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# A robust implicit measure of facial attractiveness discrimination

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# Abstract

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Decisions of attractiveness from the human face are made instantly and spontaneously, but robust implicit neural measures of facial attractiveness discrimination are currently lacking. Here we applied fast periodic visual stimulation coupled with electroencephalography (EEG) to objectively measure the neural coding of facial attractiveness. We presented different pictures of faces at 6 Hz, i.e. six faces/second, for a minute while participants attended to a central fixation cross and indicated whether the cross shortly changed color. Every other face in the stimulation was attractive and was replaced by a relatively less attractive face. This resulted in alternating more/less attractive faces at a 3 Hz rate, eliciting a significant increase in occipito-temporal EEG amplitude at 3 Hz both at the group and the individual participant level. This response was absent in two control conditions where either only attractive or only less attractive faces were presented. These observations support the view that face-sensitive visual areas discriminate attractiveness implicitly and rapidly from the human face.

Key words: facial attractiveness perception; FPVS

# Introduction

Within a split second, human observers can extract a wealth of information from the face of an individual to categorize this person according to age, gender, ethnicity, emotional expression, etc. Observers even rapidly attribute social traits to a person, such as the degree to which the person can be trusted (e.g. Bar et al., 2006; Willis and Todorov, 2006; Todorov et al., 2009). Even though the validity of personality judgments has been questioned (e.g. Alley, 1988; Cook, 1939; but see also Penton-Voak et al., 2006; Stirrat & Perrett, 2010), people generally agree on these judgments. Yet, trait attributions often have real-life consequences (e.g. Hassin and Trope, 2000; Langlois et al., 2000; Zebrowitz and Montepare, 2008), impacting cooperation (Stirrat and Perrett, 2010), political elections (Todorov et al., 2005; Little et al., 2007), court verdicts (Zebrowitz and McDonald, 1991; Blair et al., 2004), job interviews (Langlois et al., 2000), career success (Mueller and Mazur, 1996; Rule and Ambady, 2008), etc. In particular, attractiveness perception has a far-reaching influence on social behavior. It does not only affect mate choice and choice of friends, but it also influences the impressions we form about an individual—'the attractiveness halo effect' (Dion et al., 1972; Nisbett and Wilson, 1977). As a result, attractive individuals are more likely to be hired (for a review, see Hosoda et al., 2003), tend to earn more money (Hamermesh and Biddle, 1993) and experience greater dating success (Walster et al., 1966; Woll, 1986) as well as social success (Prestia et al., 2002) than their less attractive counterparts. Facial traits (e.g. symmetry and gender typicality) indicating the biological fitness of an individual are cross-culturally perceived as attractive (Perrett et al., 1999; Rhodes et al., 2001), and preferences for attractive faces are shown early in life

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This is an Open Access article distributed under the terms of the Creative Commons Attribution NonCommercial-NoDerivs licence (http:// creativecommons.org/licenses/by-nc-nd/4.0/), which permits non-commercial reproduction and distribution of the work, in any medium, provided the original work is not altered or transformed in any way, and that the work properly cited. For commercial re-use, please contact journals.permissions@oup.com with infants looking more towards attractive faces (Slater *et al.*, 1998; Slater *et al.*, 2000). Given the association of beauty and the motivational value it has, it is not surprising that processing of attractiveness recruits brain regions involved in face processing but also regions involved in the reward circuit (Aharon *et al.*, 2001; Berridge and Kringelbach, 2008; O'Doherty *et al.*, 2003; Winston *et al.*, 2007; for a review see Senior, 2003), which implies that physical attractiveness may hold incentive salience (Kawabata and Zeki, 2004; Vartanian and Goel, 2004; Cupchik *et al.*, 2009).

Despite the importance of attractiveness perception in reallife decision, a single glance at one's face appears to be enough to make an attractiveness decision of a face stimulus (Olson and Marshuetz, 2005; Willis and Todorov, 2006). Moreover, judgments made after limited time exposure are correlated with judgments made after prolonged stimulus presentation. The consensus rapidly increases as time exposure increases and reaches a plateau at presentation duration of about 200 ms, suggesting that if people are given longer viewing periods, they would only be more confident about their judgments instead of changing them (Willis and Todorov, 2006). In addition, these decisions are also mandatory, i.e. they cannot be avoided (Ritchie *et al.*, 2017).

Similarly to behavioral data, some electrophysiological studies suggest that attractiveness is extracted automatically at an early perceptual level, as indicated by differences in amplitude or peak latencies of a negativity peaking over posterioroccipital sites  $\sim$ 170 ms (i.e. the face-sensitive N170) for more or less attractive faces (Pizzagalli et al., 2002; Marzi and Viggiano, 2010; van Hooff et al., 2011; Zhang and Deng, 2012; Hahn et al., 2016). Yet, the direction of the modulation of N170 is equivocal, with some studies reporting increased amplitudes for attractive faces (e.g. Marzi and Viggiano, 2010), others finding increased amplitudes for unattractive faces (e.g. Hahn et al., 2016) and still others reporting effects of facial attractiveness only for later components (early posterior negativity, late positive component; e.g. Werheid et al., 2007; Wiese et al., 2014). The latter components reflect heightened processing referring to emotional, motivational and attentional aspects of the stimuli (e.g. Werheid et al., 2007; Zhang and Deng, 2012; Wiese et al., 2014). Some of these discrepancies could result from different task requirements, as evidence for the automatic processing of attractiveness is usually found in explicit tasks (e.g. Willis and Todorov, 2006; Zhang and Deng, 2012; Hahn et al., 2016). Furthermore, stimuli presented in electrophysiological studies often appear for fairly long intervals ranging from 450 ms (Pizzagalli et al., 2002) to 5 s (Wiese et al., 2014), allowing early perceptual coding as well as deeper emotional and motivational processing and thus providing only indirect and/or limited information about the automatic processing of attractiveness.

What would be highly desirable is an unambiguous implicit measure of facial attractiveness discrimination that could be identified objectively and relatively rapidly. To this end, we probed the automatic (i.e. effortless and without the intention to do so or being able to suppress this visual discrimination process) and implicit processing of facial attractiveness with a simple fast periodic visual stimulation (FPVS) approach coupled with electroencephalography (EEG). More attractive and less attractive faces were presented alternating at a fixed rate of 6 Hz (~167 ms), permitting only a single glance at each stimulus. This stimulation mode leads to clear frequency-tagged responses at 6 Hz and harmonics in the EEG spectrum (Adrian and Matthews, 1934; Regan, 1966; Norcia et al., 2015). Critically, if the two types of stimuli are coded by distinct spatio-temporal patterns of neural activity, an asymmetrical response in the EEG frequency data should be recorded at exactly 6 Hz/2=3 Hz (e.g. Ales et

al., 2012; Liu-Shuang et al., 2015 for asymmetrical responses between faces and scrambled faces). Thus, for example, a population of neurons responding preferentially to one stimulus category (either the more or the less attractive faces) will fire more or only when this coded category is presented, namely every 333 ms, resulting in 3 Hz response. This additional 3 Hz response can be directly quantified in the EEG frequency domain through Fourier transform and may provide an index for the perception of facial attractiveness. In earlier studies examining face identity perception with this paradigm (Retter and Rossion, 2016, 2017) given that there was no reason to expect a differential neural response at the population level between different individual faces, an asymmetrical response was generated by introducing adaptation to one of the stimuli (see also Ales and Norcia, 2009; Hoffmann et al., 2001; Tyler and Kaitz, 1977 for motion coding). Here, based on studies showing differential processing of attractive and unattractive faces, we predicted that the alternation of more and less attractive faces would generate asymmetrical responses in the EEG spectrum, even without adaptation. More importantly, in comparison to previous studies using this paradigm where only two stimuli have been alternated, we presented variable individual faces at each stimulation cycle to allow ruling out the contribution of specific characteristics of an individual face.

#### Methods

#### Participants

A total of 15 volunteers (6 males, mean $\pm$ s.d. age=23.13 $\pm$  1.81 years) participated in the study. They were all right-handed, free of neurological or psychiatric problems and had normal or corrected-to-normal vision. All participants provided signed and informed consent and were paid an amount according to their testing time. The study was approved by the Biomedical Ethical Committee of the University of Louvain. Behavioral data from one participant were excluded due to a saving failure, yet the EEG recordings were included in the final analysis.

#### Stimuli

A total of 80 color photographs of female and male faces from several databases were initially evaluated on attractiveness (1=extremely unattractive; 7=extremely attractive) by an independent participant sample (10 males, 16 females, mean  $\pm$  s.d. age = 21.46  $\pm$  1.88 years). Subsequently, faces from Face Categorization database used in previous studies (Laguesse et al., 2012; with FPVS: Liu-Shuang et al., 2014; Dzhelyova and Rossion, 2014a, 2014b) with the six highest and the six lowest attractiveness ratings for each sex were selected for the present study to avoid physical discrepancy in the image set (Figure 1). The ratings for the more attractive faces (M = 3.79, s.d. = 0.42)were significantly higher than those for the less attractive faces (M = 2.47, s.d. = 0.17), P < 0.001. All 24 faces were in a frontal view with forward eye gaze, with masked external features such as ears and hair. The image size was set to 8.04 deg (width)  $\times$  16.00 deg (height) at an 80 cm distance from the monitor ( $800 \times 600$ ), placed against a grey background (RGB: 153, 153, 153).

Several facial characteristics could influence perception of facial attractiveness: sexual dimorphism (e.g. Perrett *et al.*, 1998; Rhodes *et al.*, 2000; Debruine *et al.*, 2010; Scott *et al.*, 2010), averageness (e.g. Langlois & Roggman, 1990; Little and Hancock, 2002; Rhodes *et al.*, 2002) or facial expression (e.g. Mueser *et al.*, 1984). To evaluate if these characteristics impact the



Fig. 1. Experimental design for the CONTRAST condition. Faces rated as more attractive (A) and less attractive (B) are alternating at 6 Hz presentation rate, reaching full contrast halfway through the image presentation cycle. More and less attractive faces are repeated every 3 Hz. Faces are randomly chosen from the respective set and have the same sex within a sequence. Sequence duration is 64 s including 2 s of fade in and fade out.

attractiveness perception of our stimuli, an additional sample of 20 participants (11 males, mean  $\pm$  s.d. age = 22.05  $\pm$  1.69 years) rated the faces for sexual dimorphism on a 7-point scale (1 = not very feminine/masculine; 7=very feminine/masculine) and judged the expressed emotion (neutral, angry, fearful, disgusted, happy, sad, surprised or I do not know). Consistent with previous findings (e.g. Perrett et al., 1998; Rhodes et al., 2000; Debruine et al., 2010; Scott et al., 2010), female faces differed in perceived sexual dimorphism with attractive faces rated as more feminine than less attractive faces (mean rating scores averaged across items, M more attr  $\pm$  s.d. = 5.21  $\pm$  0.87; M less attr  $\pm$  s.d. = 3.79  $\pm$  1.11, t(19) = 9.49, P < 0.0001; mean rating scores averaged across participants, t(10) = 2.95, P = 0.014; Figure 2A), yet no difference was found for the male faces (mean rating scores averaged across items M more attr  $\pm$  s.d. = 5.60  $\pm$  0.73; M less attr  $\pm$  s.d. = 5.33  $\pm$  1.07, t(19)=1.87, P=0.077; mean rating scores averaged across participants, t(10) = 0.90, P = 0.39; Figure 2B). Considering the facial expression of the images, the majority of the stimuli were perceived as neutral (15 images out of the 24). Three of the images were more often perceived as happy, three as displaying sadness or anger and one as disgusted, yet faces were from both sets-more and less attractive (Figure 2). To statistically evaluate if the facial images differed along any of the perceived facial expressions, we compared the proportion with which an emotion was selected using a repeated measures analysis of variance (ANOVA) with factors Facial Expression (neutral, happy, angry, sad, disgusted, fearful, surprised or I do not know), Facial Attractiveness (More attractive or Less attractive) and Face Gender (female or male) as betweensubject variables. As Mauchly's test indicated a violation of the sphericity assumption, a Greenhouse-Geisser correction was applied. The main effect of Facial Expression, F(3.45, 69.06) = 15.00, P < 0.0001,  $\eta_{\rm p}^2$  = 0.43, was primarily driven by the neutral expression being significantly more often selected than all other expressions (Ps  $\leq$  0.002). Faces were rarely categorized as fearful and surprised, and the least often selected label was 'I do not know'. A trend for an interaction between Facial Expression and Facial Attractiveness was present, F(3.45, 69.06) = 2.47, P = 0.061,  $\eta_p^2$  = 0.11. Post hoc pairwise comparisons suggested that unattractive faces tended to be perceived as sad more frequently than attractive faces. Yet, due to the limited

number of images, this result should be interpreted cautiously as it could be driven by a particular image (e.g. less attractive male facial image 2). The other interactions were not significant (Ps > 0.29).

In addition, we ran a principal component analysis (PCA) on the facial shape (defined by the unique position of 137 points; see Supplementary Figure S1) to produce a mathematical index of sexual dimorphism and averageness (distance to the average of all images per sex). The technique provides a statistical description of the face images, by extracting the dimensions of variability (eigenvectors or 'eigenfaces') in the order of the variances they explain. Thus, early components capture gross variation in the image set, and later components capture more fine-grained variation (e.g. Valentin et al., 1994). All 23 PCA scores were summed to produce the indexes for sexual dimorphism and averageness. To explore if any of these factors contribute to the perceived attractiveness of the images, a binary logistic regression predicting the likelihood of an image to be categorized as more or less attractive depending on the sex of the face, the average rating of sexual dimorphism and the mathematical estimation of the sexual dimorphism and averageness were calculated in a forward model. The variables significantly predicting the likelihood of images being perceived as more/less attractive (correct classification 83.3%) were gender (P=0.047), rated sexual dimorphism (P = 0.037) and the mathematical index of averageness (P = 0.024).

#### Procedure

Participants were seated comfortably in a dimly illuminated room. The EEG recording session consisted of 18 stimulation sequences in total, the order of which was randomized for each participant. Each sequence started with a fixation cross displayed for 2–5 s, followed by 2 s of gradual stimulus fade in, 60 s of stimulation sequence and 2 s of gradual stimulus fade out. The stimulation fade in and fade out were set to avoid abrupt eye movements or blinks at the beginning or near the end of a sequence. Thus the EEG session for the current experiment lasted about 30 min including rests. In every sequence, faces were presented at a periodic frequency rate of



Fig. 2. Image characteristics. Results for female (A) and male (B) faces. Left: mean femininity/masculinity rating for each of the 12 facial images presented in the FPVS experiment. Middle: facial expression categorization for each image rated as more attractive. Right: facial expression categorization for each image rated as less attractive.

6 Hz (F) through a sinusoidal contrast modulation, as in previous studies (e.g. Rossion and Boremanse, 2011; Retter and Rossion, 2016, 2017), which is a smoother stimulation mode than square wave stimulation, thus making the experiment more comfortable for the participant. In addition, the visual stimulation is present almost all the time, creating a continuously changing percept. At each stimulus presentation cycle, the size of the facial image randomly changed (between 80% and 100%, 4% steps) to reduce the impact of low-level physical properties of the images.

Three different conditions were included and presented in random order during the whole testing. For each condition, sequences with either female or male faces were repeated three times. In the MORE ATTRACTIVE ONLY condition, faces from the same sex rated as more attractive were presented within the same sequence. Similarly, face from the same sex rated as less attractive were presented within the same sequence referred here as LESS ATTRACTIVE ONLY condition. In the critical condition, called the CONTRAST, the six faces from the same sex rated as more (A) and less (B) attractive were presented, resulting in a sequence ABABAB (Figure 1). All these faces were randomly selected from the corresponding stimulus set. For seven of the participants, the CONTRAST condition started with presenting a more attractive face, while for the remaining eight participants sequences of this condition started with a less attractive face. Faces were presented at 6 Hz; however, in the CONTRAST condition, the attractive and the less attractive faces per sex alternated at 3 Hz (f = F/2) presentation rate.

In this paradigm, symmetrical responses at the stimulation presentation rate (i.e. 6 Hz) reflect elements common to the response for each of the two alternatively presented facial stimuli, which would be present in all three conditions. However, if tuned populations respond differently to more and less attractive faces, asymmetry in the spectrum responses would be expected at the alternation rate (i.e. 3 Hz) in the CONTRAST condition, indicating the spectral signature of attractiveness discrimination. The MORE ATTRACTIVE ONLY and LESS ATTRAC-TIVE ONLY conditions were conducted to ensure that the asymmetrical EEG response would be specific to the alternation of more and less attractive faces. If this is the case, then the asymmetrical neural response in these control conditions should be absent or reduced (much weaker than the one observed in the CONTRAST condition).

To keep the attention of the participants high and constant during the experiment, they were asked to press a response key when a fixation cross randomly changed its color from black to red, 10 times for each sequence. The duration of the color change was 300 ms. The fixation cross was presented in the center of the face stimuli, just below the eyes, which is the optimal fixation point for face perception (Peterson and Eckstein, 2012). Participants were also instructed to pay attention to the faces that appeared on the screen. The mean accuracy and correct response times (RTs) of color change detection were calculated for each condition with no significant differences either for the accuracy scores, F (1.258, 16.354)=0.05, P=0.88 (M=0.93, s.d.=0.03), or for the RTs of correct responses, F (2, 26)=0.39, P=0.68 (M=0.46 s, s.d.=0.04), among the three main conditions.

It is noteworthy that 12 images per sex were available during the CONTRAST condition sequences, while only 6 images per sex were displayed in the control condition sequences. This would result in different face repetitions and possibly familiarity effects between the CONTRAST and the control conditions. In order to rule out the possibility that the different number of images presented in the conditions could lead to the asymmetrical response, an additional CONTRAST (i.e. HALF CONTRAST) condition with the three faces per sex rated the highest and the lowest, respectively, were presented for 10 of the 15 participants (see Supplementary Material). Except for the number of images presented, the design for the HALF CONTRAST condition was the same as the one for the CONTRAST condition.

#### **EEG** acquisition

EEG activity was recorded via a BIOSEMI Active two amplifier system (Biosemi, Amsterdam, Netherlands), with 128 Ag/AgCl electrodes sampled at 512 Hz. The electrodes include standard 10–20 system locations as well as additional intermediate positions. Eye movements were monitored with four electrodes, one placed at the outer canthi of each eye (HEOG) and one placed above and one below the right eye (VEOG).

## EEG pre-processing

All EEG pre-processing steps were carried out by using Letswave 6 (http://nocions.webnode.com/letswave) and Matlab (R2014a, Math works) following a similar procedure as in previous studies with this approach (e.g. Retter and Rossion, 2016, 2017). EEG data was segmented to include 4 s before and after each sequence, resulting in 72 s segments (-4–68 s). Then it was digitally bandpass filtered at 0.10–120 Hz with a Butterworth filter (fourth order). A fast Fourier transform (FFT) multi-notch filter with a width of 0.5 Hz was implemented to remove electrical noise at 50 Hz and its two harmonics. Artifact-ridden or noisy channels were replaced using linear interpolation of the three neighboring channels; less than 2% of the channels were interpolated per participant, on average only two channels for each participant. After that, a common average reference computation was applied to all channels for each participant.

#### Frequency domain analysis

Pre-processed data segments were cropped to an integer number of 3 Hz cycles, beginning 2 s after the onset of the sequence until  $\sim$ 62 s (60 s, corresponding to 179 cycles of 3 Hz, 30 554 time bins in total). The first 2 s of each sequence (i.e. fade in) were excluded to avoid any contamination by the initial transient responses. Segments of the same condition were averaged separately for sequences with female and male images. An FFT was then applied to these averaged segments, and normalized amplitude spectra were extracted for all channels (square root of the sum of squares of the real and imaginary parts divided by the number of data points). Thanks to the long time window (60 s), frequency analysis yielded spectra with a high frequency resolution of 0.0167 Hz (1/60), thus increasing the signal-to-noise ratio (SNR; Regan, 1989) and allowing unambiguous identification of the response at the frequency bins of interest (i.e. 3-3.0167 Hz and 6-6.0167 Hz).

In order to identify the presence of statistically significant responses at the frequencies of interest, Z-scores were calculated (the difference between amplitude at the frequency of interest and mean amplitude of 20 surrounding frequency bins, divided by the standard deviation of the 20 surrounding bins). The 20 bins were the 12 bins on each side, excluding the immediately adjacent bin to avoid contamination in case of spectral leakage and the local maximum and minimum amplitude bins to avoid projecting the signal in the noise estimation. Thus, baseline correction was applied by taking into account a signal of roughly 0.2 Hz on each side of the bin of interest. Only significant responses were taken for analysis (Z-score > 2.32, P < 0.01 one-tailed, i.e. signal > noise). Firstly, amplitude spectra across subjects were averaged separately for each condition (i.e. grand averaged), and then the resulting grand-averaged spectra were pooled across all 128 channels. The asymmetrical responses at 3 Hz were only significant in the CONTRAST condition, with no significant harmonics. The symmetrical responses at 6 Hz

were significant in all conditions, along with seven consecutively significant harmonics, up to 48 Hz.

For data visualization, the SNR spectra, expressed as the proportion of the signal of interest divided by the average noise measured from the 20 surrounding frequency bins (same selection criterion as above), were computed for each condition and electrode separately. To quantify the response, the baselinecorrected amplitudes for the symmetrical and asymmetrical responses were calculated by subtracting the average amplitude of the 20 surrounding bins (same selection criterion as above) and summed for the significant harmonics. The final values were obtained by averaging the responses for sequences with female and male images.

To define the regions of interest (ROIs) we normalized the baseline-corrected amplitudes for the CONTRAST condition, showing the strongest asymmetrical response (see results), by dividing the value at each electrode by the scalp-wide rootmean-square value (i.e. the square root of the sum of squares for all 128 electrodes) (McCarthy and Wood, 1985). This procedure equalizes the scalp-wide global magnitude of the response. Then 15 regions were formed based on the proximity of the channels (Supplementary Figure S2). Maximal activation was observed over the right occipito-temporal (OT) region followed by the occipital region (Supplementary Figure S2). Furthermore, the highest Z-scores were found for channels in the middle occipital (MO) region: Oz (z = 7.20) and Oiz (z = 7.29), followed by channels in the right occipito-temporal (ROT) region: PO10 (z = 7.14) and P10 (z = 6.99), as well as channel PO9 (z = 6.74) in the left occipito-temporal (LOT) region. These observations were also confirmed with a visual examination of the topographical distribution of the response on the grand-averaged data. Thus, three ROIs were defined: ROT, the corresponding LOT and MO. The summed baseline-subtracted amplitudes were averaged across five electrodes for each ROI: LOT- PO7, PO9, PO11, P7, P9; MO- POz, POOz, Oz, Oiz, Iz; ROT- PO8, PO10, PO12, P8, P10. The response was evaluated with a repeated measures ANOVA with factors Condition (CONTRAST, MORE ATTRACTIVE ONLY and LESS ATTRACTIVE ONLY) and ROI (ROT, LOT and MO). A Greenhouse-Geisser correction for degrees of freedom was applied if Mauchly's test of sphericity was significant. Correction for multiple comparisons was conducted via the Bonferroni-Holm method (Hochberg & Tamhane, 1987). To further quantify the evidence for observed differences, accompanying Bayes factors (BFs) were calculated using Bayes-paired samples t-test as implemented in JASP (Love et al., 2015) with a Cauchy prior distribution (width=0.707). The BF represents the likelihood of the data under H1 relative to H0. For example, a BF of 2.00 indicates that the data is twice more likely under the alternative hypothesis than under the null hypothesis, while a BF of 0.50 indicates that the data is twice more likely under the null hypothesis than under the alternative hypothesis. As such, the BF allows us to quantify evidence in favor of the alternative as well as the null hypothesis. As a rule of thumb,  $1 < BF \le 3$ indicates anecdotal evidence,  $3 < BF \le 10$  indicates substantial evidence and BF > 10 indicates strong evidence (Jeffreys, 1961). A directional hypothesis was tested with the Bayesian analysis; the asymmetrical 3 Hz response will be larger for the CONTRAST condition than for the other two control conditions.

### Results

#### Frequency domain analysis

Symmetrical responses (6 Hz) . Grand-averaged SNR spectra showed clear symmetrical responses at 6 Hz and its harmonics.



Fig. 3. Spectral representation and scalp distribution of EEG signal during FPVS. (A) Symmetrical response. Grand-averaged SNR spectra at 6 Hz at electrode Oz for CONTRAST (red), MORE ATTRACTIVE ONLY (yellow) and LESS ATTRACTIVE ONLY (brown) conditions. Topographical maps illustrate the distribution of the 6 Hz responses. Bar graph (Mean ± SEM) displaying summed baseline-corrected amplitudes (μV) for the 6 Hz response and its harmonics for each condition across the three ROIs, MO, LOT and ROT, indicates that the symmetrical response is largest over MO sites with no significant differences across conditions. (B) Asymmetrical response. Grand-averaged SNR spectra at 3 Hz at P10 for the CONTRAST (red), MORE ATTRACTIVE ONLY (yellow) and LESS ATTRACTIVE ONLY (brown) conditions across the three ROIs, MO, LOT and ROT, indicates that the asymmetrical response is largest over MO sites with no significant differences across conditions. (B) Asymmetrical response. Grand-averaged SNR spectra at 3 Hz at P10 for the CONTRAST (red), MORE ATTRACTIVE ONLY (yellow) and LESS ATTRACTIVE ONLY (brown) condition across the condition across the three ROIs, MO, LOT and ROT, indicates that the asymmetrical response is observed only for the CONTRAST condition, particularly over the ROT region.

The symmetrical response represents elements common to the response for stimulus and background alternation, which was expected to dominate over the MO area and not to differ across conditions.

As predicted, the repeated measures ANOVA with withinsubject factors Condition and ROI on the summed baselinecorrected amplitudes for the symmetrical response indicated a significant main effect of ROI, F(2, 28) = 41.85, P < 0.001,  $\eta_p^2 = 0.75$ , with larger responses over the MO than LOT and ROT regions, Ps < 0.001. No significant main effect of Condition, F(2, 28) = 0.34, P = 0.71, nor an interaction with ROI, F(2.603, 36.445) = 0.55, P = 0.63, were found (Figure 3A).

Asymmetrical response (3 Hz) . The 3 Hz response, indicating an asymmetry (i.e. differentiation) in the response to more and less attractive faces, was significant for the CONTRAST condition (z=4.98 over all 128 channels) but not for the control conditions: MORE ATTRACTIVE ONLY (z = 2.12 over all 128 channels)<sup>1</sup> and LESS ATTRACTIVE ONLY (z=-0.48 over all 128 channels) conditions. In the CONTRAST condition, this response was distributed over ROT channels, peaking at the low OT channel P10 (SNR=2.13) but also spreading to MO sites (Figure 3B).

To further evaluate the distribution across the scalp of the asymmetrical responses for attractiveness discrimination an ROI analysis was performed. Repeated measures ANOVA with factors ROI (LOT, MO and ROT) and Condition (CONTRAST, MORE ATTRACTIVE ONLY and LESS ATTRACTIVE ONLY) was performed on the baseline-corrected amplitude of the asymmetrical response (3 Hz). The main effect of Condition was significant, F(2, 28) = 7.46, P = 0.003,  $\eta_p^2 = 0.35$ . Post hoc pairwise comparisons indicated that the largest asymmetrical response was in the CONTRAST condition, which was significantly larger than that in the LESS ATTRACTIVE ONLY (P = 0.017,  $BF_{10} = 15.18$ ) and MORE ATTRACTIVE ONLY (P = 0.029,  $BF_{10} = 3.61$ ) conditions (Figure 3B). The response amplitudes between the latter two conditions were not significantly different, P = 0.32,  $BF_{10} = 0.69$ . No ROI difference was found, F(2, 28) = 0.69, P = 0.51. The interaction between ROI and Condition also did not reach significance, F(2.155, 30.174) = 1.97, P = 0.15.

Individual responses. The asymmetrical response was present at an individual level (Figure 4A) although the topographical distribution was variable (Figure 4B). All participants had at least four significant electrodes at a threshold of z > 2.32, P < 0.01. For 10 of the participants, at least one of the significant channels was within the OT regions (range: 1–9 electrodes). Reducing the threshold to z = 1.64, P < 0.05 revealed that channels within the OT region were significant for another three of the participants (yet the maximal activation was found over channels dorsal to the left OT ROI (P#5) or dorsal to the right OT ROI (P#10) and MO sites (P#8)). The last two participants showed significant responses over the central cluster (P#13, P#15) and the MO ROI (P#15).

# Discussion

We present original evidence for a population of neurons projecting to OT channels tuned to discriminate faces based on

<sup>1</sup> The asymmetrical response in the MORE ATTRACTIVE ONLY condition was dispersedly distributed, with the largest response localized at fronto-central channels FC3h, FCz and FCC1.



Fig. 4. Individual asymmetrical response. (A) Individual asymmetrical response at 3 Hz for the CONTRAST condition. Individual displays are centered at 3 Hz and show data from 2.83 Hz to 3.18 Hz corresponding to the 10 surrounding bins with resolution = 0.0167. Channels are indicated above the displays. (B) Individual scalp maps showing the topography of the asymmetrical response at 3 Hz. SNR responses are displayed and the individual range indicated above the topographies (1 = noise level).

attractiveness. More and less attractive faces were shown very briefly at 6 Hz (~167 ms), allowing only a single glance at the images, leading to an asymmetrical response (3 Hz) discriminating between the two categories. Importantly, this asymmetrical response was not observed when only the less attractive faces were presented. A small asymmetrical response was observed for the more attractive only face, yet importantly this response was much weaker than the asymmetrical response observed when the less and more attractive faces alternated. This facial attractiveness discrimination signal is significant at an individual subject level, and it is obtained without requiring any explicit task within a few minutes of visual stimulation.

Consistent with behavioral findings, our results support the idea that facial attractiveness is processed rapidly (Olson and Marshuetz, 2005; Willis and Todorov, 2006). The asymmetrical response (3 Hz) in the present study reflects the robust and specific discrimination of more and less attractive faces at a single glance. In contrast to previous EEG studies, investigating facial attractiveness (e.g. Pizzagalli et al., 2002; van Hooff et al., 2011; Zhang and Deng, 2012), with the FPVS paradigm, all visual stimuli were presented briefly for 167 ms (allowing only a single glance, i.e. no eye movement exploration of the image) and were quickly replaced (backward and forward masked) by other stimuli, diminishing the ability to process deeper the facial stimuli (Liu-Shuang et al., 2014; Dzhelyova et al., 2016). This coding of attractiveness can be driving the spontaneous and rapid perception of attractiveness observed in behavioral studies (Olson and Marshuetz, 2005; Willis and Todorov, 2006). Together with the emotional and motivational aspects of attractiveness, they can affect the inferences one forms based on facial appearance (Dion et al., 1972).

The asymmetrical response was distributed over posterior OT channels, suggesting a response originating from higher level visual areas (e.g. Norcia *et al.*, 2015). In comparison, an MO distribution, often observed with higher stimulation frequencies, is often linked to activation within lower-tier visual cortex with strong contributions from V1 (e.g. Di Russo *et al.*, 2007; Weiser *et al.*, 2012). Although it is impossible to define the exact neuronal population producing this OT scalp topography, based on previous findings and face perception models (e.g. Haxby *et al.*, 2000; O'Doherty *et al.*, 2003; Kranz and Ishai, 2006; Proverbio *et al.*, 2010), it is likely to be within the fusiform gyrus, superior temporal sulcus or lateral occipital cortex (see the discussion in Jacques et al., 2019). Increased activation within the ventral

OT cortex has been found during judgments of attractiveness (Kranz and Ishai, 2006; O'Doherty et al., 2003; Proverbio et al., 2010), which potentially reflects the initial perceptual processing of facial attractiveness. The asymmetrical response was slightly stronger over the right hemisphere, consistent with typical face processing, yet the individual response varied substantially, possibly obscuring consistent lateralization.

This scalp topography is also similar to those of the facesensitive event-related potentials (ERPs) to transient stimulation (i.e. N170). Enhanced N170 component has been found for high compared to low attractive faces, revealing elaborate structural and cognitive encoding for the former stimuli (Werheid *et al.*, 2007; Wiese *et al.*, 2014; but see Roye *et al.*, 2008; Schacht *et al.*, 2008). Although similarities are shared between the asymmetrical response and the face-sensitive ERP components, it is difficult to draw a parallel between standard ERP components and the response observed with FPVS since the present 3 Hz asymmetrical response results from the difference between the more and less attractive faces, rather than a response to a single image category (either more or less attractive images).

The observed asymmetrical response is unlikely to be explained by low-level processing such as pixel-wise differences in luminance or contrast between the alternated images. Firstly, several images were used as stimuli as well as substantial random changes in size at each stimulus cycle were applied, preventing pixel by pixel discrimination (Liu-Shuang et al., 2014; Dzhelyova and Rossion, 2014a, 2014b). Secondly, the 3 Hz response peaked over the right occipital-temporal cortex, suggesting contributions from high-level visual areas (Retter and Rossion, 2017). Also, it cannot be explained by different attentional demands across the conditions, since the performance on the orthogonal tasks did not differ across these conditions and the strength of the 6 Hz response was equivalent among them. Furthermore, even when the HALF CONTRAST was tested, an asymmetrical response was observed, which makes it unlikely to explain the 3 Hz response as a result of different number of images or memory requirements. It is also important to note that in the CONTRAST condition, the images are repeated fewer times than in the two control conditions that could possibly lead to a stronger neuronal response due to less adaptation than in the two control conditions. Yet, this factor is unlikely to explain our results firstly because the general visual response was not different across the conditions and secondly because the asymmetrical response was found and even was stronger when presenting only the six images in the HALF CONDITION than in the CONTRAST condition.

# Furthermore, we have observed this asymmetrical response using an implicit task, which does not require the participants to form impressions of attractiveness or to judge any other aspect of the faces. This manipulation provides some initial evidence that attractiveness is processed capacity free by tuned populations of neurons. Further studies could embark on this research avenue and explore how task manipulation and cognitive load modulate the automatic processing of attractiveness. Nevertheless, the use of an implicit task and the robust responses obtained within a few minutes provide the unique opportunity to investigate, independently of linguistic abilities, facial attractiveness processing through development or crossculturally.

Which facial cues, differing between more and less attractive faces, could explain the symmetrical response? Our image analysis suggests that facial averageness (distinctiveness) and perceived sexual dimorphism differed between the more attractive and less attractive faces and thus could possibly account for the observed asymmetries. These two facial aspects have been shown to influence perception of facial attractiveness in numerous studies (e.g. Little and Hancock, 2002; Langlois and Roggman, 1990; Perrett et al., 1998; Rhodes et al., 2002) and also to modulate EEG waveforms (e.g. Halit et al., 2000; Freeman et al., 2010). Other aspects like facial expression have been also shown to affect perceived attractiveness with happy faces perceived as more attractive than faces with negative expressions (e.g. Mueser et al., 1984), yet in our set the individuals were photographed with neutral facial expression, thus there was no clear influence of perceived expression on attractiveness. Nevertheless, our initial attempt to understand which features contribute to the discrimination of more and less attractive faces indicate that facial aspects impacting on attractiveness perception differed for our stimuli and thus can be driving the asymmetrical processing of attractiveness. Admittedly, determining which of these features contributed to the observed asymmetrical response is beyond the scope of the reported study. Therefore, future studies could look more precisely if a particular aspect of facial attractiveness-averageness/distinctiveness, sex typicality, etc.-impacts mostly on the automatic coding of attractiveness.

In summary, by rapidly alternating between high and low attractive faces, we provide evidence for tuned populations of neurons within higher visual face-sensitive areas coding for attractiveness discrimination. Importantly, this effect is not observed when only high or low attractive faces were presented. Thus, this technique may be considered as a simple and powerful tool to investigate the perceptual underpinnings of attractiveness discrimination by carefully manipulating different facial aspects contributing to attractiveness. Given the short experimental duration, the lack of explicit response required and the robustness of the response with the FPVS–EEG technique, this paradigm may also be extended to test infants, children and cross-cultural populations.

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#### **References**

- Adrian, E.D., Matthews, B.H. (1934). The Berger rhythm: potential changes from the occipital lobes in man. Brain, 57(4), 355–85.
- Aharon, I., Etcoff, N., Ariely, D., Chabris, C.F., O'Connor, E., Breiter, H.C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron*, 32(3), 537–51.
- Ales, J.M., Norcia, A.M. (2009). Assessing direction-specific adaptation using the steady-state visual evoked potential: results from EEG source imaging. *Journal* of Vision, **9**(7), 8–8.
- Ales, J.M., Farzin, F., Rossion, B., Norcia, A.M. (2012). An objective method for measuring face detection thresholds using the sweep steady-state visual evoked response. *Journal of Vision*, 12(10), 18–8.
- Alley, T.R. (1988). Physiognomy and social perception. In: Social and Applied Aspects of Perceiving Faces, pp. 167–86.
- Bar, M., Neta, M., Linz, H. (2006). Very first impressions. Emotion, 6(2), 269.
- Berridge, K.C., Kringelbach, M.L. (2008). Affective neuroscience of pleasure: reward in humans and animals. *Psychopharmacology*, 199(3), 457–80.
- Blair, I.V., Judd, C.M., Chapleau, K.M. (2004). The influence of Afrocentric facial features in criminal sentencing. Psychological Science, 15(10), 674–9.
- Cook, S.W. (1939). The judgment of intelligence from photographs. The Journal of Abnormal and Social Psychology, 34(3), 384.
- Cupchik, G.C., Vartanian, O., Crawley, A., Mikulis, D.J. (2009). Viewing artworks: contributions of cognitive control and perceptual facilitation to aesthetic experience. *Brain & Cognition*, **70**(1), 84–91.
- DeBruine, L.M., Jones, B.C., Smith, F.G., Little, A.C. (2010). Are attractive men's faces masculine or feminine? The importance of controlling confounds in face stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, **36**(3), 751.
- Di Russo, F., Pitzalis, S., Aprile, T., *et al.* (2007). Spatiotemporal analysis of the cortical sources of the steady-state visual evoked potential. *Human Brain Mapping*, **28**(4), 323–34.
- Dion, K., Berscheid, E., Walster, E. (1972). What is beautiful is good. Journal of Personality and Social Psychology, **24**(3), 285.
- Dzhelyova, M., Jacques, C., Rossion, B. (2016). At a single glance: fast periodic visual stimulation uncovers the Spatio-temporal dynamics of brief facial expression changes in the human brain. *Cerebral Cortex*, **27**, 4106–23.
- Dzhelyova, M., & Rossion, B. (2014a). The effect of parametric stimulus size variation on individual face discrimination indexed by fast periodic visual stimulation. BMC Neuroscience, **15**, 1–12. doi: 10.1186/1471-2202-15-87
- Dzhelyova, M. & Rossion, B. (2014b). Supra-additive contribution of shape and surface information to individual face discrimination as revealed by fast periodic visual stimulation. *Journal* of Vision, **14**(14):15. doi:10.1167/14.14.15
- Freeman, J.B., Ambady, N., Holcomb, P.J. (2010). The face-sensitive N170 encodes social category information. *Neuroreport*, **21**(1), 24.
- Hahn, A.C., Symons, L.A., Kredel, T., et al. (2016). Early and late event-related potentials are modulated by infant and adult faces of high and low attractiveness. Social Neuroscience, **11**(2), 207–20.

- Halit, H., de Haan, M., Johnson, M.H. (2000). Modulation of eventrelated potentials by prototypical and atypical faces. *Neuroreport*, **11**(9), 1871–5.
- Hamermesh, D.S., Biddle, J.E. (1993). Beauty and the labor market (no. w4518). National Bureau of Economic Research.
- Hassin, R., Trope, Y. (2000). Facing faces: studies on the cognitive aspects of physiognomy. *Journal of Personality and Social Psychology*, **78**(5), 837.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, **4**(6), 223–33.
- Hochberg, J., Tamhane, A.C. (1987). Multiple comparison procedures (No. 519.535 H655m Ej. 1). John Wiley & Sons,.
- Hoffmann, M.B., Unsöld, A.S., Bach, M. (2001). Directional tuning of human motion adaptation as reflected by the motion VEP. Vision Research, 41(17), 2187–94.
- van Hooff, J.C., Crawford, H., Van, V.M. (2011). The wandering mind of men: ERP evidence for gender differences in attention bias towards attractive opposite sex faces. Social Cognitive & Affective Neuroscience, 6(4), 477.
- Hosoda, M., Stone-Romero, E.F., Coats, G. (2003). The effects of physical attractiveness on job-related outcomes: a metaanalysis of experimental studies. *Personnel Psychology*, 56(2), 431–62.
- Jacques, C., Jonas, J., Maillard, L., Colnat-Coulbois, S., Koessler, L., Rossion, B. (2019). The inferior occipital gyrus as a major cortical source of the face-evoked N170: evidence from simultaneous scalp and intracerebral human recordings. *Human Brain Mapping*, 40, 1403–1419.
- Jeffreys, H. (1961). Theory of probability, 3rd edn, New York, NY: Oxford University Press.
- Kawabata, H., Zeki, S. (2004). Neural correlates of beauty. Journal of Neurophysiology, **91**(4), 1699.
- Kranz, F., Ishai, A. (2006). Face perception is modulated by sexual preference. *Current Biology*, **16**(1), 63–8.
- Laguesse, R., Dormal, G., Biervoye, A., Kuefner, D., Rossion, B. (2012). Extensive visual training in adulthood significantly reduces the face inversion effect. *Journal of Vision*, **12**(14), 1–13.
- Langlois, J.H., Roggman, L.A. (1990). Attractive faces are only average. Psychological Science, 1(2), 115–21.
- Langlois, J.H., Kalakanis, L., Rubenstein, A.J., Larson, A., Hallam, M., Smoot, M. (2000). Maxims or myths of beauty? A metaanalytic and theoretical review. *Psychological Bulletin*, **126**(3), 390.
- Little, A.C., Hancock, P.J. (2002). The role of masculinity and distinctiveness in judgments of human male facial attractiveness. British Journal of Psychology, **93**(4), 451–64.
- Little, A.C., Burriss, R.P., Jones, B.C., Roberts, S.C. (2007). Facial appearance affects voting decisions. *Evolution and Human Behavior*, **28**(1), 18–27.
- Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2014). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia*, **52**, 57–72. doi: 10.1016/j.neuropsychologia.2013.10.022
- Liu-Shuang, J., Ales, J.M., Rossion, B., Norcia, A.M. (2015). The effect of contrast polarity reversal on face detection: evidence of perceptual asymmetry from sweep VEP. Vision Research, 108, 8–19.
- Love, J., Selker, R., Marsman, M. et al. (2015). Jasp (version 0.7). [computer software]. Retrieved from https://jasp-stats.org
- Marzi, T., Viggiano, M.P. (2010). When memory meets beauty: insights from event-related potentials. *Biological Psychology*, **84**(2), 192–205.

- McCarthy, G., Wood, C.C. (1985). Scalp distributions of eventrelated potentials: an ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophys*iology, **62**(3), 203–8.
- Mueller, U., Mazur, A. (1996). Facial dominance of West Point cadets as a predictor of later military rank. Social Forces, 74(3), 823–50.
- Mueser, K.T., Grau, B.W., Sussman, S., Rosen, A.J. (1984). You're only as pretty as you feel: facial expression as a determinant of physical attractiveness. *Journal of Personality and Social Psychology*, **46**(2), 469.
- Nisbett, R.E., Wilson, T.D. (1977). The halo effect: evidence for unconscious alteration of judgments. *Journal of Personality and Social Psychology*, **35**(4), 250.
- Norcia, A.M., Appelbaum, L.G., Ales, J.M., Cottereau, B.R., Rossion, B. (2015). The steady-state visual evoked potential in vision research: a review. *Journal of Vision*, **15**(6), 4.
- O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D.M., Dolan, R.J. (2003). Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, **41**(2), 147–55.
- Olson, I.R., Marshuetz, C. (2005). Facial attractiveness is appraised in a glance. *Emotion*, **5**(4), 498.
- Penton-Voak, I.S., Pound, N., Little, A.C., Perrett, D.I. (2006). Personality judgments from natural and composite facial images: more evidence for a 'kernel of truth' in social perception. Social *Cognition*, **24**(5), 607–40.
- Perrett, D.I., Lee, K.J., Penton-Voak, I., et al. (1998). Effects of sexual dimorphism on facial attractiveness. Nature, 394(6696), 884.
- Perrett, D.I., Burt, D.M., Penton-Voak, I.S., Lee, K.J., Rowland, D.A., Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, **20**(5), 295–307.
- Peterson, M.F., Eckstein, M.P. (2012). Looking just below the eyes is optimal across face recognition tasks. Proceedings of the National Academy of Sciences of the United States of America, **109**(48), E3314–23.
- Pizzagalli, D.A., Lehmann, D., Hendrick, A.M., Regard, M., Pascual-Marqui, R.D., Davidson, R.J. (2002). Affective judgments of faces modulate early activity (approximately 160 ms) within the fusiform gyri. *NeuroImage*, **16**(3), 663–77.
- Prestia, S., Silverston, J., Wood, K., Zigarmi, L. (2002). The effects of attractiveness on popularity; an observational study of social interaction among college students. *Perspectives in Psychology*, 40, 3–11.
- Proverbio, A.M., Riva, F., Martin, E., Zani, A. (2010). Face coding is bilateral in the female brain. PLoS One, **5**(6), e11242.
- Regan, D. (1966). Some characteristics of average steadystate and transient responses evoked by modulated light. *Electroencephalography and Clinical Neurophysiology*, **20**(3), 238–48.
- Regan, D. (1989). Human Brain Electrophysiology: Evoked Potentials and Evoked Magnetic Fields in Science and Medicine.
- Retter, T.L., Rossion, B. (2016). Visual adaptation provides objective electrophysiological evidence of facial identity discrimination. Cortex, 80, 35–50.
- Retter, T. L., & Rossion, B. (2017). Visual adaptation reveals an objective electrophysiological measure of high-level individual face discrimination. *Scientific Reports*, 7, 1–10. doi: 10.1038/s41598-017-03348-x
- Rhodes, G., Hickford, C., Jeffery, L. (2000). Sex-typicality and attractiveness: are supermale and superfemale faces super-attractive? British Journal of Psychology, **91**(1), 125–40.

- Rhodes, G., Yoshikawa, S., Clark, A., Lee, K., McKay, R., Akamatsu, S. (2001). Attractiveness of facial averageness and symmetry in non-Western cultures: in search of biologically based standards of beauty. *Perception*, **30**(5), 611–25.
- Rhodes, G., Geddes, K., Jeffery, L., Dziurawiec, S., Clark, A. (2002). Are average and symmetric faces attractive to infants? Discrimination and looking preferences. *Perception*, **31**(3), 315–21.
- Ritchie, K.L., Palermo, R., Rhodes, G. (2017). Forming impressions of facial attractiveness is mandatory. *Scientific Reports*, 7(1), 469.
- Rossion, B., Boremanse, A. (2011). Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. *Journal of Vision*, **11**(2), 16–6.
- Roye, A., Höfel, L., Jacobsen, T. (2008). Aesthetics of faces: behavioral and electrophysiological indices of evaluative and descriptive judgment processes. *Journal of Psychophysiology*, 22(1), 41–57.
- Rule, N.O., Ambady, N. (2008). The face of success: inferences from chief executive officers' appearance predict company profits. Psychological Science, 19(2), 109–11.
- Schacht, A., Werheid, K., Sommer, W. (2008). The appraisal of facial beauty is rapid but not mandatory. Cognitive, Affective, & Behavioral Neuroscience, 8(2), 132–42.
- Scott, I.M., Pound, N., Stephen, I.D., Clark, A.P., Penton-Voak, I.S. (2010). Does masculinity matter? The contribution of masculine face shape to male attractiveness in humans. PLoS One, 5(10), e13585.
- Senior, C. (2003). Beauty in the brain of the beholder. Neuron, 38(4), 525-8.
- Slater, A., Von der Schulenburg, C., Brown, E., et al. (1998). Newborn infants prefer attractive faces. Infant Behavior and Development, 21(2), 345–54.
- Slater, A., Bremner, G., Johnson, S.P., Sherwood, P., Hayes, R., Brown, E. (2000). Newborn infants' preference for attractive faces: the role of internal and external facial features. *Infancy*, 1(2), 265–74.
- Stirrat, M., Perrett, D.I. (2010). Valid facial cues to cooperation and trust: male facial width and trustworthiness. Psychological Science, 21(3), 349–54.
- Todorov, A., Mandisodza, A.N., Goren, A., Hall, C.C. (2005). Inferences of competence from faces predict election outcomes. *Science*, **308**(5728), 1623–6.

- Todorov, A., Pakrashi, M., Oosterhof, N.N. (2009). Evaluating faces on trustworthiness after minimal time exposure. Social Cognition, **27**(6), 813–33.
- Tyler, C., Kaitz, M. (1977). Movement adaptation in the visual evoked response. *Experimental Brain Research*, **27**(2), 203–9.
- Valentin, D., Abdi, H., O'Toole, A.J. (1994). Categorization and identification of human face images by neural networks: a review of the linear autoassociative and principal component approaches. *Journal of Biological Systems*, 2(03), 413–29.
- Vartanian, O., Goel, V. (2004). Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport*, **15**(5), 893–7.
- Walster, E., Aronson, V., Abrahams, D., Rottman, L. (1966). Importance of physical attractiveness in dating behavior. *Journal of Personality and Social Psychology*, 4(5), 508.
- Werheid, K., Schacht, A., Sommer, W. (2007). Facial attractiveness modulates early and late event-related brain potentials. *Biological Psychology*, **76**(1–2), 100.
- Wiese, H., Altmann, C.S., Schweinberger, S.R. (2014). Effects of attractiveness on face memory separated from distinctiveness: evidence from event-related brain potentials. *Neuropsy*chologia, 56(1), 26.
- Wieser, M.J., McTeague, L.M., Keil, A. (2012). Competition effects of threatening faces in social anxiety. *Emotion*, **12**(5), 1050–1060. http://dx.doi.org/10.1037/a0027069
- Willis, J., Todorov, A. (2006). First impressions: making up your mind after a 100-ms exposure to a face. Psychological Science, 17(7), 592–8.
- Winston, J.S., O'Doherty, J., Kilner, J.M., Perrett, D.I., Dolan, R.J. (2007). Brain systems for assessing facial attractiveness. *Neuropsychologia*, 45(1), 195.
- Woll, S. (1986). So many to choose from: decision strategies in videodating. Journal of Social and Personal Relationships, **3**(1), 43–52.
- Zebrowitz, L.A., McDonald, S.M. (1991). The impact of litigants' baby-facedness and attractiveness on adjudications in small claims courts. *Law and Human Behavior*, **15**(6), 603.
- Zebrowitz, L.A., Montepare, J.M. (2008). Social psychological face perception: why appearance matters. Social and Personality Psychology Compass, **2**(3), 1497–517.
- Zhang, Z., Deng, Z. (2012). Gender, facial attractiveness, and early and late event-related potential components. *Journal of Integrative Neuroscience*, **11**(4), 477–87.