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Time course of the use of chromatic and achromatic facial information for sex categorization

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ABSTRACT

The most useful facial features for sex categorization are the eyes, the eyebrows, and the mouth. Dupuis-Roy et al. reported a large positive correlation between the use of the mouth region and rapid correct answers [*Journal of Vision 9* (2009) 1–8]. Given the chromatic information in this region, they hypothesized that the extraction of chromatic and achromatic cues may have different time courses. Here, we tested this hypothesis directly: 110 participants categorized the sex of 300 face images whose chromatic and achromatic content was partially revealed through time (200 ms) and space using randomly located spatio-temporal Gaussian apertures (i.e. the Bubbles technique). This also allowed us to directly compare, for the first time, the relative importance of chromatic and achromatic facial cues for sex categorization. Results showed that face-sex categorization relies mostly on achromatic (luminance) information concentrated in the eye and eyebrow regions, especially the left eye and eyebrow. Additional analyses indicated that chromatic information located in the mouth/philtrum region was used earlier—peaking as early as 35 ms after stimulus onset—than achromatic information in the eye regions—peaking between 165 and 176 ms after stimulus onset—as was speculated by Dupuis-Roy et al. A non-linear analysis failed to support Yip and Sinha's proposal that processing of chromatic variations can improve subsequent processing of achromatic spatial cues, possibly via surface segmentation [*Perception 31* (2002) 995-1003]. Instead, we argue that the brain prioritizes chromatic information to compensate for the sluggishness of chromatic processing in early visual areas, and allow chromatic and achromatic information to reach higher-level visual areas simultaneously.

1. Introduction

What are the respective roles of chromatic and achromatic cues in face-sex categorization? More specifically, which chromatic and achromatic facial cues does the brain use to perform this perceptual task, and what is the time course of their extraction? Research on face recognition has long underestimated the role of color, probably in part as a result of the popularity of earlier *edge-based* object recognition theories emphasizing the role of shape and spatial cues (Biederman & Ju, 1988; Marr & Hildreth, 1980). This view seems difficult to reconcile with the emergence of trichromatic perception in primates (see Rowe, 2002). It is usually assumed that trichromatic perception has emerged through natural selection because it helped with the detection of certain fruits against approximately equiluminant green foliage (i.e. the foraging hypothesis, see Caine et al., 2003; Dominy & Lucas, 2001). Evolutionary theorists have long speculated (see Allen, 1892) that once the appropriate biological apparatus for trichromatic perception had emerged through natural selection, it became useful in primate species for discriminating the spectral modulations on the facial skin of conspecifics, presumably for the purpose of discriminating emotional states, socio-sexual signals and threat displays (e.g. redder skin is related to higher testosterone and dominance level in male mandrills; ovulation in female chimpanzees is linked to redder skin; see Setchell & Dixson, 2001; Surridge, Osorio & Mundy, 2003). It was even recently argued that color vision in primates was originally selected specifically for social facial communication purposes (Changizi, Zhang & Shimojo, 2006; Hiramatsu et al., 2017).

Surprisingly, thus, it is only a few years ago that researchers began accumulating evidence that color is an important cue for face recognition in humans. Indeed, the chromatic properties of facial skin and features, particularly on the red-green axis, were shown to play an important role in facial categorization of socially relevant information such as emotion (Young, Elliot, Feltman & Ambady, 2013; Benitez-Quiroz, Srinivasan & Martinez, 2018), attractiveness (Stephen, Oldham, Perrett & Barton, 2012; Fink, Grammer & Matts, 2006; Jones, Russel & Ward, 2015), health (Stephen, Coetzee, Smith, & Perrett, 2009; Fink,

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et al., 2006; Stephen et al., 2009; Jones et al., 2016; Russell, Sweda, Porcheron, & Mauger, 2014; Russell et al., 2016), dominance (Elliott et al., 2010; Stephen et al., 2012; Mileva et al., 2016), aggressiveness (Stephen et al., 2012), identity (Chang, Bao & Tsao, 2017; Nestor et al., 2013), sex categorization (Nestor & Tarr, 2008a; Nestor et Tarr., 2008b; Dupuis-Roy, Fortin, Fiset, & Gosselin, 2009; Dupuis-Roy, Fiset, Dufresne, Caplette, & Gosselin, 2014; Russell, Kramer & Jones; 2017; Russell, 2009) and sex typicality (Fink, Grammer & Matts, 2006; Stephen and McKeegan, 2010). For instance, Stephen and McKeegan (2010) instructed participants to adjust the color of the lips along each axis of the CIELab colorspace to enhance the apparent attractiveness and sex-typicality of faces. They found that women were perceived as more feminine and attractive when red contrast was increased between the lips and the surrounding skin. Similar studies indicated that men are perceived as more masculine and dominant when they possess a darker and redder complexion across the entire face (Stephen et al., 2012; Jones, Russell & Ward, 2015; Stephen and McKeegan, 2010).

Nestor & Tarr (2008a) asked participants to categorize the sex of androgynous faces embedded in white chromatic noise, and used reverse correlation to reveal which color variations drove their perception of sex. They found that human observers mostly relied on color variations in the eyes, nose and mouth regions along the red-green axis of the CIELab color space. These results indicate that observers' memory representations for sex categorization contain chromatic elements; they do not indicate, however, that these color elements reflect real-world face-sex variations or, relatedly, that they contribute to correct face-sex categorization.

In fact, there is evidence that chromatic surface properties are important cues for face sex categorization (Dupuis-Roy, Fortin, Fiset, & Gosselin, 2009; Hill, Bruce & Akamatsu., 1995; Kemp, Pike, White, & Musselman, 1996). Nestor & Tarr, (2008b) found that an algorithm designed to categorize the sex of frontal view color faces, reached a higher accuracy when all three color CIELab channels were available than when only luminance was available, suggesting that color conveyed sex-related information beyond that carried by brightness alone. A similar conclusion was reached independently by Dupuis-Roy et al. (2009; see Fig. 3c below).

A hypothesis formulated by Yip and Sinha (2002, also see Nestor & Tarr, 2008a), who have observed similar benefits of color in a face identification task, states that color could improve the segmentation of the facial features' surfaces and thus indirectly help the visual system to process the relevant facial cues. Dupuis-Roy et al. (2014) found further support for this hypothesis in a face-sex categorization task. They compared performances of human observers to that of an ideal observer designed to make use of all available information. Subjects had to categorize the sex of three sets of color and grayscale male and female faces: (1) a set of androgynous faces that varied only in terms of their real-life interattribute distances (i.e. all pairwise distances between the eyes, the nose and the mouth), (2) a set of faces that varied in all respects except that they all displayed the same androgynous set of interattribute distances and (3) a set of original faces. Overall, subjects obtained higher performances with the color faces than with their grayscale version, suggesting that they made correct use of face-sex color information in faces. Moreover, the authors observed higher efficiencies (i.e. ratio of human to ideal performance) in the color than in the grayscale conditions. This was the case even when faces only varied in terms of their real-world interattribute that is, when color was not task-relevant. Then, in this condition at least, the increase of efficiency must have originated from an improvement at a relatively low-level of visual processing, as predicted by Yip and Sinha's low-level segmentation hypothesis.

Gegenfurtner and Rieger (2000) found evidence for such a low-level mechanism for scene recognition. They employed a delayed match-to-sample task with three scene image conditions: 1) encoded and retrieved in luminance, 2) encoded in color and luminance and retrieved in luminance, and 3) encoded and retrieved in color and luminance. Scenes presented from 16 to 54 ms were better recognized when encoded in color and luminance compared to luminance alone, even if they were later retrieved in luminance. This is consistent with an early, low-level, segmentation process. Interestingly, scenes that were encoded *and* retrieved in color and luminance led to higher accuracy than scenes encoded in color and luminance and retrieved in luminance only for presentation times of 64 ms. This suggests a high-level color (i.e. representational) advantage in addition to the low-level one (Goffaux, Jacques, Mouraux, Oliva, Schyns, & Rossion, 2005).

In the face recognition literature, data supporting a fast, low-level advantage of color information remains scarce. Dupuis-Roy et al. (2009) gathered *indirect* evidence of an early extraction of color information in the context of face-sex categorization task. In this study, male and female color face images were spatially sampled with randomly generated *bubbles* masks—i.e. uniform gray masks punctured by randomly located small 2D Gaussian apertures. Multiple linear regression was used to assess the relationship between the position of these *bubbles* on the face, and the accuracy and latency of the responses. This first revealed that the eyes/eyebrows regions were linked to accurate sex categorization (see also Brown & Perrett, 1993; Russell, 2003). Of particular relevance here was the finding that the mouth region was significantly linked to *fast* accurate responses (but not to fast incorrect responses). In other words, subjects responded correctly and relatively fast on trials in which the mouth area of face stimuli tended to be revealed by bubbles. A statistical analysis of the face images revealed that the most discriminative information for the task within the mouth area was concentrated in the red-green color channel. Together, these results suggest that the processing of chromatic and achromatic facial cues follows a distinct time course, with color-based cues being processed earlier than luminance-based cues.

Here, we *directly* tested this hypothesis by examining the time course of the extraction of chromatic and achromatic cues in a face-sex categorization task. To do so, 110 participants were asked to categorize the sex of 900 unique stimuli created from a dataset of 300 real-life face images. The stimuli were made by sampling randomly the chromatic and the achromatic content of the face images through time and space with spatiotemporal Gaussian apertures. Computing the weighted sums of these spatiotemporal samples with accuracy on a trial-by-trial basis allows to determine the achromatic and chromatic voxels that were the most useful for categorizing the sex of a face through time. This experiment also gave us the opportunity to compare directly the relative importance of chromatic and achromatic facial cues for sex categorization and to test a sequential prediction of Yip and Sinha's low-level segmentation ypothesis.

2. Methods

2.1. Participants

One hundred and ten healthy participants (54 men) with normal color vision and normal or corrected-to-normal visual acuity were recruited on the campus of the Université de Montréal. Participants were aged between 20 and 30 years. An informed consent was obtained prior to the experiment and a monetary compensation of 10$/h was provided upon its completion. All procedures were carried out with the approval of the Université de Montréal ethics committee.

2.2. Face database

We used the face database of Dupuis-Roy et al. (2009). It contains 300 Caucasian frontal-view face images (150 males and 150 females) with a neutral expression. Rotations, scalings, and translations in the image plane were applied to the face images in order to minimize the distance between handpicked landmarks around the eyes (four landmarks each), the eyebrows (2 landmarks each), the nose (four landmarks) and the mouth (four landmarks). Note that these so-called

Procrustes transformations do not modify the relative distances between features.

2.3. Stimuli

The chromatic and achromatic content of a face image were revealed through Gaussian apertures randomly located in space (128 × 128 pixels for a given frame) and at random moments in the time (17-frames) dimension. This required four steps. A face image was first converted from its original RGB map to the HSV color map. Second, two volumes of 128 × 128 × 17 voxels, henceforth referred to as chromatic (Saturation, M1) and achromatic (Value, M2) volumes, with the same number of randomly located 3D Gaussian apertures were generated.

Each of these 3D Gaussian apertures ($\sigma_{xy} = 0.15^\circ$ of visual angle, $\sigma_{time} = 23.53$ ms) were scaled and truncated so that their probability density ranged from zero (at the tails ± 2.18 σ) to one (at the center). The spatial and temporal extents of the bubbles were selected to provide the resolution necessary to reveal the expected signals in the classification volumes. A spatial standard deviation of 0.15 deg of visual angle corresponds to a Full Width at Half Maximum (FWHM) of 0.35 deg of visual angle that is, approximately the period of the finest spatial information used by human observers to categorize the sex of faces (e.g. Willenbockel et al., 2010). A temporal standard deviation of 23.53 ms corresponds to a FWHM of 54.75 ms that is, slightly less than the smallest temporal period that has been observed in similar experiments (e.g. Vinette, Gosselin & Schyns, 2004; Blais, Arguin, & Gosselin, 2013). Third, the following calculations were performed on the 17 frames of the H (hue), S (saturation) and V (value) channels of a given face image:

$$H'_i = H$$
$$S'_i = M1_i \cdot\!* S$$
$$V'_i = M2_i \cdot\!* (V - \mu) + \mu \qquad (1)$$

where i = [1:17]; H, S and V are the original channels of a given face image; H′, S′ and V′ are the resulting sampled volumes (128 × 128 × 17 voxels); and μ is the average of all pixels in V. In conjunction with the H channel, each bubble of the chromatic volume M1 reveals hue information with the maximum saturation at its centre. Each bubble of the achromatic bubbles volume M2 reveals the maximum value at its centre. When bubbles of the chromatic and achromatic volume do not overlap, the areas revealed through the chromatic bubbles have approximately the same average luminance (± 5 cd/m^2, which represents 3.7% of the full range), whereas the areas revealed through the achromatic bubbles have a null saturation and thus no hue. When bubbles of the chromatic and achromatic volumes overlap perfectly, they reveal all the information to its full contrast. Consequently, the degree of spatial overlapping between both M1 and M2 bubbles volume establish how much of the whole HSV face information is revealed. Finally, the H′, S′ and V′ volumes are converted to RGB values. Fig. 1a illustrates one iteration of the sampling process that was repeated for each time frame, 17 times. Note that face images were set at a low resolution of 128 × 128 pixels to keep statistical power high while exploring two tridimensional search spaces.

2.4. Apparatus

The experimental programs were run on four Macintosh computers in the Matlab (Mathwork Inc.) environment, using functions from the Psychophysics Toolbox (Brainard & Vision, 1997; Pelli, 1997). The computers' high-resolution CRT monitors were set to display 1024 by 768 pixels at a refresh rate of 85 Hz. The relationship between RGB values and luminance levels (measured with a Samsung SyncMaster 753df photometer) was computed for each color channel independently; the three best-fitted gamma functions were then used to convert each image of the face database into HSV space. Participants were seated in a dim-lighted room. Their viewing distance was maintained by a chin-rest so that the stimuli interpupillary distance was 1.03 deg of visual angle (face width was 3.28 deg of visual angle) as in Dupuis-Roy et al. (2009), which is equivalent to viewing a real face from approximately 3.50 m. Thus proximal stimuli fell within the fovea—a ~5 deg area on the retina where fine details and colors are best distinguished. Although the relatively small angular size of our face images might have promoted the use of information at slightly lower spatial frequencies than in the typical face recognition experiment, it probably had a limited impact on our spatio-temporal results (Loftus & Harley, 2005; Näsänen, 1999; Willenbockel et al., 2010; but see Yang et al., 2014).

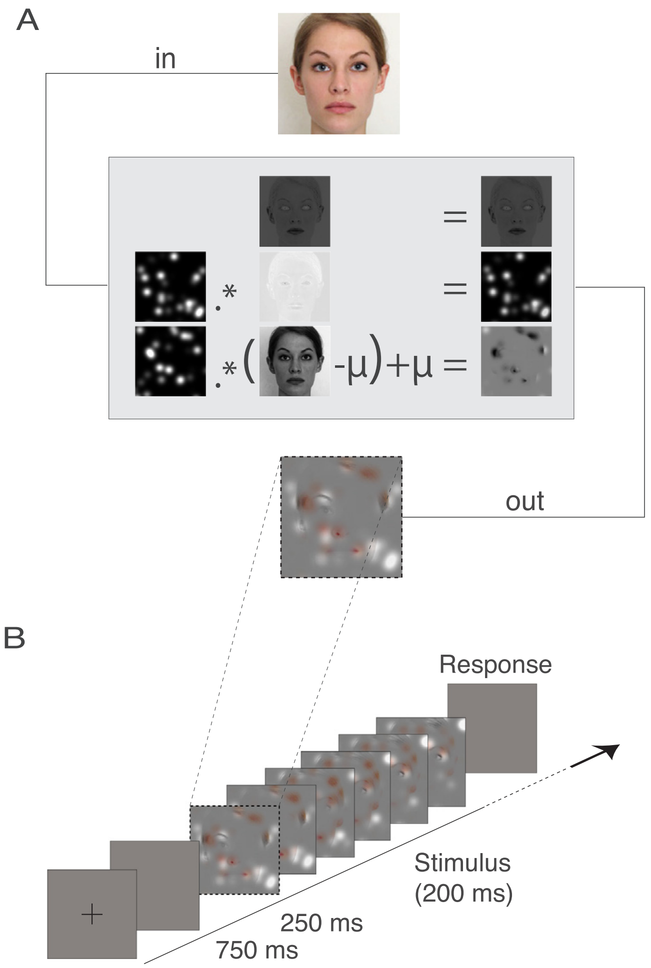

Fig. 1. A) Illustration of the construction of one of the 17 frames of a face stimulus. First, a face image is converted from its original RGB color map to the HSV color map. Second, two volumes of Gaussian apertures randomly located in space (128 x 128 pixels) and at random moments in time (17 frames) were generated (only one frame shown per volume). One volume is used to samples the S channel (saturation) of the face image, while the other volume is used to sample the V channel (value). The H (hue) channel of the image is fully revealed in the face stimulus. Each volume had the same number of randomly located 3D Gaussian apertures. Finally, the H, S and V volumes are converted to RGB volumes. B) On each trial, a fixation cross is presented at the center of the computer monitor for 750 ms; immediately after a homogeneous gray field is presented for 250 ms; immediately after the 17 frames of a face stimulus are shown at a rate of 85 Hz (for a total duration of 200 ms); immediately after a homogeneous gray field is presented until a response is provided by the participant.

2.5. Procedure

First, participants were screened for possible color vision deficiencies with the Ishihara Color Test (Ishihara, 1936). Then, they were brought in a dark lighted experimental room where they completed three blocks of 300 trials in each of which a different face from the face database was shown, in a random order, partially revealed in space (128x128 pixels for a given frame) and time (200 ms) through 3D bubble masks. Face photos were rotated 180 deg about its vertical axis with a 0.5 probability on every trial to eliminate possible information asymmetries (e.g. illumination differences). The sequence of visual events in a given trial unfolded as follows (see Fig. 1b): A black fixation cross was shown at the center of the computer monitor against a uniform gray background for 750 ms; a uniform grey field immediately followed for 250 ms; a video containing the 17 frames of a stimulus immediately followed at the center of the screen against a uniform gray background for 200 ms (i.e., 17 frames presented at 85 Hz); and, finally, a uniform grey field immediately followed and remained until the participant had indicated the sex of the sampled face by pressing a labeled computer keyboard key. No feedback was provided. The number of bubbles was adjusted on a trial-by-trial basis with Quest (Watson & Pelli, 1983) to maintain 75% of correct responses.

3. Results

Participants required an average of 97.23 Gaussian apertures (SD = 35.95) to reach the target of 75% of correct responses. Four participants were excluded from the rest of the data analyses because the number of bubbles they required was at least three standard deviations above the group average. Thus the following analyses were carried out on a total of 106 subjects (for a total of 95,400 trials).

3.1. Linear classification volumes

Two weighted sums were calculated for every participant to determine the achromatic and chromatic voxels that were the most useful for categorizing the sex of a face through time. We summed the volumes of chromatic Gaussian apertures weighted by the participant's response accuracy transformed in z-scores on a trial-by-trial basis; and we summed the volumes of achromatic Gaussian apertures and the participant's response accuracy transformed in z-scores on a trial-by-trial basis. The resulting classification volumes ($128 \times 128 \times 17$) revealed how each participant extracted achromatic and chromatic face-sex information through time.

To assess the relative use of achromatic and chromatic cues, we summed, for each participant, the unsmoothed standardized voxels found within the left eye, the right eye and the mouth areas—defined anatomically—for both the achromatic and chromatic individual classification volumes. This led to two sums of z-scores per participant that is, one for the achromatic and another for the chromatic classification volume. The values obtained for the two classification volumes were then compared with a two-tailed paired sample *t*-test. This revealed that achromatic facial information was 4.01 times more potent than that of chromatic facial information for sex-categorization ($M_{achromatic} = 0.75$, SD = 0.95; $M_{chromatic} = 0.19$, SD = 0.98; $t(105) = 4.32$, $p < 0.001$, Cohen's $d = 0.58$).

The group-average chromatic and achromatic classification volumes were also computed by summing the appropriate individual classification volumes. These group classification volumes were then smoothed with the same 3D Gaussian kernel as the one used in the experiment ($\sigma_{xy} = 0.15^\circ$ of visual angle, $\sigma_{time} = 23.53$ ms) and finally transformed into z-scores. This transformation was based on a bootstrap estimation (278 528 voxels) of the null hypothesis population mean and standard deviation (e.g., Efron and Tibshirani, 1986; Chauvin, Worsley, Schyns, Arguin, & Gosselin, 2005).

The remaining statistical analyses performed on the group classification volumes were restricted to the face area, i.e. a region of 3,469 pixels per frame that excluded the hair and other external facial cues. Any significant positive local divergence from uniformity in our group classification volumes would indicate that the corresponding part of the stimuli led to more accurate responses. A one-tail Pixel test was done on each z-scored group classification volume ($S_r = 58{,}973$ voxels, $Z_{thresh} = 3.05$, $p < 0.05$). This test — which was derived from the Random Field Theory — predicts what statistical values should be expected (whether Z, F or t-stat) when a tensor of a given random distribution is convolved with a given kernel. It thus corrects for multiple comparisons while taking the spatial correlation inherent to smoothed classification volumes into account. Further details about this test are provided in Chauvin et al. (2005).

3.2. The use of spatial features

Each blob of Fig. 3b represents a spatiotemporal cluster of significant voxels that was collapsed on the temporal dimension. The blobs are depicted over the average face to help with interpretation. The results show that the eyes and eyebrows, especially the left eye and eyebrow, in the achromatic classification volume (green shaded areas) are the most important facial regions for sex categorization followed by the mouth region (i.e. the philtrum and the mentolabial sulcus) in the chromatic classification volume (red shaded areas).

We tested the apparent asymmetry between use of the left and right eye with a two-way repeated measure ANOVA (2 eye regions × 17 frames) over the two classification volumes. We found a significant main effect for the eye regions in the achromatic classification volume—a greater use of the left eye/eyebrow than the right from the observer's point of view ($F(1,105) = 4.36$, $p = 0.04$, $M_{left} = 0.20$, $SD_{left} = 0.96$, $M_{right} = 0.13$, $SD_{right} = 1.01$). Importantly, this asymmetry in the use of facial information cannot be attributed to physical differences between the left and right side of face stimuli because the partially revealed face images were mirror-reversed about their vertical axis with a probability of 0.5 on each trial. There was no such effect in the chromatic classification volume ($F(1,105) = 0.64$, $p = 0.43$).

Fig. 3c, adapted from Dupuis-Roy et al., (2009, Fig. 3), shows the available chromatic and achromatic information in the face database that we used. Each face images was first converted to *Lab* color space: *L* corresponds to the light-dark—or achromatic—color map, *a* to the red-green color map, and *b* to the yellow-blue color map. Then, we computed an index of the information available at each pixel of each color map to discriminate the sex of a face. More specifically, we calculated *d'*s—the distance between the mean of the distributions of this pixel's values for male and for female faces in standard deviation units. The three *d'* maps are represented as contour plots in Fig. 3c. Warm colors indicate regions where men are lighter, redder or yellower than women and, cold colors, regions where men are darker, greener or bluer than women. To help with interpretation, the contour plots are superimposed to the face average. Thick white dotted lines delineate the main significant achromatic (see light-dark color map) and chromatic (see red-green and yellow-blue color maps) blobs in our classification volumes.

3.3. The use of spatial features through time

At the temporal level, the achromatic clusters in both eyes are significant for the entire sampling period, i.e. from 12 to 200 ms after stimulus onset, whereas the chromatic clusters in the mouth region are significant from 12 to 24 ms and from 165 to 200 ms after stimulus onset (see Fig. 2). The time at which clusters are significant, however, only provides an incomplete measure of the time course of information extraction because it lacks granularity and also because of the large differences in z-scores between the chromatic and achromatic classification volumes. To overcome these shortcomings, we divided the maximum z-score found in the eye and mouth areas defined

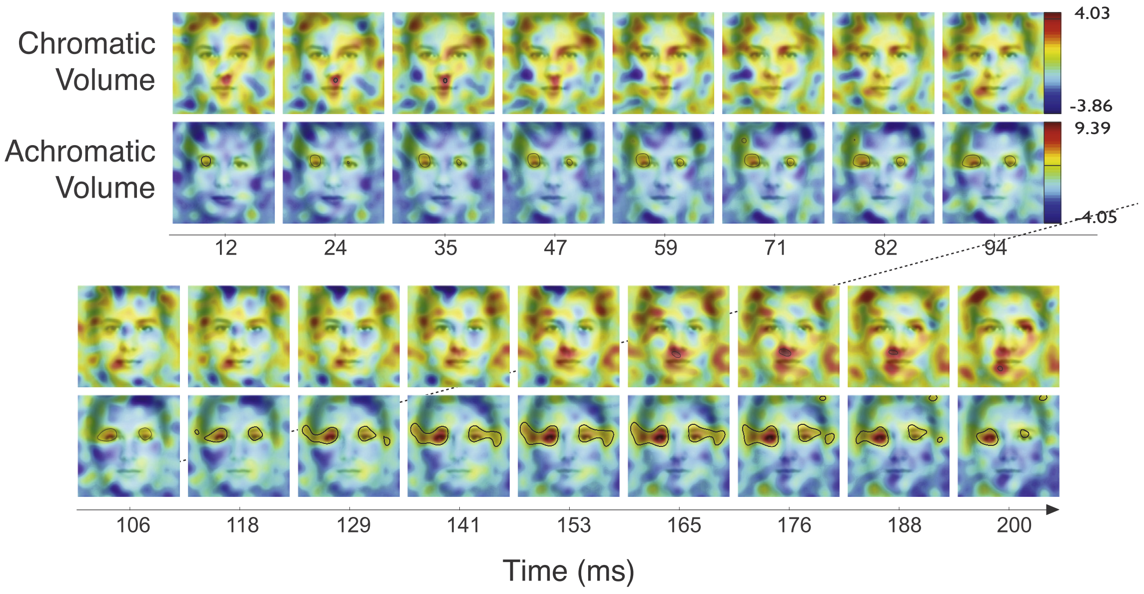

Fig. 2. Linear classification volumes for facial sex categorization. A sum of the volumes of chromatic Gaussian apertures weighted by the participant's response accuracy was computed. The same computation was performed on the volumes of achromatic Gaussian apertures. Spatio-temporal regions containing significant regression coefficients for chromatic (2nd and 4th row) and chromatic face information (1st and 3rd row) are delimited by thin black lines (pixel-test, $p < 0.05$). The frames of the classification volumes were superimposed on the average face to help with interpretation.

anatomically at each point in time by the overall maximum z-score found in the appropriate classification volume. A bootstrap analysis was also conducted to simulate the distribution of maximum z-scores found in each region of interest given the null hypothesis (on a total of 278,528 voxels), and to compute a statistical threshold.

The resulting curves provide the time course of chromatic information extraction in the mouth region (red curve) as well as the time course of achromatic information extraction in the left (green curve) and in the right eye (dotted green curve) regions from the point of view of the observer (Fig. 3a), factoring out the absolute usefulness of achromatic and chromatic information. Note that the maximum of the curves within each classification volume was set to 1. The colored circles indicate time points that attain statistical significance ($p < 0.05$). Chromatic information extraction within the mouth region peaks at 35 ms and then again at 176 ms after the stimulus onset, whereas the achromatic information extraction within the left and right eye regions respectively peaks at 165 and 176 ms after the stimulus onset.

3.4. *Yip and Sinha's segmentation hypothesis*

Yip and Sinha (2002) proposed that processing of chromatic variations, whether task-relevant or not, could facilitate the segmentation and, therefore, subsequent processing of achromatic spatial features. Contrary to this hypothesis, we did not find any facial region in which significant voxels in the chromatic classification volume peaked *before* significant voxels in the achromatic classification volume. Our linear analysis, however, can only reveal cases of chromatic segmentation and subsequent use of achromatic cues occurring systematically at the same latencies after stimulus onset. To test more thoroughly the chromatic-before-achromatic hypothesis, we first selected, for each participant, the trials that revealed chromatic voxels at least 5 frames (corresponding to the FWHM of the gaussian aperture on the temporal dimension) before achromatic voxels in each of the three facial regions of interest ($M = 272.17$ trials per participant), and then computed the mean accuracy. One-tailed paired sample t-tests between these mean accuracies and the ones obtained similarly for the alternative achromatic-before-chromatic hypothesis failed to reveal any significant difference (left eye: $t(105) = -0.33$, $p = 0.74$; $M_{\text{chromatic-before-achromatic}} = 0.756$, $M_{\text{achromatic-before-chromatic}} = 0.757$; right eye: $t(105) = 0.04$, $p = 0.97$; $M_{\text{chromatic-before-achromatic}} = 0.755$, $M_{\text{achromatic-before-chromatic}} = 0.755$; mouth: $t(105) = 1.83$, $p = 0.07$; $M_{\text{chromatic-before-achromatic}} = 0.758$, $M_{\text{achromatic-before-chromatic}} = 0.752$).

4. General discussion

Which chromatic and achromatic facial cues does the brain use to perform sex categorization, and what is the time course of their extraction? Research on face recognition has long underestimated the role of color. Recent studies showed that the chromatic properties of facial skin and features, particularly on the red-green axis, play an important role in many socially relevant facial judgments, including sex categorization (e.g. Nestor & Tarr., 2008a; Nestor & Tarr, 2008b; Dupuis-Roy et al., 2009; Dupuis-Roy et al., 2014; Russell, et al.; 2017; Russell, 2009). Studies are also starting to unravel how chromatic and achromatic information interact through time during face categorization. Findings by Dupuis-Roy et al. (2009), for example, suggest that the extraction of chromatic cues from the mouth region precedes the extraction of achromatic cues from the eye regions (see also Gegenfurtner and Rieger, 2000; Oliva & Schyns, 2000).

Here, we examined directly the time course of local chromatic and achromatic face information extraction during a face-sex categorization task in more than 100 observers. We found that achromatic information was about four times more useful for sex categorization than chromatic information. We also showed that the most useful chromatic facial information was concentrated in the mouth region (i.e. the philtrum and the mentolabial sulcus) of the face, and that the most useful achromatic information was concentrated in the eye and eyebrow regions. Furthermore, we revealed, for the first time, that chromatic information extraction peaks as early as 35 ms while achromatic information extraction peaks later, between 165 and 176 ms. Finally, we tested, and refuted, one possible explanation for this chromatic-before-achromatic-information extraction, namely that it could reflect a coarse chromatic segmentation of facial features prior to their fine achromatic analysis (Yip & Sinha, 2002).

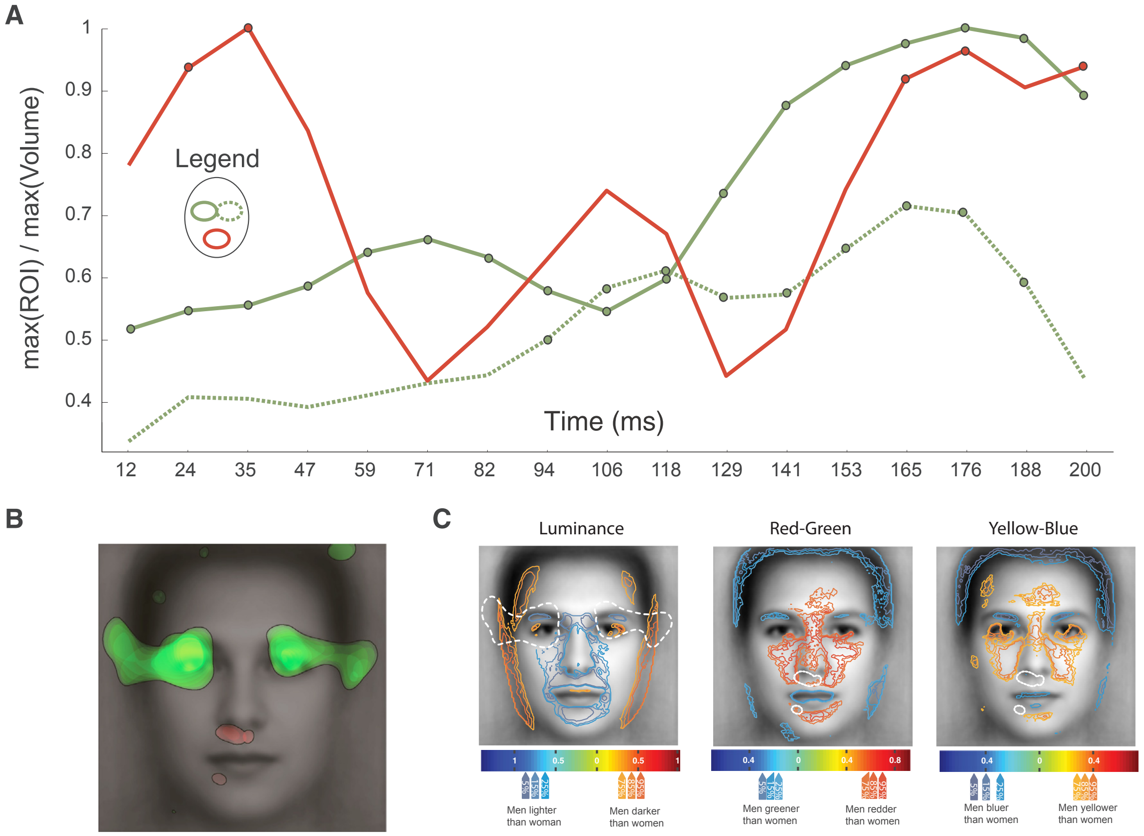

Fig. 3. Spatiotemporal use of chromatic and achromatic facial cues for facial sex categorization. A) The solid red curve represents the time course of the use of chromatic information in the mouth region; the green curves represent the time course of the use of the left (solid line) and right eye region (dotted line) from the observer's perspective. Open circles indicate statistically significant curve segments ($p < 0.05$). B) Green and red blobs represent, respectively, the spatio-temporal regions that contained regression coefficients significantly greater than zero in the achromatic and chromatic classification volumes ($p < 0.05$). These blobs were collapsed on the temporal dimension and superimposed on the average face to help with interpretation. C) Contour plots of the available color/luminance information for face-sex discrimination are superimposed to the average face. The contour plot summarizes the spatial modulation of available information (d's) in the dark-light (1st image from the left), red-green (2nd) and yellow-blue (3rd) channels. Warm colors were used for regions where men are lighter, redder or yellower than women; and cold colors for regions where men are darker, greener or bluer than women. Clusters significantly correlated with accurate achromatic (see white dotted line in the light–dark color map) and accurate chromatic responses (full white lines in the red-green and yellow-blue color maps) from Fig. 3B reveal which specific available information may be used by observers.

4.1. The spatial distribution of chromatic and achromatic face-sex cues

The magnitude of z-scores obtained in the group achromatic classification volume was approximately four times greater than that of the z-scores obtained in the group chromatic classification volume. In other words, achromatic information is much more useful to human observers to categorize the sex of faces than chromatic information. This is in line with previous studies on face image statistics which revealed that there is little information *available* to categorize sex in the chromatic compared to the achromatic channel (Fig. 3c; see also Kemp, Pike, White, & Musselman, 1996; Nestor & Tarr, 2008b, Russell, 2003; Russell, 2009; Jones, Russell & ward, 2015; Dupuis-Roy et al., 2009; Dupuis-Roy et al., 2014). This is also compatible with previous results indicating that human observers do represent chromatic information for sex categorization (Nestor & Tarr, 2008a), and that they use this scarce information quite efficiently (Dupuis-Roy et al., 2014).

We replicated the findings that the eye, eyebrow and mouth regions are the most prominent face-sex cues for human observers (e.g. Dupuis-Roy et al., 2009; Brown & Perrett, 1993; Nestor & Tarr, 2008a; Roberts & Bruce, 1988; Schyns, Bonnar, & Gosselin, 2002; Gosselin & Schyns, 2001; Russell, 2003). We further discovered that it is the chromatic information within the philtrum and mentolabial sulcus areas, and the achromatic information within the eye and eyebrow areas specifically which are the most useful to human observers. In the chromatic classification volume, the significant spatiotemporal clusters in the philtrum and mentolabial sulcus areas, as well as the marginally significant cluster in the left oral commissure area from the observer's perspective (see Fig. 2, frames 7–12; maximum z-score = 2.936, $p = 0.10$) all match real-world chromatic sexual dimorphisms. As shown in Fig. 3c, these sexual dimorphisms are concentrated in the red-green face color maps: e.g., men tend to have greener lips and redder skin in the philtrum and mentolabial sulcus areas. In the achromatic classification volume, the significant clusters in the eye and eyebrow regions contain all featural achromatic sexual dimorphisms. Dupuis-Roy et al. (2009) speculated that this was the case based on the use of spatial information—achromatic and chromatic information combined—by human observers and the available information in these different facial regions but this had never been shown empirically.

Several prior studies reported an asymmetric use of information favoring the left over the right eye and eyebrow region from the observer's perspective, both using the Bubbles procedure (e.g. Faghel-Soubeyrand et al., Submitted; Ince et al., 2016; Rousselet et al., 2014; Schyns, et al., 2002; Vinette, et al., 2004) and other experimental procedures, such as divided visual field, chimeric faces or gaze-tracking (e.g. Bourne, 2008; Butler et al., 2005; Jansari, Rodway, & Goncalves, 2011; Innes et al., 2016; Yovel et al., 2008). Here, we extend these findings by showing for the first time that this asymmetry is driven exclusively by achromatic cues, and that it is present as soon as 12 ms after stimulus onset and lasts at least 200 ms.

4.2. Time course of chromatic and achromatic cues

Our experiment showed that achromatic and chromatic facial information are extracted according to distinct time courses.

The use of achromatic information within the left and right eye regions, respectively, attain local maxima at ~71 ms and at ~118 ms, and then culminate at ~176 ms and ~165 ms. It is tempting—but it would be an error—to associate the peaks of these time courses with the N170, an event related-potential component associated to face processing that occurs about 170 ms after stimulus onset and that is widely believed to originate from the inferotemporal cortex (IT, Bentin, Allison, Puce, Perez, & McCarthy, 1996; for a review see Rossion, 2014). The moment at which information is processed is function of both the time window of extraction and the processing speed of the visual system. Indeed, we know that it takes at least 45 ms for a neural signal to travel from the photoreceptors to V1, and at least an additional 60 ms to reach IT (Bullier, 2001). This implies that information impinging the retina during the 165–176 time window after the first frame of our stimuli is actually processed more than 105 ms later in IT, that is more than 270–281 ms after stimulus onset. These concepts—processing and extraction—are often confused in the literature; this can lead to processing-oriented interpretations, when in fact the results are about extraction, and vice-versa (see also VanRullen, 2011).

The local maxima of the achromatic time courses (~71 ms and ~118 ms, respectively, for the left- and right-eye regions) are, however, consistent with the timing of the N170. Smith, Gosselin & Schyns (2004) showed that this early face-sensitive brain components are mainly driven by the contralateral eye, irrespective of the categorization task (see also De Lissa, McArthur, Hawelka, Palermo, Mahajan, & Hutzler, 2014; Rousselet et al., 2014; Ince et al., 2016), whereas selective attention to diagnostic information for categorizing stimuli—achromatic eye information and chromatic mouth information for the task at hand—correlates with late brain activity in the 250–300 ms time window (see also Hachemi et al., 2018). This late brain activity could reflect the processing of the peaks in the achromatic time courses (as well as the late burst in the chromatic time course).

The most important contribution of this study is without a doubt the uncovering of the time course of the use of isoluminant chromatic face information. Chromatic cues from the mouth area are extracted in two successive bursts, the first of which happens as early as 35 ms after stimulus onset while the second one happens around 176 ms. Importantly, the early chromatic burst occurs about 135 ms before the peak of the extraction of achromatic cues, and 35 ms earlier than its first local maxima. This offers direct support for the hypothesis formulated by Dupuis-Roy et al. (2009) that chromatic information in the mouth area is extracted prior to achromatic information in the eye areas. It seems, however, at odd with several studies that have reported that the parvocellular system—specialized in the processing of fine chromatic information—is generally slower than the magnocellular system—specialized in the processing of coarse achromatic information (Merigan & Maunsell, 1993). For example, Nowak, Munk, Girard, and Bullier (1995; see also Maunsell et al., 1999) found that V2 color cells were activated 10–20 ms after V2 non-color cells when stimulated with simple spots of light. But this story appears to change with more complex face stimuli. Edwards, Xiao, Keysers, Földiák, and Perrett (2003) examined the effect of the presence of color in face stimuli on the response of IT neurons in monkeys. They found no evidence to support the hypothesis that chromatic information about faces is delayed with respect to achromatic information in IT. They proposed that the brain compensates for the relative sluggishness of color processing in early visual areas such as V1 and V2 to allow chromatic and achromatic information to reach higher-level visual areas simultaneously. Our results suggest that the brain could achieve this goal by prioritizing the extraction of chromatic facial information ~135 ms earlier than achromatic information.

A proposal by Yip and Sinha (2002) suggests that the brain could actually take advantage of the processing of chromatic before achromatic information in low- to mid-level ventral stream brain areas—prior to the integration of chromatic and achromatic information. They proposed that chromatic variations, whether task-relevant or not, contribute to the segmentation of surfaces in different regions and, thus, improve the subsequent processing of achromatic spatial cues (see also De Valois & Switkes, 1983; Nestor & Tarr, 2008b; Dupuis-Roy et al., 2014). Our results, however, failed to support this hypothesis. First, our linear classification volumes contain no facial region for which the extraction of chromatic information precedes the extraction of achromatic information. Second, and more conclusively, trials on which chromatic information was presented before achromatic information within a given facial region of interest—irrespective of the interval between the sources of information—did not lead to greater performances than trials on which achromatic information was presented before chromatic information.

The integration of chromatic and achromatic facial cues could occur in a subset of four recently discovered color-selective brain areas anterior to the V4/hV4 color area (Zeki et al.,1991; Brewer, Liu, Wade, & Wandell, 2005) and “sandwiched” between face and place-sensitive regions along IT of humans and primates (Chang, et al., 2017; Lafer-Sousa, Conway & Kanwisher, 2016). These hue-sensitive modules tend to have a higher overlap with face-selective patches as they go through a posterior-to -anterior axis of IT (Lafer-Sousa, Conway & Kanwisher, 2016). Interestingly, the most anterior of these color modules, called the “anterior medial color” region, is highly responsive to chromatic information about faces and bodies (Chang, et al., 2017; see also Simmons et al., 2007). However, more research will be required to examine when and where in the brain are processed the chromatic and achromatic face-sex information extracted in different time windows.

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