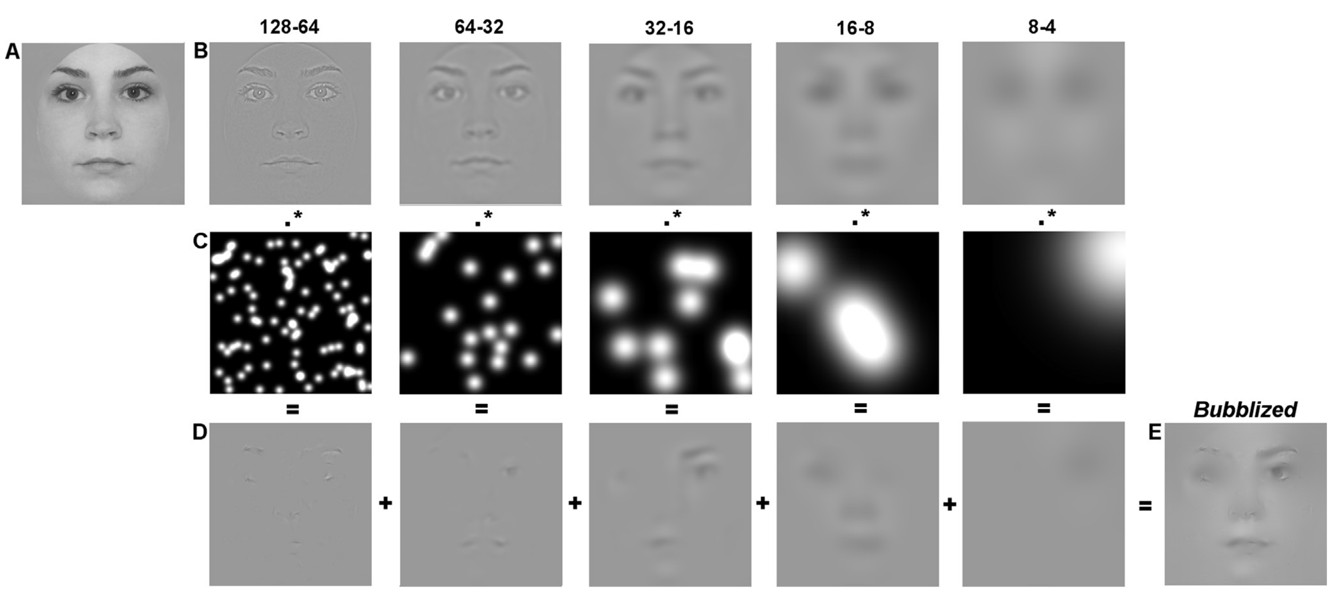


**Fig. 2.** Creation of the bubblized stimulus using one of the stimuli of our study. The original stimulus (A) is filtered into the five spatial frequency bands in B. In each band, a number of randomly positioned Gaussian apertures puncture a homogeneous black field (C). Applying the punctured masks to the filtered stimulus reveals the information in each band (D). This spatially filtered information is then summed, producing a bubblized stimulus (E). Cycles per image for each band are written over the corresponding SF bands.

were confident that they could identify the ten faces. A 500 ms fixation point initiated each trial and disappeared at stimulus onset. Participants were also instructed to look at the fixation point, which fell approximately in the nose area of the test face. Then, one of the randomly chosen ten faces was presented, and remained onscreen until the participant provided a response by pressing one of the response keys. An unrestricted stimulus presentation time seemed more appropriate for our study of individual differences in face processing ability to ensure the task was not made too difficult for certain participants. Indeed, it is possible that lower-ability recognizers would have been unable to complete the bubbles task with a restricted presentation time or would have needed a very high number of Bubbles to complete the task, thereby making it potentially difficult to analyze their results (see below for details on bubbles task and analyses). Furthermore, applying the bubbles method to tasks using restricted and unrestricted presentation times (e.g. Smith et al., 2005; Blais et al., 2012 in facial expression categorization) have led to similar results. The participants were asked to complete additional 100-trial blocks until the accuracy criterion of 95% was reached in two consecutive blocks. This ensured that any interindividual differences observed with bubbles were not merely the product of variations in learning or memorizing the faces, and that the use of information reflects each observers' own perceptual strategy in face recognition (see, for example, Caldara et al., 2005 for a similar procedure with a prosopagnosic patient and healthy controls). Once this condition was met, the bubbles experiment began. The practice and bubbles experiments were programmed in Matlab using functions from the Psychophysics toolbox. The procedure for the bubbles experiment was identical to the practice, with the exception that the face images were now sampled with bubbles. Each participant completed 20 blocks of 100 trials each for a total of 2000 trials. The number of bubbles was adjusted using QUEST (Watson & Pelli, 1983) to maintain an accuracy rate of 55% (i.e. midway between a perfect (100%) and random (10%) performance). A single adjustment procedure was used for all spatial scales; the amount of information revealed in each scale was manipulated so that an equal amount of information (i.e. the same number of pixels) was revealed, on average, across the SF bandwidths.

## 3. Results

### 3.1. Analyses of bubbles data

We first computed a weighted sum with Z-scored accuracies as weights, which amounts to a multiple linear regression between bubbles locations and the participants' accuracy. The plane of regression coefficients yielded by this operation is called a classification image (CI): It reveals how the processing of different regions of the face image is correlated with accuracy. We computed one such raw classification image per subject, per SF band. Of note, a weighted sum (i.e. a special case of the linear regression equation with the identity matrix instead of the inverse covariance matrix—the inverse covariance matrix becomes the identity matrix because the bubbles are randomly distributed) as we perform has been shown to be the optimal estimate of the internal template under the assumption that we apply a linear amplifier model (Murray, Bennett, & Sekuler, 2005; see also Chauvin, Worsley, Schyns, Arguin, & Gosselin, 2005). To transform the resulting values into Z-Scores, we used a permutation procedure, meaning that we repeated the above procedure with random permutations of the response vector, thus obtaining a permutation-CI, or PCI. This procedure generates a noise distribution. The individual CIs and PCIs were smoothed using Gaussian kernels of same standard deviations as the ones used to create the bubblized stimuli during the experiment. Each observer's CI was then transformed into Z-scores using the mean and standard deviation of the PCI. More specifically, the pixel values in each observer's CI in each SF band was subtracted by the mean of all pixel values contained in the PCI of the corresponding SF band, and the result was then divided by the standard deviation of all pixels values in this same PCI. Finally, we grouped all observers' Z-scored CIs by summing them and dividing the result by the square root of the number of observers (i.e. fifty). This group CI either consisted of the unweighted individual CIs (as described here) or the individual CIs weighted with face recognition performance (see Section 3.3). To determine what visual information was significantly correlated with accuracy in the bubbles task, we applied the pixel test to these grouped classification images. The statistical threshold provided by this test corrects for multiple comparisons (for details, see Chauvin et al., 2005).

A separate analysis was also conducted where SF information was combined across all five bands (see Blais et al., 2012 for a similar procedure). In short, this analysis consisted of summing the bubbles' center across scales and smoothing the resulting 2D plane by a unique filter. Similar to our previous analysis preserving separate SF information, this procedure was conducted for each observer. The individual CIs were first converted to Z-Scores using a permutation procedure (see above for details). The raw CIs were then smoothed with a Gaussian kernel defined by the same standard deviation as the one used in the third SF band during the experiment. All observers' smoothed CIs were summed, and the result was divided by the square root of the number of observers. Similar to the separate SF results, the group CI was either composed of the unweighted individual CIs (see Section 3.2) or the individual CIs weighted with face recognition performance (see Section 3.3). To determine what visual information was significantly correlated with accuracy in the bubbles task, we again applied the Pixel test (Chauvin et al., 2005).

### 3.2. Group average

We first verified whether our participants used, on average, facial regions similar to what has been obtained in past experiments using the bubbles method in face identification tasks (see, for example, Gosselin & Schyns, 2001; Schyns, Bonnar, & Gosselin, 2002; Caldara et al., 2005; Butler et al., 2010). Fig. 3 shows the information significantly linked to accuracy on our bubbles task, i.e. the facial areas and SFs that were diagnostic for face identification. The regions that reached statistical significance are shown in color and are superimposed on one of the

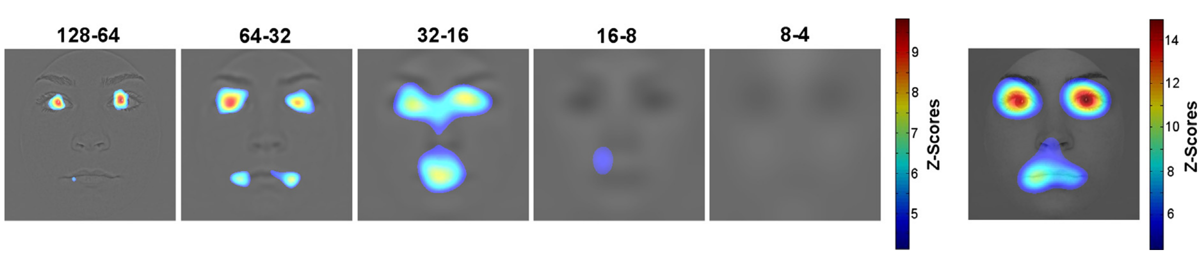


**Fig. 3.** Visual information significantly linked to accuracy decomposed by SF band (left) and combined across all bands (right). The significant portions of the CIs (depicted as heat maps of Z-scores) are superimposed on one of the faces used in the study. Note that the face stimulus presented here was darkened to better illustrate the coloured areas of the image. Cycles per image for each band are written over the corresponding SF bands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

faces used in our experiment ($p < .001$; Z-score threshold criterion [$Z_{crit}$] = 5.02; 4.73; 4.43; 4.12; 3.82, from finer to coarser scales).

As shown in Fig. 3, we see that the eye and mouth areas are particularly correlated with recognition accuracy. The eyebrow area was also significant used on average ($p < 0.05$), but less so than the eyes and mouth. More specifically, the eye region is more important in higher SF bands, while the diagnosticity of the mouth area is slightly shifted towards mid to lower SF bands. Thus, these facial regions appeared to be, on average, useful for the task. The absence of significant diagnostic information in low SFs is consistent with previous results that investigated the use of SF information for face recognition using different methods (e.g. Costen, Parker, & Craw, 1994, 1996; Gaspar, Sekuler, & Bennett, 2008; Gold et al., 1999; Näsänen, 1999; Royer et al., 2017; Willenbockel, Fiset, et al., 2010). We obtain similar results when computing the CIs with a non-parametric approach that does not use the Pixel test from the Stat4CI (see Fig. S1 in the supplemental materials). Of note, the pattern of significant facial information shown in Fig. 3 was similar when using a residual measure of reaction times that regresses out accuracy (see supplemental material). This suggests that areas of the face image that are associated with accurate responses also tend to be associated with fast responses, even when factoring out response accuracy.

The present study used identical face images in the training phase and bubbles experiment which may have influenced the use of features and SFs, and raises the question of whether these results reflect the use of information in everyday face recognition or only when recognition of identical face images is required. The fact that results highly similar to our own are obtained (1) across bubbles studies using different stimulus sets (e.g. Royer et al., 2016; Schyns et al., 2002; Vinette et al., 2004) and (2) in studies that do not rely on training with specific images (e.g. celebrity faces in Butler et al. (2010)) suggests that our results shed light on face processing in natural settings.

While some observers show a pattern of diagnostic information closely resembling this group average, this is not the case for all of our participants. We conducted a second round of analyses where individual ability in face processing was taken into account before grouping the individual CIs. This procedure allowed us to pinpoint the facial information significantly associated with the best performance in the three face recognition tests.

### *3.3. Diagnostic facial information and face processing ability*

To obtain a single measure of face processing ability, we carried out a principal components analysis (PCA), a technique that reduces the dimensionality of a dataset into a more manageable number of variables (components). We submitted the data obtained on the three face tests to a PCA of the correlation matrix with Varimax rotation of the resulting eigenvector components (see Furl et al., 2011, Royer et al., 2015). We retained the first factor in our analysis (i.e. the only factor that yielded an eigenvalue over 1) and computed our participants' factor scores on this factor. As evidenced by the Varimax-rotated principal component weights, each face test loaded, as expected, on this factor, suggesting that it indeed captures general face processing ability (0.851 loading for the CFMT; 0.732 loading for the GFMT; −0.723 loading for the CFPT, note that the scores on the CFPT represent error rates, and are thus inversely correlated with the other two face processing tests). Of note, as in a previous study using bubbles and different measures of face and object processing ability, we obtained a strong negative correlation between the participants' factor scores on the retained component and the number of bubbles required by each observer to reach the target accuracy rate in the bubbles task ($r = -0.6711$; $p < 0.001$; see Royer et al., 2015 for a discussion).

To obtain a first approximation of the facial information correlated with face recognition ability, the individual CIs were weighted using the rank of individual factor scores for the factor retained in our PCA. The weights applied to the individual CIs were based on our participants' performance in the behavioural tests administered in our study. All of the weighted CIs were then summed. The values of the pixels in the weighted-group-CI were then converted to Z-scores using the mean and standard deviation of the portion of the CI corresponding to the face image's gray background (see Royer et al., 2016 for a similar procedure). The facial regions that were associated with face-related processing ability according to the Pixel test (Chauvin et al., 2005) are shown in color in Fig. 3 ($Z_{crit}$ = 4.30, 3.95, 3.58, 3.19, and 2.81, from finer to coarser scales; $p < .025$).

When all SF bands were combined, only the eye area was significantly associated with face processing abilities. These results demonstrate that face processing ability is associated with an increase in the use of the eyes. Together, our data suggests that, within the normal population, better face recognizers tend to make more efficient use of multiple facial areas, particularly the eyes. Also, individual differences in object recognition abilities were not related to the use of the eyes or any other specific visual information as measured in the Bubbles task. Similar results are obtained when using a bootstrap to investigate the facial areas significantly linked to face processing ability (see Fig. S3 in the supplemental materials for details).

However, the results presented so far do not take into account the covariance within the individual CIs, as it only considers the contribution of each individual pixel in the image. It is possible that lower-ability face recognizers use the general area of the eyes, but show high inter-observer variability in the precise use of this feature. If this is true, we could expect similar results to what is obtained in the weighted CI, but a correlation between the peak value in the general eye region and face processing ability would be weak. To assess this possibility, we performed a multiple linear regression on face processing ability (dependent variable) and the peak Z-score in two anatomically-defined regions of interest (ROI, i.e. the eyes) of the individual CIs combining information across SF bands (predictors). This regression thus complements the results of the weighted-CI analysis presented in Fig. 4. We considered the peak Z-score in these regions in each observer's individual CI to determine if the use of these features could predict face processing ability. We chose to run this analysis on the CIs combining SF information as we aimed to determine the variance explained by a specific feature, irrespective of SF band. As the information linked to face processing ability is variable across SF bands, we only used the SF-combined individual CIs to minimize the number of predictors included in the model given our relatively small sample size. Including SF-specific information could add noise to the regression model, as the bubbles method used here does not allow a fine sampling of SF information.

Note that we refer to the position of each eye according to their position on the face image from the observer's point of view. The model significantly predicted face processing ability ($F(2,47) = 5.85$;

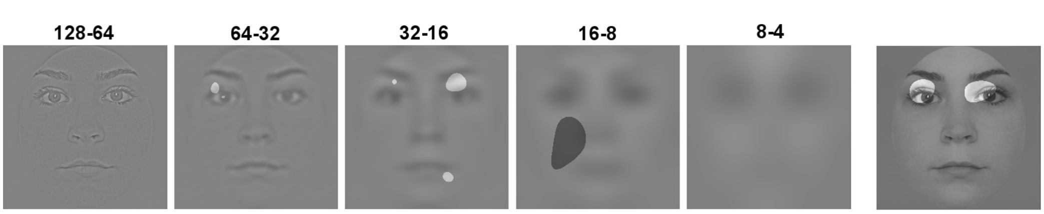


**Fig. 4.** Visual information significantly linked to accuracy when weighing the individual classification images by face processing ability measured with a PCA. Higher-ability observers significantly used regions with positive Z-scores (light gray areas), while lower-ability observers significantly used regions with negative Z-scores (dark gray areas).

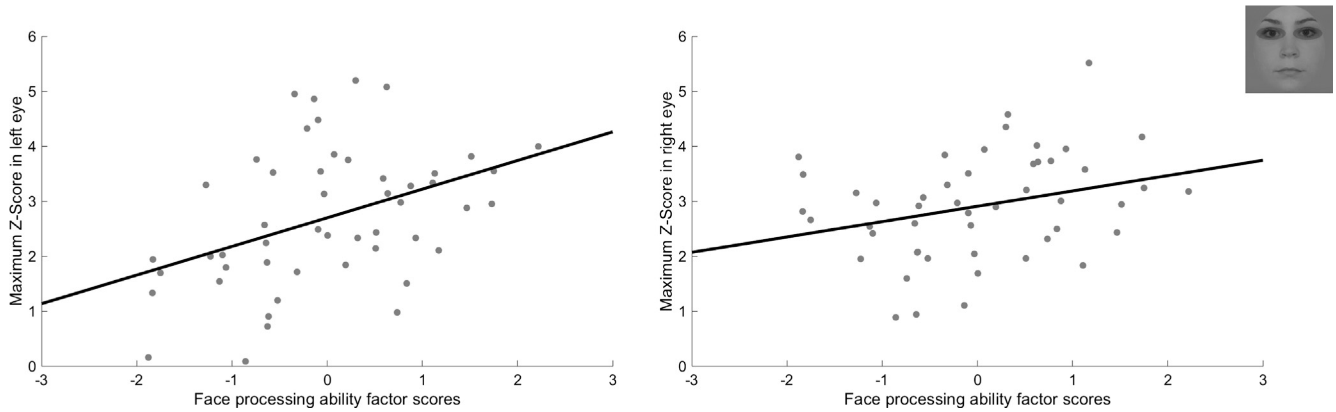


**Fig. 5.** Correlations between face processing ability and maximum Z-scores in each eye ($r_{left} = 0.4176$, $p = .003$; $r_{right} = 0.2949$, $p = .04$ after removing an outlier).

$p = .005$; $r^2 = 0.20$). The peak Z-score in the left eye ($\beta = 0.369$; $p = .009$) significantly predicted individual differences in ability, but the use of the right eye ($\beta = 0.165$; *ns*) did not reach statistical significance (see Fig. 5). The conclusions of this analysis were unchanged after removing an outlier that shows a very high maximum Z-score in the right eye (Z = 6.6), i.e. only the use of the left eye is retained as a significant predictor. Thus, in terms of feature utilization, it is the use of the left eye that best accounts for individual differences in face processing ability. When computing the correlations separately for both ROIs, the correlation between the peak Z-score in the right eye is significant, but is not as strong as what we obtain for the left eye (Fig. 5). The difference between the use of both eyes, i.e. to what extent the participants relied on the left eye over the right eye, was not significantly correlated with face processing ability ($r = 0.16$; *ns*).

We then computed a second PCA using only the three object-recognition tests, which also resulted in retaining a single factor (i.e. eigenvalue $> 1$; 0.796 loading for the HMT; 0.619 loading for the CCMT; 0.554 loading for the CHMT). This aimed to verify if a similar pattern of results could be obtained in a second regression analysis when using a purer measure of face processing ability that took into account the variance attributable to the object recognition ability factor. Indeed, many authors suggest that face processing may involve both face-specific mechanisms and more general visual recognition strategies such as those involved in the recognition of different categories of objects (see Wang et al., 2012 for a similar approach). This second regression analysis was computed using the residuals between the face processing ability factor and object recognition ability factor as the dependent variable. As in the previous regression, the individual peak Z-Score in each eye were used as predictors. The model significantly predicted the face processing ability residuals ($F(2,47) = 3.80$; $p = .029$; $r^2 = 0.14$). The peak Z-score in the left eye ($\beta = 0.305$; $p = .036$) significantly predicted individual differences in ability, but the peak Z-score in the right eye ($\beta = 0.143$; *ns*) did not reach statistical significance. Thus, eliminating the variance in object recognition ability from the correlation observed between face processing ability and perceptual strategies ensures that this link cannot not solely be explained by the use of general visual recognition mechanisms.

## 4. Discussion

The goal of this study was to assess whether varying levels of face recognition ability are linked to changes in the perceptual strategies used to extract visual information to identify faces. Fifty participants were first asked to complete multiple tests measuring their individual ability to recognize faces and objects. Next, a face identification task in which the facial stimuli were sampled in the image and SF domains with Bubbles (Gosselin & Schyns, 2001) was administered to the same subjects.

Our first analysis aimed to verify if, on average, we obtain similar results to previous studies using the set of stimuli selected in the present paper. In line with previous results, our data indeed shows the crucial role of the eyes for accurate face recognition (Butler et al., 2010; Caldara et al., 2005; Gosselin & Schyns, 2001; Schyns et al., 2002; Vinette et al., 2004). Our main analyses aimed to evaluate the link between (1) the individual face recognition strategies uncovered in our bubbles task and (2) individual face processing ability, quantified using the first component of a PCA computed on the three face recognition tasks included in our study. Our results demonstrate a systematic link between the use of the eyes and face processing ability. Interestingly, the best face recognizers rely to a greater extent on the eyes, especially the left eye (from the observer's perspective) compared to the low-ability face recognizers. The use of this feature accounts for approximately 20% of the variance in face processing ability. Our data did not reveal information that was systematically linked to lower face processing ability, i.e. information that was found to be significant both in the weighted CI analysis and in a correlation between the use of a specific area and face processing ability. In the present study, we show that the best face recognizers, who tend to obtain higher z-score values in the eye region, also require fewer bubbles to accurately recognize faces. Importantly, the link we obtain between use of facial features and face processing ability cannot be explained by the number of bubbles modulating the z-score values of the individual CIs. We obtain strikingly similar results to those presented in Fig. 4 when controlling for z-score magnitudes in individual CIs either by equating their standard deviations or their range. This implies that there are differences in the templates of the observers as a function of face recognition ability, and that these differences are the main driving force behind the association we find between use of the left eye and face processing ability.

Our study is one of the first to use an individual differences approach to clarify how face recognition ability is linked to the perceptual strategies used to extract visual information to identify faces. A growing number of authors are now using individual differences to uncover the nature of the cognitive mechanisms reflected by various face-specific neural responses, which offers an interesting framework to interpret our results. For instance, Furl et al. (2011) showed a significant association between face recognition ability and peak face selectivity in the right and left individually defined Fusiform Face Area (FFA; Kanwisher, McDermott, & Chun, 1997), as well as with the size of the right FFA, in a sample of developmental prosopagnosic individuals and age-matched controls (see also Garrido et al., 2009). Similar results were obtained in a cohort of healthy participants, i.e. a significant correlation between face recognition ability and the face-selective responses in the FFA and Occipital Face Area (OFA; Huang et al., 2014; Elbich & Scherf, 2017). It is thus possible that the activation of regions in the core face-processing network may reflect the allocation of greater resources towards the eye—especially the left eye—region of faces. Relatedly, it has been shown that the latency of the N170, a well-documented ERP component thought to reflect early face processing, is related to individual accuracy in perceiving, learning, and recognizing faces (Herzmann, Kunina, Sommer, & Wilhelm, 2010). Using a face adaptation paradigm, a recent study demonstrated that N170 adaptation-effect for individual faces is correlated with face abilities (Turano, Marzi, & Viggiano, 2016). Considering that the N170 seems to be modulated by the mere presence or absence of the eye region, irrespective of task demands (Schyns, Jentzsch, Johnson, Schweinberger & Gosselin, 2003; Smith, Gosselin, & Schyns, 2004), these results also suggest a link between eye processing and face recognition ability. Importantly, our results make a much more direct link between efficient processing of the eye region of faces and face processing abilities.

This proposition is compatible with data from acquired prosopagnosia patients, i.e. individuals showing significant impairment in face processing due to acquired brain injury. Pancaroglu et al. (2016) recently proposed that the impairment in the processing of the eyes observed in some prosopagnosic individuals might be more typical of patients with occipitotemporal lesions than those with more anterior temporal lesions. This is consistent with data from patient PS, a case of pure prosopagnosia due to bilateral occipito-temporal lesions. Three distinct studies using bubbles have shown impairment in using the eye area of faces in both face identification and facial expression categorization in this patient (Caldara et al., 2005; Fiset et al., 2017; Ramon, Busigny, Gosselin, & Rossion, 2017). These three case studies of PS's use of information in face processing conclude that her condition stems from a deficit in extracting the information conveyed by the eye area. This is compatible with previous studies suggesting a causal role of the OFA (the region lesioned in PS) in facial feature extraction (e.g. Duchaine & Yovel, 2015) from static face images (Pitcher, Duchaine, & Walsh, 2014). Hence, it is possible that the impairment observed in certain cases of acquired prosopagnosia in extracting visual information in the eye region of faces may be similar to the deficits found in individuals in the general population at the low-end of the continuum of face processing ability. Relatedly, the brain regions involved in the earlier steps of face processing (i.e. occipitotemporal regions such as the OFA and FFA) may be directly linked to the greater use of the eye region observed in the best face recognizers (see Furl et al., 2011; DeGutis, Cohan, Mercado, Wilmer, & Nakayama, 2012; Fisher, Towler, & Eimer, 2016 for congruent data with developmental prosopagnosia).

Our results further support the relevance and interest of an approach based on individual differences in order to reach a better understanding of the cognitive and visual mechanisms involved in expert face processing. Indeed, the present study establishes the existence of systematic differences in the use of information in accordance with individual face recognition ability. These findings may seem to conflict with the results of eye-tracking studies that have failed to show a link between individual idiosyncratic fixation patterns and face recognition ability (Mehoudar, Arizpe, Baker, & Yovel, 2014; Arizpe, Walsh, Yovel, & Baker, 2017; see also Peterson & Eckstein, 2013). It is important to note, however, that eye-tracking and methods such as bubbles do not necessarily reflect the same cognitive and perceptual processes. Indeed, the features that are fixated foveally by an observer when completing a given task are not necessarily *used* for this task. For instance, previous data has shown that Asian observers fixate the nose in face recognition, but use the eye and mouth area in lower SFs to carry out this task (Blais, Jack, Scheepers, Fiset, & Caldara, 2008; Miellet, Vizioli, He, Zhou, & Caldara, 2013; see Caldara, 2017 for a review). Thus, it is possible that observers directly fixate different parts of the face, while processing and ultimately utilizing other features at the extra-foveal level.

Numerous studies suggest that faces are processed holistically (Farah et al., 1998; Maurer, Le Grand, & Mondloch, 2002; Richler et al., 2011; Richler, Tanaka, Brown, & Gauthier, 2008; Schiltz, Dricot, Goebel, & Rossion, 2010; Tanaka and Farah, 1993; Wang et al., 2012; Young et al., 1987). However, some studies do not support this proposition (e.g. Sekuler et al., 2004; Gold, Mundy, & Tjan, 2012; Gold et al., 2014), and the association between individual differences in face processing abilities and holistic processing remains unclear (e.g. Konar et al., 2010; Richler et al., 2014). We replicate a previously published result showing a strong negative correlation between face processing abilities and the amount of information required to accurately recognize faces. Indeed, better face recognizers tend to need less available information for accurate face identification. This result seems at odds with previous studies showing a significant correlation between individual differences in face processing ability and reliance on holistic processing of faces (Richler et al., 2011; DeGutis et al., 2013; Wang et al., 2012; but see Biotti et al., 2017; Konar et al., 2010; Richler et al., 2014). Overall, our observations suggest that those with superior face recognition abilities make a more efficient utilization of the visible features to activate their identity representations. Whether these representations are more holistic in these skilled face recognizers certainly warrants further investigation. Future studies could also specifically investigate whether efficiency in processing multiple features simultaneously is linked to individual differences in face processing abilities. As such, superior face recognizers may be more efficient in processing multiple features at the same time. These interesting questions, however, are beyond the scope of the present work.

Many questions remain unanswered regarding the nature of the mechanisms supporting face processing ability and its variations in the general population. The present work shows that these individual differences are partly reflected by the use of certain facial features in different SF bands. The bubbles method used here, however, gives a relatively coarse idea of each observer's SF tuning. In fact, although many studies have investigated SF tuning in face identification using group average approach, little is known about the importance of individual differences in this domain. Furthermore, the role of other types of low-level visual information such as orientation structure could also benefit from an approach based on individual differences. Pachai et al. (2013) demonstrated that tuning for horizontal information was significantly correlated with upright face identification accuracy as measured within the same recognition task. Our results are consistent with these findings, likely related to the fact that the eyes contain a great amount of horizontal information compared to other facial features. Future work using precise and unbiased SF and orientation sampling methods (e.g. SF bubbles and orientation bubbles; Willenbockel, Fiset, et al., 2010; Duncan et al., 2017) as well as independent tasks to measure face identification ability are warranted in order to better understand the link between the use of low-level visual information and face processing ability. Furthermore, it is important that our results be replicated with methods other than bubbles, as any technique that aims to investigate the use of visual information may influence or interact with the use of this information.

Our study provides one piece of the puzzle to better understand the mechanisms underlying individual differences in face recognition ability. Thus, our findings may be useful for the development of effective training programs aimed at individuals at the lower-end of the continuum of face processing ability to help them become better face recognizers. Future work could also verify if the systematic variations in the use of the eye region uncovered in the present work generalizes to individuals with developmental prosopagnosia. If so, this would allow such training programs to also be effectively applied to this clinical population.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.cognition.2018.08.004.

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