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Beyond the west: Chemosignaling of emotions transcends ethno-cultural boundaries

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ABSTRACT

Accumulating evidence has pointed to a human capacity to communicate emotions to others via sweat. So far, these studies have relied exclusively on Western Caucasian samples. Our aim was to test whether the chemosensory communication of emotions extended beyond ethno-cultural boundaries, from Western Caucasians ($N = 48$) to East Asians ($N = 48$). To test this, we used well-validated materials and procedures, a double-blind design, a pre-registered analysis plan, and a combination of facial electromyography (EMG) and continuous flash suppression techniques to measure unconscious emotions. Our results show that East Asian (and Western Caucasian) female *receivers* exposed to the sweat (body odor) of fearful, happy, and neutral Western Caucasian male *senders* emulate these respective states based on body odors, outside of awareness. More specifically, East Asian (and Western Caucasian) receivers demonstrated significantly different patterns of facial muscle activity when being exposed to fear odor, happy odor, and neutral odor. Furthermore, fear odor decreased the suppression time of all faces on an interocular suppression task (IST), indicating subconscious vigilance, whereas happy odor increased the detection speed of happy faces. These combined findings suggest that the ability to perceive emotional signals from body odor may be a universal phenomenon.

1. Introduction

The human sense of smell has long been underestimated, from the ancient Greeks, to Sigmund Freud, and beyond (Le Guérer, 2002). Currently, pseudoscientific ideas about poor human olfaction are being replaced by empirical studies showing excellent human smell skills (McGann, 2017). Indeed, one capacity humans share with super smeller species is social communication (Stevenson, 2010): Human body odor can convey a person's identity (Kuhn and Natsch, 2008), gender (Penn et al., 2007), age (e.g., Haze et al., 2001), sickness (Olsson et al., 2014), and emotions: from transient fear, stress, and anxiety (de Groot et al., 2012; Mujica-Parodi et al., 2009; Pause et al., 2004; Wudarczyk et al., 2016; Zhou and Chen, 2009), to happiness (Chen and Haviland-Jones, 2000; de Groot et al., 2015a).

Although these studies have alluded to a *shared human* capacity to communicate social information via smell, a critical limitation concerns the exclusive use of Western Caucasian study samples. Not knowing whether effects presumed to be universal hold beyond Western Caucasians is a major problem in scientific research in general (Henrich et al., 2010), and a particularly pressing issue when human chemosensory communication is concerned, which may rely on universal chemosensory signals ("chemosignals") eliciting *species-wide* effects (de Groot et al., 2017). Understanding universal human chemosignals is one of the most compelling puzzles facing scientists this century (Kennedy and Norman, 2005), and part of its solution lies in examining whether the human chemosensory communication of emotions trans-

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cends Western Caucasian ethno-cultural boundaries.

When moving beyond Western Caucasians to discover the potentially universal chemical communication of emotions, East Asians seem the most informative comparison group. There is evidence (Martin et al., 2010) that most East Asians (80–95%) carry a single gene variant (ABCC11, allele A/A) that Caucasians lack (0–3% A/A; vs. G/A, G/G), causing their apocrine sweat glands to produce fewer axillary odor precursors, and fewer volatile odorants (Harker et al., 2014; Yoshiura et al., 2006). As apocrine sweat gland activity has been related to emotions (Harker, 2013), East Asians' may have a limited capacity to *express* emotions through apocrine sweat secretions, which raises the question whether their *perception* of emotion-related body odors is impeded. Examining East Asian (vs. Caucasian) receivers' responses to senders' emotion-related body odors will advance our understanding of the *scale* of the human chemosensory emotion communication.

Prior (Western Caucasian-based) research also focused on the receiver, and determined the successful chemosensory emotion communication from *receivers'* perceptual, affective, and behavioral processes matching the initial experience of *senders* who produced the body odor (e.g., de Groot et al., 2012; Zhou and Chen, 2009). In the present research, we focus on the chemosensory communication of *fear* and *happiness* in East Asians. Essentially, these emotions have adaptive significance for all humans, with fear facilitating vigilance to detect threat (Susskind et al., 2008), and happiness contributing to social bonding, and restoring the harmful impact of negative emotions on our cardiovascular, immune, and neuroendocrine system (Steptoe et al., 2005). Moreover, there is prior support for the chemosensory communication of these emotions in Caucasian receivers (reviewed in: de Groot et al., 2017): Exposure to Caucasian fear odor (i.e., sweat sampled from the axilla of senders induced to be fearful) evoked in receivers a fearful facial expression (increased *medial frontalis*, and reduced *zygomaticus major* muscle activity) and sensory vigilance processes (e.g., enhanced visual search), whereas happy odor elicited a genuine "Duchenne" smile (increased *zygomaticus major* and *orbicularis oculi* muscle activity; Ekman et al., 2002) and a broader perceptual processing style typical for positive affect (de Groot et al., 2015a).

To test whether this capacity to emulate emotions based on body odor extends from Caucasian receivers to East Asians, we exposed both receiver groups to emotional (fearful, happy, and neutral) sweat from Caucasian senders. Caucasian sweat was used, as prior research showed that it can signal emotions (reviewed in: de Groot et al., 2017). Successful chemosensory communication of emotion was inferred from a novel combination of implicit measures, namely facial emotion expression using electromyography (EMG), and a paradigm called interocular suppression, which is sensitive to olfactory influence (Zhou et al., 2010, 2012). Through interocular suppression, we could assess if fear and happy (vs. neutral) odor subconsciously modulated receivers' readiness to perceive fearful and happy faces, respectively.

2. Materials and methods

Approval for these studies came from Utrecht University's Faculty Ethics Review Board (FETC15-103; Dutch sender and receiver study), the Shanghai Clinical Research Center (SW.000438.1; Chinese sender study), and the Institutional Review Board of the Institute of Psychology (Chinese Academy of Sciences, Beijing, China) (H16005; Chinese receiver study).

We report how we determined sample size, all data exclusions, all manipulations, and all measures. Based on effect sizes from comparable prior research (de Groot et al., 2015a), a power analysis (α = .05, power = 90%) computed 48 receivers per ethno-cultural group; given a 4:1 standard ratio, this means 12 donors per group (for details, see Supplementary method 1.1).

2.1. Part 1: senders

2.1.1. Participants and design

Twenty-four Caucasian Dutch males (M_{age} = 24.42 years; *SD* = 3.76; range: 19–34 years; ABCC11 genotype G/A, G/G: *n* = 23; A/A: *n* = 1[2]) provided written informed consent to donate sweat in three emotion-induction sessions (fear, happy, neutral) for €50. Only healthy, non-smoking, Caucasian males were included (cf. de Groot et al., 2015a).

2.1.2. Materials and procedure

Dutch donors recruited both in China (expats) and the Netherlands (*n* = 12, per location) followed a well-validated 48-hour protocol to avoid sweat contamination (e.g., de Groot et al., 2015a): Participants shaved their armpits, and heavily flavored food items (e.g., garlic, onions), alcohol, drugs, and excessive exercise were prohibited.

Each donor wore 10 x 10 cm sterile absorbent pads (Cutisorb, BSN Medical, Hamburg, Germany) under their armpits to absorb sweat, a pre-washed t-shirt, and a hooded sweater, and watched on three different donation days 30-minute film clips that induced fear, happiness, and a neutral state (in that order).

The fear condition contained nine horror clips (Schaefer et al., 2010; database codes: 7;16;28;32;38;46;50;55;66), including scenes from *The Shining* and *The Blair Witch Project*. The happy condition: "Bear Necessities" (*The Jungle Book*); *Validation*; a comical opera scene (*Intouchables*); and an elaborate televised prank. The neutral condition: First-person view of a car/boat/train traveling through the Dutch countryside, and Swiss Alps, followed by outdated weather forecasts (cf. de Groot et al., 2015a).

Afterward, participants rated their feelings. The first question involved a dichotomy (yes/no), and if "yes", participants rated emotion degree (1: "a little bit"; 5: "extreme"). Sixteen items from the affective circumplex (Russell, 1980), including "happy" and "sad", were complemented by four remaining discrete emotion terms (i.e., surprise, anger, fear, and disgust), to gain a completer understanding of senders' emotional experience. Core affect (arousal, valence) was also directly measured on a two-dimensional 7 × 7 affect grid (Russell et al., 1989).

Sweat production was determined by subtracting pad weight before emotion-induction from the post-induction weight (Δ), and summing the Δ-weight of the left and right armpit.

To verify ABCC11 genotype, DNA samples were collected with buccal swabs (Isohelix SK-1S, Cell Projects Ltd., Harrietsham, UK). All samples were anonymized, frozen (−27 °C), and analyzed by a specialized lab (BaseClear BV, Leiden, the Netherlands) (Section 2.1.1: DNA results senders; Section 2.2.1: DNA receivers).

2.1.3. Statistical analysis

Donors neither dropped-out, nor were excluded; all adhered to experimental protocols. Data were subjected to non-parametric Friedman tests. Follow-up Wilcoxon signed-rank tests without hypothesized direction were Bonferroni corrected. Target analyses were accompanied by effect sizes (*r* = 0.1, 0.3, 0.5: small, moderate, large; Cohen, 1988).

2.2. Part 2: receivers (East asians, western caucasians)

2.2.1. Participants and design

Written informed consent was obtained from 96 females (East Asians: 48 Chinese females: M_{age} = 22.38; *SD* = 2.35; ABCC11 genotype: G/A: *n* = 2; A/A: *n* = 46; Western Caucasians: 48 Dutch females: M_{age} = 21.17; *SD* = 2.41; ABCC11 genotype: G/G: *n* = 35; G/A: *n* = 11; A/A: *n* = 2). Each participant received €12.

Only females were recruited, because their generally superior sense

[2] As sweat samples were pooled across multiple subjects, the one A/A-genotyped donor (identified post-experiment) had a negligible impact.

of smell (Brand and Millot, 2001) and their capacity for odor-based emotional contagion (de Groot et al., 2014) makes them the most sensitive sample to detect chemosensory communication in East Asians. The interocular suppression task required participants to have normal vision or lenses.

A standardized odor threshold test (Hummel et al., 1997) using "Sniffin' Sticks" (Burghart Instruments, Wedel, Germany) indicated that all participants had a functional sense of smell (East Asian phenethyl alcohol (PEA) threshold: *Mdn* = 3.41 × 10^{-2}%, range = .59%–3.45 × 10^{-4}%; *n* = 44 normosmic; *n* = 4 hyposmic; classification criteria: Wolfensberger et al., 2000); Western Caucasian PEA threshold: *Mdn* = 5.52 × 10^{-3}%, range = .71%–2.90 × 10^{-4}%; *n* = 46 normosmic; *n* = 2 hyposmic).

Both studies were double-blind, with body odor (fear, happy, neutral) being the within-subjects factor. Odors were counterbalanced, and each odor was presented twice.

2.2.2. Materials and procedure

2.2.2.1. Odor presentation. Body odors (sweat pads) were presented in polypropylene jars, held by an adjustable clamp attached to the head-and-chin rest, ~2 cm below the participant's nose. Odors were presented during a 5 s fixation cross (a typical, visually neutral EMG recording interval), and during the subsequent interocular suppression task.

2.2.2.2. Handedness scale. The Edinburgh handedness inventory (Oldfield, 1971) verified East Asians' (*M* = 16.65, *SD* = 3.69); Western Caucasians' (*M* = 16.44, *SD* = 2.56) right-handedness on 10 items (-2: "always left"; 2: "always right").

2.2.2.3. Facial EMG. Facial muscle activity was recorded with small (4 mm ø) sintered bipolar Ag/AgCl electrodes (Easycap GmbH, Herrsching, Germany) placed on the left *orbicularis oculi* and *zygomaticus major* muscle, and left *medial frontalis* (Dimberg and Petterson, 2000; Fridlund and Cacioppo, 1986) (Fig. 1A; for more details: Supplementary method 1.2).

2.2.2.4. Interocular suppresion task (IST). The IST uses two dichoptically presented visual stimuli; at trial start, the test image is interocularly suppressed from being consciously perceived (e.g., Tsuchiya and Koch, 2005; Zhou et al., 2010, 2012). To ensure interocular suppression, a mirror stereoscope (adjusted for each participant) was placed between the computer monitor and the head-and-chin rest (Fig. 1B). Stimuli were presented using MATLAB (MathWorks, Natick, MA) with PsychToolbox (Brainard, 1997; Pelli, 1997).

The IST contained 48 trials per odor exposure. Each trial started with a 1-s fixation cross. Participants twice viewed 24 Ekman faces (4 unique male actors, 4 unique female actors) displaying fearful, happy, and neutral facial expressions (Ekman and Friesen, 1976). To each eye, a frame (9.1° x 9.1°) was always displayed that extended beyond the outer border of the visual stimuli with a central fixation point (0.57° x 0.57°) to facilitate stable convergence. Faces (1.8° x 2.3°) were presented at a random location (i.e., in a rectangle area (0.57° x 0.86°) 1.7° horizontally to the left or right of the central fixation cross) to the *nondominant* eye, whereas a high contrast dynamic noise pattern (7.4° x 7.4°) was presented to the *dominant* eye (see Supplementary method 1.2, for determining eye dominance). The face picture contrast was gradually ramped up from 0% to full contrast within a 2 s-period from trial onset, and then remained constant; after 1 s, the reverse occurred for the dynamic noise pattern (Fig. 2).

Participants had to press as fast as possible the left (vs. right) arrow key when they perceived (any part of) the face image on the left (vs. right) side of the central fixation cross. Emotion or face recognition was not required. After 2 s, the face remained at full contrast until key press. Accuracy and reaction time were measured. There was a brief practice session, and a 1 min mid-way break.

2.2.2.5. Odor rating, discrimination, awareness. Participants were again exposed to the body odors they faced during the behavioral task, and they rated these odors (pleasantness, intensity) and discriminated between them while blindfolded. A short post-experimental debriefing questionnaire verified if participants were aware of the study's purpose (one Caucasian was excluded because of this). Post hoc, one East Asian and 13 Caucasians listed the smells as sweat/body odor.

2.2.2.6. Procedure. A female experimenter, fragrance-free and blind to the odor conditions, instructed participants. After an eye dominance test (required for the IST; Supplementary materials 1.2), the participant's face was cleaned, before EMG electrodes were applied. In-between cleaning sessions, a handedness questionnaire was completed. The experimenter then put the first jar (containing the body odor) in the adjustable clamp attached to the head-and-chin rest. This jar was opened after IST instructions, while at the same time a nose clip (preventing preliminary sniffs) was removed from participants' noses; this exact moment of odor exposure was determined by a camera. While being exposed to the odor, participants first looked at a fixation cross for 5 s (critical EMG window). Then, the IST started. This sequence was repeated six times (~4 min each; 5 min odor wash-out), with each counterbalanced odor (fear, happy, neutral) being presented twice. Finally, olfactory sensory tests and debriefing questions were administered.

2.2.3. Statistical analysis

Following our pre-registered analysis plan (osf.io/d2pv3) and prior research (e.g., de Groot et al., 2015a), EMG analysis concerned the first five seconds of EMG activity (per 200 ms) after nose clip removal; this was right before the start of the IST. EMG endpoints included per muscle the mean, standard deviation, peak, and time to peak activity.

Prior to EMG analysis, artifacts were removed (Supplementary materials 1.3.1) and data were prepared for confirmatory and exploratory discriminant analysis (DA) following prior procedures (de Groot et al.,

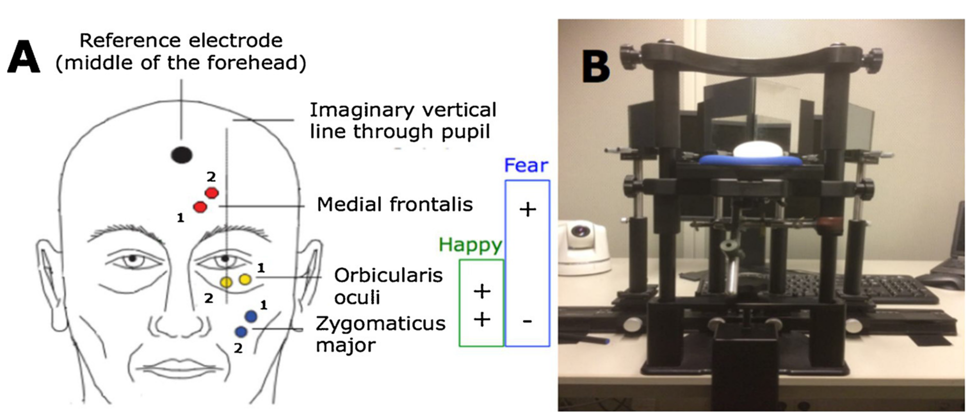

Fig. 1. (**A**) EMG recording sites (and muscle activity related to emotion). (**B**) Experiment set-up.

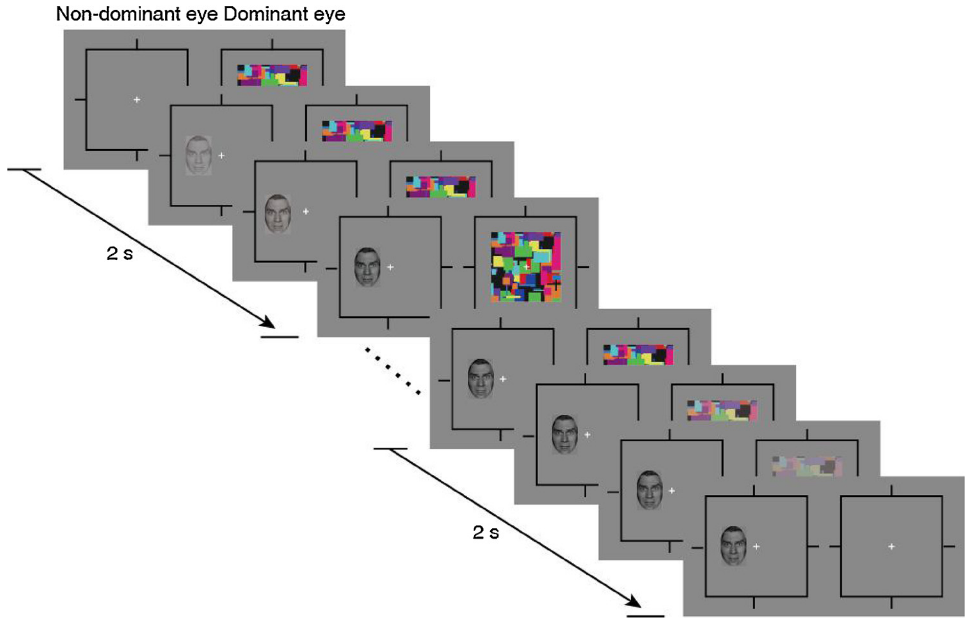

Fig. 2. IST exemplar trial.

2015a; osf.io/d2pv3): (i) all data were natural log-transformed; (ii) a baseline (600 ms) was subtracted from each following data point (600-5,000 ms; 200 ms increments) per muscle, per body odor condition, per exposure round; (iii) data were mean-centered around zero per participant across conditions to account for individual differences in facial EMG activity. The *confirmatory* part entailed classifying participants' EMG responses into fear vs. neutral, fear vs. happy, happy vs. neutral, based on *the exact same* EMG parameters that significantly discriminated odor conditions in prior research (see Table S4). However, as "confirmatory" EMG parameters were based on a single study sample, unconstrained (exploratory) stepwise DA was also performed to identify parameters that *best* classified responses into odor conditions for East Asians and Western Caucasians separately. DA does not pre-suppose a well-defined model and endpoint, and is preferred over general linear models (GLMs) when making unbiased *observations* in our first attempt to separate East Asians' EMG responses to emotion-related body odors.

Model adequacy was assessed via leave-one-out cross-validation (LOO-CV). This unbiased approach sequentially omits each participant's response and then repeats DA to verify the classification accuracy of the omitted case. LOO-CV should offer reassurance that discriminant models were not driven by an influential subset of observations. Classification outcomes were again assessed with a binomial test, which compared to chance (.25) the proportion of receivers for whom *both responses* (i.e., to fear *and* happy odor; fear *and* neutral odor; happy *and* neutral odor) were correctly classified (e.g., into fear and happy, et cetera), with *each* response having a 50% chance of being correctly classified (hence: $.50 \times .50 = .25$ chance proportion). Because DA may classify responses based on parameters that may not be intelligible from theory, we also inspected patterns of mean facial muscle activity to reflect fearful/happy expressions.

Details about IST pre-processing, subject exclusion, and analysis, can be found in the Supplementary method (1.3.2).

3. Results

Before testing whether East Asian *receivers* emulated the sender's emotion, we first assessed emotion induction effectiveness in *senders*, based on their self-reported feelings and sweat production. Because sampling location (the Netherlands, China) did not affect the results, this factor was collapsed.

3.1. Part 1: senders

A non-parametric Friedman test yielded significant effects of emotion induction (fear, happy, neutral) on self-reported fear, $\chi^2(2, N = 24) = 32.00$, $p < .001$; happiness, $\chi^2(2, N = 24) = 33.60$, $p < .001$; and calmness, $\chi^2(2, N = 24) = 15.10$, $p = .001$. Planned Wilcoxon signed-rank tests supported our hypotheses (cf. de Groot et al., 2015a): (i) fear was experienced more in the fear condition compared to the happy condition, $Z = 3.62$, $p < .001$, $r = .52$, *and* neutral condition, $Z = 3.62$, $p < .001$, $r = .52$ (happy-neutral: $Z = 0$) (Fig. 3A); (ii) happiness was experienced more in the happy condition versus the fear condition, $Z = 4.23$, $p < .001$, $r = .61$, *and* neutral condition, $Z = 3.83$, $p < .001$, $r = .55$ (neutral-fear: $Z = 2.20$, $p = .027$); and (iii) calmness was higher in the neutral condition (vs. fear), $Z = 3.05$, $p = .002$, $r = .44$, and in the happy condition (vs. fear), $Z = 3.22$, $p = .001$ (neutral-happy: $Z < 1$). Because (i) males may underreport their fear on direct self-report questions (Jansz et al., 2000; Pierce and Kirkpatrick, 1992), and (ii) 30 min movies could induce a mix of calmness, happiness, and fear, we examined (i) additional fear-related indicators of negative arousal (affective circumplex), and (ii) overall arousal/valence (affect grid), next to overall objective physiological arousal (sweat production).

Analyses on feelings mapping on the affective circumplex (Fig. 3B; Supplementary results 2.1.2) painted a complimentary picture for the fear condition ("tense", "nervous"), happy condition ("content", "elated"), and neutral condition (less "excited", less "alert"). Moreover, non-targeted discrete states (e.g., disgust, anger, sadness) did not vary across conditions (Fig. 3A; Table S1). Another Friedman test on *core affect* experience yielded significant effects for both valence, $\chi^2(2, N = 24) = 22.35$, $p < .001$, and arousal, $\chi^2(2, N = 24) = 24.09$, $p < .001$ (Fig. 3C). Whereas happiness induction evoked more positive feelings than both the fear, $Z = 3.74$, $p < .001$, $r = .54$, and neutral condition, $Z = 3.47$, $p = .001$, $r = .50$ (fear-neutral: $Z < 1$), the fear condition was most arousing (vs. happy, $Z = 2.06$, $p = .039$, $r = .30$; vs. neutral, $Z = 4.04$, $p < .001$, $r = .58$), followed by happy, and then neutral (happy-neutral: $Z = 3.35$, $p = .001$, $r = .48$).

As expected (cf. de Groot et al., 2015a), senders induced to be fearful *and* happy also produced more sweat than in the neutral condition (fear-neutral: $Z = 4.00$, $p < .001$, $r = .58$, happy-neutral: $Z = 3.47$, $p = .001$, $r = .50$ (happy-fear: $Z < 1$), $\chi^2(2, N = 24) = 16.23$, $p < .001$ (Fig. 3D). Because ambient temperature

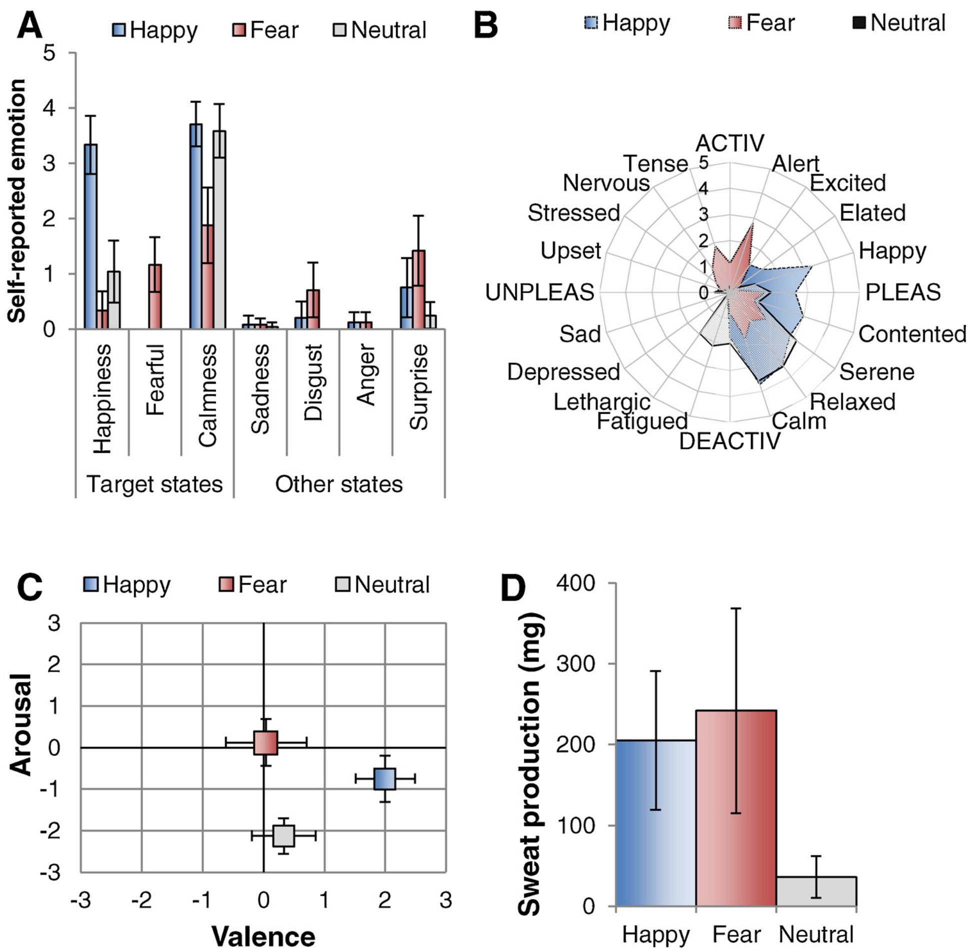

Fig. 3. Mean scores of sweat donors (N = 24) on (non-)subjective indicators of experienced affect per emotion induction condition (happy, fear, neutral). Error bars: 95% confidence interval (CI) based on the standard error of the mean (SEM). (**A**) Self-reported feelings (scale: 0–5); (**B**) Feelings on affective circumplex (scale: 0–5); (**C**) Feelings of core affect; (**D**) Sweat production (mg).

did not differ between conditions (fear: M = 23.1 °C; SD = 0.18; happy: M = 23.2 °C; SD = 0.16; neutral: M = 23.1 °C; SD = 0.16), $\chi^2(2, N = 24) = 2.33$, p = .31, the differences in sweat production can arguably be ascribed to changes in physiological arousal accompanying experienced fear and happiness.

Overall, even without additional indicators of physiological arousal (e.g., heart rate), the combined results (self report, sweat production) show that emotion induction was largely effective.

3.2. Part 2: receivers

3.2.1. Facial EMG

First, successful chemosensory communication of fear and happiness was inferred from receivers' facial expressions. Facial EMG data were subjected to discriminant analysis (DA) per ethno-cultural group (East Asians, Western Caucasians), using (i) the exact same "confirmatory" models that best discriminated between body odor conditions in prior Caucasian-based research (de Groot et al., 2015a), and (ii) unconstrained "exploratory" models that provided the best fit to the *current* data. Before reporting on model performance (Section 3.2.1.2), we document first whether confirmatory and exploratory models yielded mean facial muscle activity in line with our predictions. Since EMG responses did not meaningfully change on the second round of odor exposure (see Supplementary results, 2.2.2), and since comparable research used a single odor exposure (e.g., de Groot et al., 2015a), we focus on EMG responses following the first odor exposure.

3.2.1.1. Patterns of mean muscle activity

3.2.1.1.1. Fear vs. Happy. Confirmatory DA classifying receivers' EMG data into fear vs. happy revealed, as expected, that higher zygomaticus and orbicularis activity (i.e., a genuine smile) was characteristic of "happy" for *both* East Asians (zygomaticus, happy: M = .16, SE = .04; fear: M = -.17, SE = .04; orbicularis, happy: M = .16, SE -.04; fear: M = -.11, SE = .04) *and* Caucasians (zygomaticus, happy: M = .01, SE = .04; fear: M = -.03, SE = .02; orbicularis, happy: M = .08, SE = .05; fear: M = -.04, SE = .04) (Fig. 4). Furthermore, "happy" responses were characterized by a slowed orbicularis peak for East Asians, a fast zygomaticus peak for Caucasians, and higher orbicularis peaks for both groups (Tables S6-17). Also, East Asians' higher peak frontalis activity was classifed into "fear"; yet, potentially reflecting surprise, higher mean frontalis activity was characteristic of "happy" (vs. fear) in both East Asians (M = .02, SE = .04; vs. fear: M = -.03, SE = .05) and Caucasians (M = .04, SE = .02; vs. fear: M = -.01, SE = .03). Importantly, consistent with our predictions (Fig. 4; Table S5), and with prior research (de Groot et al., 2015a), happy odor evoked a genuine smile in both samples, regardless of their ethno-cultural differences.

Exploratory DA models fitting Western Caucasians' EMG data showed that a happy response was best characterized by high variation in frontalis activity (M = .10, SE = .03; vs. fear: M = .06, SE = .01), whereas the best predictor of East Asians' responses being classified into happy was high peak zygomaticus activity (M = .17, SE = .06; vs. fear: M = -.30; SE = .04) (for remaining exploratory DA predictor(s), if applicable, see Supplementary results 2.2.2.3).

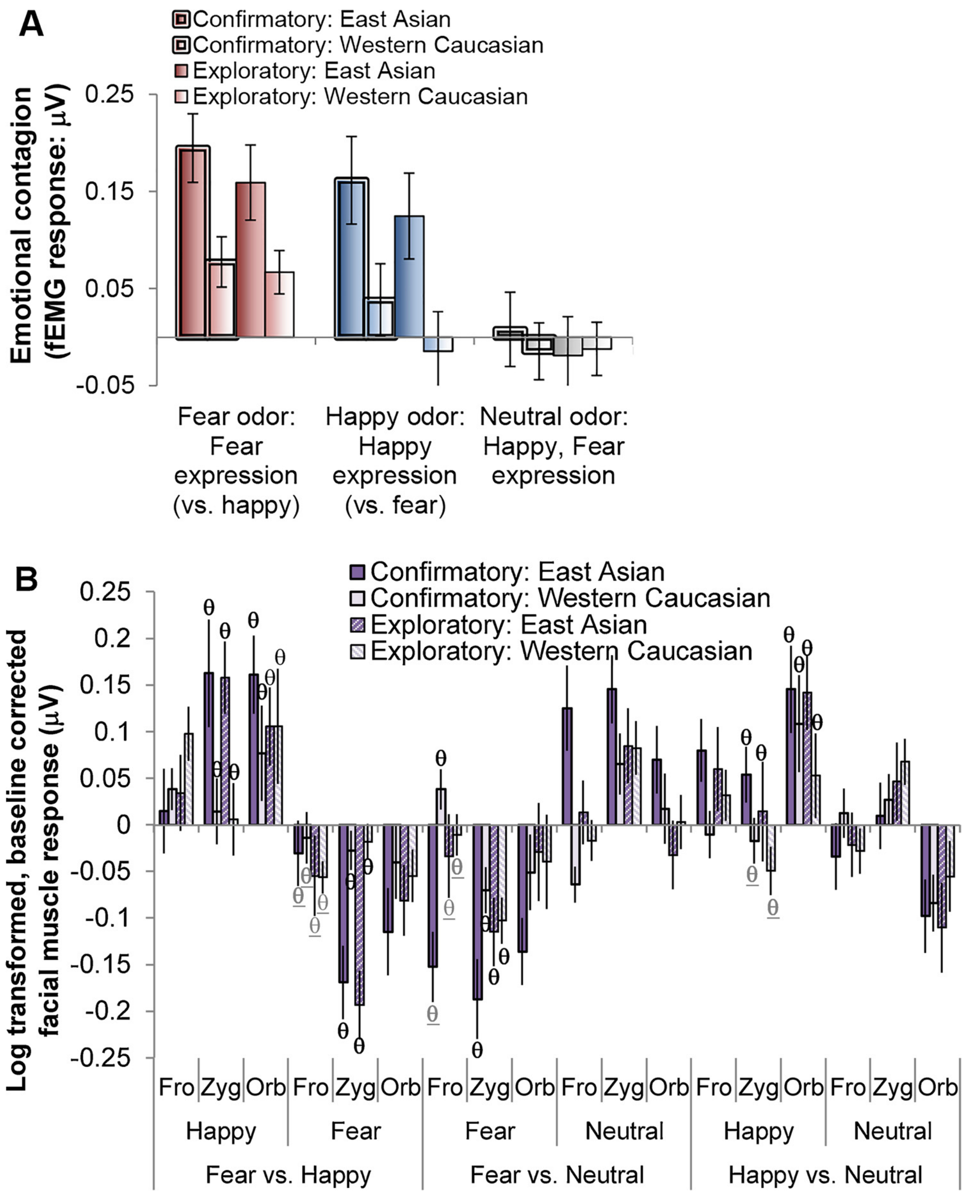

Fig. 4. Mean facial expression of East Asian and Western Caucasian receivers, as classified by confirmatory and exploratory discriminant analysis (1st odor exposure). (**A**) Fear odor evoked a stronger expression of fear (higher frontalis activity, lower zygomaticus activity) than happiness (higher zygomaticus and orbicularis activity), whereas happy odor generally evoked the opposite pattern, and neutral odor induced neither expression. Combining activity from multiple muscles more coherently shows the emotional facial expression assumed by receivers (cf. Kamiloğlu et al., 2018). (**B**) EMG activity classified by discriminant analysis per comparison pair (e.g., happy-fear). "Fro": *Medial frontalis* muscle; "Zyg": *Zygomaticus major*; "Orb": *Orbicularis oculi*. θ: Muscle activity in predicted (vs. opposite: θ) direction. Value of .1 on this scale: .1 unit (unlogged scale: e^{-1}: 11%) higher muscle activity than average across body odor conditions. Error bars: ± 1 SE.

3.2.1.1.2. Fear vs. Neutral. A confirmatory DA on EMG responses classfied into fear vs. neutral revealed partially different patterns for both samples (Fig. 4; Tables S6-11). Whereas consistent with theory, Caucasian "fear" was classified as high frontalis activity (M = .04, SE = .02; vs. neutral: M = -.06, SE = .02) and low zygomaticus activity (M = -.06, SE = .02; vs. neutral: M = .06, SE = .03), East Asian "fear" was also characterized by low zygomaticus activity (M = -.19, SE = .03; neutral: M = .15, SE = .04), next to—unexpectedly—*lower* frontalis activity (M = -.15, SE = .03; vs. neutral: M = .13, SE = .04). Arguably, whereas Caucasians *expressed* a negative affective fearful facial expression, East Asians displayed an inhibited version of this negative expression.

Exploratory models fitting Western Caucasians' muscle responses showed that fear was best characterized by low variation in zygomaticus activity (M = -.11, SE = .02; vs. neutral: M = .08, SE = .02), whereas East Asians' fear responses were best predicted by low peak zygomaticus activity (M = -.23, SE = .05; vs. neutral: M = .23, SE = .06).

3.2.1.1.3. Happy vs. Neutral. Confirmatory models classifying East Asian responses into the happy condition (vs. neutral) revealed that their responses were characterized by higher zygomaticus (M = .05, SE = .06; vs. neutral: M = .01, SE = .04) and orbicularis activity (M = .15, SE = .04; vs. neutral: M = -.10, SE = .05) (reflecting a genuine smile). Caucasians also demonstrated higher activity on the orbicularis (M = .11, SE = .05; vs. neutral: M = -.08, SE = .03), but not zygomaticus (M = -.02, SE = .02; vs. neutral: M = .03, SE = .03). However, consistent with prior Caucasian-based research (de Groot et al., 2015a), responses classified into "happy" contained high peaks and high variation in orbicularis activity (Table S6-17). For the majority part, EMG data were consistent with our predictions (Table S5).

Exploratory models classifying Western Caucasians' responses showed that happiness and neutral were best separated by high variation in frontalis activity (happy: M = .10, SE = .06; vs. neutral: M = -.05, SE = .06), whereas East Asians' happy responses were best predicted by high peak orbicularis activity (happy: M = .17, SE = .06; vs. neutral: M = -.17, SE = .05).

3.2.1.2. Discriminant model performance. Assessing DA model performance with LOO-CV showed that unconstrained exploratory models performed better in classifying EMG responses into body odor conditions (classification errors: 29–42%; cf. Table S2) than constrained

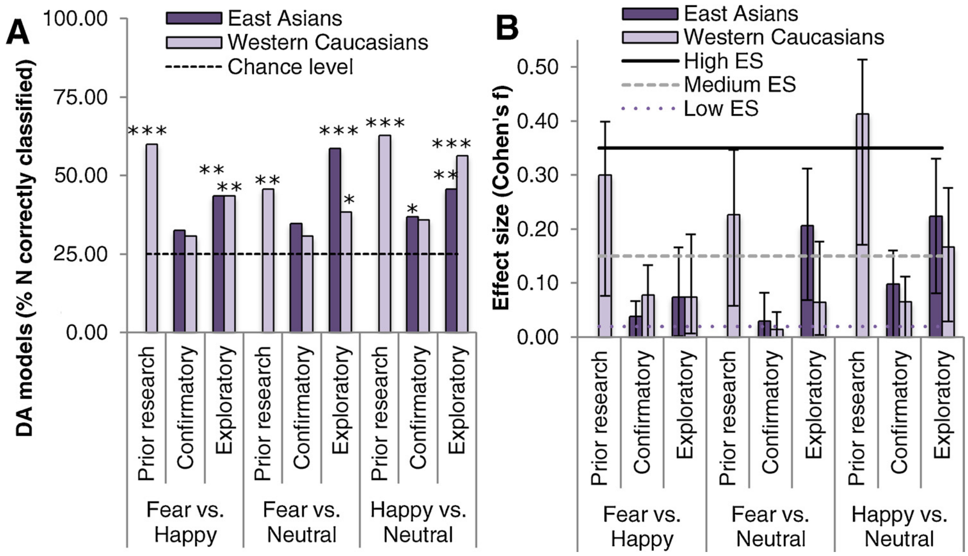

Fig. 5. Discriminant Analysis (DA) classification model performance for East Asians and Western Caucasians (1st odor exposure). "Prior research": Results of comparable prior Caucasian-based research (de Groot et al., 2015a). "Confirmatory": Constrained DA models using the exact same EMG parameters identified in de Groot et al. (2015a). "Exploratory": Unconstrained DA models following stepwise selection of *best fitting* EMG parameters based on current data (**A**) Binomial analysis, based on the percentage of receivers (vs. chance) whose facial EMG responses were correctly classified into *both* conditions by leave-one-out cross-validation (LOO-CV) (Table S3). **p* < .05, ***p* < .01, ****p* < .001. (**B**) Effect size (ES) of DA models ± 90% CI. ES ≥.02: "small"; ≥.15: "medium"; ≥.35 "large".

confirmatory models (42–54% errors). Binomial tests underlined this (Fig. 5A; Figure S2; Table S3): Whereas one confirmatory model classified East Asians' responses above chance (happy vs. neutral: $p = .048$; Western Caucasians: $p = .086$), all exploratory models (for both ethno-cultural groups) significantly discriminated between all body odors (happy-neutral: $ps \leq .002$; happy-fear: $ps \leq .005$; fear-neutral: $ps \leq .044$).

Exploratory discriminant models yielded small-to-moderate effect sizes, with CIs overlappping with prior Caucasian-based findings (Fig. 5B). Although confirmatory models' effect sizes were small at most, exploratory models showed that different body odors (fear, happy, neutral) evoked distinctive facial expressions; this counts for Western Caucasians *and* East Asians.

3.2.2. Interocular suppression

An interocular suppression task (IST) assessed whether fear odor and happy odor increased East Asians' and Western Caucasians' unconscious readiness to detect faces containing fear and happiness. The time needed for a face image to break from interocular suppression (henceforth: suppression time) served as subconscious facial affect processing index.

A mixed ANOVA was conducted on mean suppression time (RT), with within-subjects factors odor (fear, happy, and neutral), face emotion (happy, fear, and neutral), face gender (male, female), and exposure round (1st, 2nd), and between-subjects factor ethno-cultural group (East Asian, Caucasian). As there was no effect of ethno-cultural group on suppression time, $F(1, 84) = .631$, $p = .429$, $\eta_p^2 = .01$, East Asians' ($n = 43$) and Western Caucasians' ($n = 43$) data were collapsed. Aside from main effects of body odor, $F(2, 168) = 3.25$, $p = .041$, $\eta_p^2 = .04$, and face emotion, $F(2, 168) = 5.33$, $p = .007$, $\eta_p^2 = .06$ (see Supplementary results 2.2.1 for more (significant) main effects and interactions that were not of a priori interest), the interaction body odor x face emotion did not reach significance, $F(4, 336) = 1.89$, $p = .112$, $\eta_p^2 = .02$. As such, one should interpret with caution the a priori contrast (pre-registered: osf.io/d2pv3) testing the *congruency* hypothesis (one-tailed), which revealed a small-to-medium effect: Fear odor and happy odor shortened suppression times for fear faces and happy faces, respectively, $F(1, 85) = 3.31$, $p = .073$, $\eta_p^2 = .04$ (Fig. 6). Since fear is associated with heightened vigilance (e.g., de Groot et al., 2012; Low et al., 2008), we also tested a *general vigilance* hypothesis, and showed that fear odor shortened suppression times to all facial expressions, $F(1, 85) = 6.95$, $p = .010$, $\eta_p^2 = .08$. Hence, regardless of receivers' ethno-cultural background, happy body odor caused a tendency for happy faces to break from suppression faster, whereas fear odor subconsciously shortened suppression times across the board, indicating vigilance.

3.2.3. Control measures

The aforementioned social communication effects could not be attributed to the sweat's explicit hedonic features, as the three stimuli (fear, happy, neutral odor) did not differ in perceived pleasantness, $F(2, 166) = 2.44$, $p = .091$ (fear: $M = 3.54$, $SD = 1.10$; happy: $M = 3.71$, $SD = 1.28$; neutral: $M = 3.40$, $SD = 1.24$), and intensity, $F < 1$ (fear: $M = 3.28$, $SD = 1.42$; happy: $M = 3.42$, $SD = 1.38$; neutral: $M = 3.52$, $SD = 1.59$); no differences appeared between East Asians and Caucasians (pleasantness: $F(194) = 1.41$, $p = .237$; intensity: $F < 1$). All receivers were unaware of the study's hypothesis (barring one excluded participant), and odors could not be discriminated above chance (fear vs. neutral: $N = 51/85$, $p = .082$; happy vs. neutral, happy vs. fear: $N = 44/85$, $p = .828$).

4. Discussion

The present research was the first to elucidate that human chemosensory communication of fear and happiness extended beyond ethno-cultural boundaries, from Western Caucasians to East Asians. Combining facial EMG with interocular suppression, we demonstrated that *receivers* emulated the senders' fear and happiness, regardless of ethno-cultural background. East Asians' and Western Caucasians' patterns of mean EMG activity ostensibly reflected fearful and happy facial expressions following fear odor and happy odor exposure. Indeed, both groups showed significantly distinctive expressions to fear, happy, and neutral odor; yet, "confirmatory" discriminant models that *only* used EMG parameters based on prior Caucasian research (de Groot et al., 2015a) were outperformed by unconstrained data-driven models using *all* EMG parameters. Aside from modulating facial expressions, emotion-related sweat also subconsciously altered interocular suppression, with happy odor increasing the speed at which happy faces became visible (congruency effect), whereas fear odor—like before (de Groot et al., 2012, 2015b)—increased participants' detection speed across the board (vigilance effect). Since these combined effects were not driven by the sweat's intensity and pleasantness, receivers' perceptual, affective, and behavioral simulacrum of fear and happiness on this novel combination of implicit language-independent measures (facial EMG, interocular suppression) replicates and extends prior research showing the subconscious human communication of emotions via sweat (e.g., Mujica-Parodi et al., 2009; Zhou and Chen, 2009).

One notable cross-sample difference, however, is that compared to Western Caucasians, East Asians' facial response to fear odor was

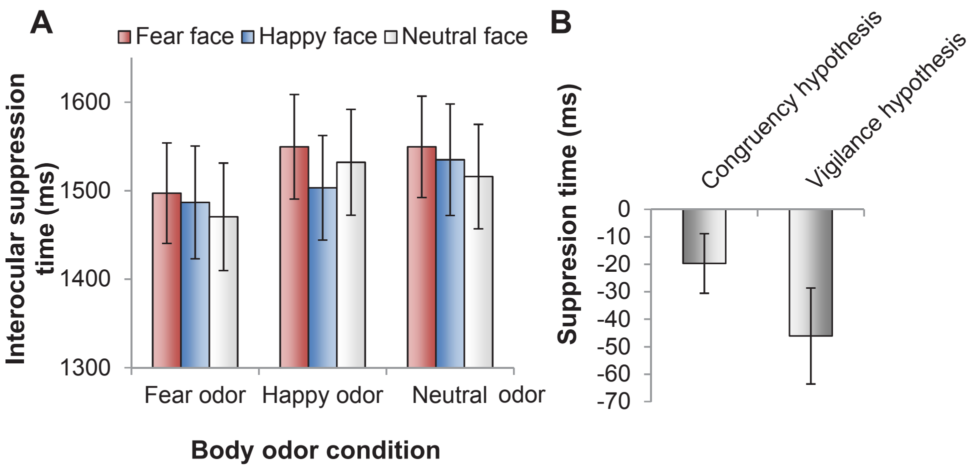

Fig. 6. Emotion-related body odor modulated visual processing in the absence of visual awareness. (**A**, **B**) Suppression times of happy (fearful) facial expressions were shorter during happy (fear) odor exposure (congruency), and suppression times of all facial expressions (fear, happy, neutral) were shorter during fear odor exposure (vigilance). Error bars represent the SEM.

characterized by *diminished* medial frontalis (and zygomaticus major) activity, which contrasts earlier Caucasian-based chemosignaling research (meta-analysis: de Groot and Smeets, 2017) and universal emotion theory. According to Darwin (1872/1998); Darwin, 1872, emotional facial expressions can be self-serving for the expresser, by preparing organisms for perception and action. For example, a fearful facial expression involves lifting the eyebrow (i.e., medial frontalis activity), which increases one's visual field size to better detect threat (Susskind et al., 2008). For East Asians, however, this arguably pre-wired self-serving emotional facial expression might have been overridden by cultural norms dictating *emotion moderation* (e.g., Kitayama et al., 2000; Klineberg, 1938; Potter, 1988; Tsai and Levenson, 1997). Since visible negative emotions can be disruptive to *social harmony*, another valued trait in the East (Soto et al., 2005), East Asians' expression to fear odor may instead have assumed a more restrained form. Being socially visible emotion indicators, facial expressions thus formed a window through which cross-cultural differences in emotion display were observed. Notably, our socially invisible measure of subconscious affect (interocular suppression) indicated that fear odor induced vigilance in *all* receivers, regardless of ethno-cultural group, converging with literature showing that restrained *expressions* do not automatically imply the dampening of emotion *experience* (e.g., Tsai et al., 2006; review: Levenson et al., 2007).

Data-driven discriminant analysis (DA) was combined with the inspection of patterns of mean facial muscle activity. This approach allowed us to show not only that the different samples (East Asians, Western Caucasians) showed discriminable facial muscle responses to fear, happy, and neutral odor, but also that these expressions involved facial muscles that were understandable from theory (fear: higher medial frontalis activity, and lower zygomaticus activity; happiness: higher zygomaticus, and higher orbicularis activity). Although previous research on emotion chemosignaling almost exclusively used general linear modeling (GLM; e.g., Zhou and Chen, 2009), this research—like the most comparable Western-Caucasian based research (de Groot et al., 2015a)—used DA to make *unbiased* observations on our first attempt to separate East Asians' EMG responses into categories of happiness, fear, and neutral. The advantage of DA over GLM is that DA does not present an unduly favorable set of outcomes, as DA does not pre-suppose a well-defined model and endpoint for both ethno-cultural groups. A downside of this approach is our inability to compare whether East Asians' responses were stronger than those of Western Caucasians, which was not our primary goal: We wanted to observe the presence or absence of a chemosensory communication capacity in both samples. To verify whether our data-driven results fitted theory-based predictions, we combined DA with theory-driven inspection of patterns of mean facial EMG activity following fear, happy, and neutral odor exposure.

A limitation of our work is the lack of control over the sweat stimuli. Despite using well-validated procedures and materials from prior research (de Groot et al., 2015a), different donors enrolled in the current study, with different appraisals of the video clips meant to induce fear, happiness, and a neutral state. Whereas donors did produce more sweat in the fear condition, some reported relatively low amounts of fear (yet, they could have underreported their fear: Jansz et al., 2000; Pierce and Kirkpatrick, 1992). We mitigated inter-individual variance in (fear) sweat production by presenting receivers with sweat stimuli pooled over four different donors. Despite our relative lack of control over the odor stimulus, receivers showed remarkable consistencies in emulating the senders' emotions in terms of behavior, affect, and perception.

By demonstrating that the chemosensory communication of emotions extended beyond Western Caucasians, this research seemingly hints at species-wide human chemosensory communication that is largely learning-independent; yet, at present, we cannot rule out alternative mechanisms. For instance, East Asians may have learned an olfactory emotion signature from being exposed to a minority of (G/A- or G/G-genotyped) East Asians' or Western Caucasians' body odor (we could not verify this), or there may be an olfactory emotion signature in A/A-genotyped sweat, despite this variant causing a different/weaker armpit odor (Harker et al., 2014; Yoshiura et al., 2006). Future research could explore similarities in the *production* and *perception* of various emotion-related body odors of A/A (vs. G/A, G/G) genotyped individuals, and could extend our findings to yet different ethno-cultural groups, using additional indicators of emotion (e.g., skin conductance, heart rate, avoidance behavior) to assess general expressiveness. These issues were outside the scope of the current research, but they form important building blocks to advance our understanding of human chemosensory communication, and its scale.

5. Conclusion

The capacity to emulate emotions based on another person's body odor had already been shown for Western Caucasians; yet, the present research elucidated a similar prowess in an ethno-culturally different group of East Asians, a finding that contributes to one of the most compelling puzzles facing scientists today (Kennedy and Norman, 2005), by assessing the *scale* of human chemosensory communication.

Conflict of interest

The authors have no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.psyneuen.2018.08.005.

References

Brainard, D.H., 1997. The psychophysics toolbox. Spat. Vision 10, 433–436.
Brand, G., Millot, J.-L., 2001. Sex differences in human olfaction: between evidence and enigma. Q. J. Exp. Psychol. B 54, 259–270.
Chen, D., Haviland-Jones, J., 2000. Human olfactory communication of emotion. Percept. Mot. Skills 91, 771–781.
Cohen, J.E., 1988. Statistical Power Analysis for the Behavioral Sciences. Lawrence Erlbaum Associates, Hillsdale, NJ.
Darwin, C. (1872/1998). The Expression of the Emotions in Man and Animals, Oxford University Press, New York.
de Groot, J.H.B., Smeets, M.A.M., 2017. Human fear chemosignaling: evidence from a meta-analysis. Chem. Senses 42, 663–673.
de Groot, J.H.B., Smeets, M.A.M., Kaldewaij, A., Duijndam, M.J.A., Semin, G.R., 2012. Chemosignals communicate human emotions. Psychol. Sci. 23, 1417–1424.
de Groot, J.H.B., Semin, G.R., Smeets, M.A.M., 2014. Chemical communication of fear: a case of male–female asymmetry. J. Exp. Psychol. Gen. 143, 1515–1525.
de Groot, J.H.B., Smeets, M.A.M., Rowson, M.J., Bulsing, P.J., Blonk, C.G., Wilkinson, J.E., Semin, G.R., 2015a. A sniff of happiness. Psychol. Sci. 26, 684–700.
de Groot, J.H.B., Smeets, M.A.M., Semin, G.R., 2015b. Rapid stress system drives chemical transfer of fear from sender to receiver. PLoS ONE 10, e0118211.
de Groot, J.H.B., Semin, G.R., Smeets, M.A.M., 2017. On the communicative function of body odors: a theoretical integration and review. Perspect. Psychol. Sci. 12, 306–324.
Dimberg, U., Petterson, M., 2000. Facial reactions to happy and angry facial expressions: evidence of right hemisphere dominance. Psychophysiology 37, 693–696.
Ekman, P., Friesen, W., 1976. Pictures of Facial Affect. Consulting Psychologists Press, Palo Alto.
Ekman, P., Friesen, W.V., Hager, J.C., 2002. Facial Action Coding System Investigator's Guide, A Human Face, Salt Lake City.
Fridlund, A.J., Cacioppo, J.T., 1986. Guidelines for human electromyographic research. Psychophysiol. 23, 567–589.
Harker, M., 2013. Psychological sweating: a systematic review focused on aetiology and cutaneous response. Skin Pharmacol. Physiol. 26, 92–100.
Harker, M., Carvell, A.M., Marti, V.P.J., Riazanskaia, S., Kelso, H., Taylor, D., Grimshaw, S., Arnold, D.S., Zillmer, R., Shaw, J., Kirk, J.M., Alcasid, Z.M., Gonzales-Tanon, S., Chan, G.P., Rosing, E.A.E., Smith, A.M., 2014. Functional characterisation of a SNP in the ABCC11 allele-Effects on axillary skin metabolism, odour generation and associated behaviours. J. Dermatol. Sci. 73, 23–30.
Haze, S., Gozu, Y., Nakamura, S., Kohno, Y., Sawano, K., Ohta, H., Yamazaki, K., 2001. 2-Nonenal newly found in human body odor tends to increase with aging. J. Invest. Dermatol. 116, 520–524.
Henrich, J., Heine, S.J., Norenzayan, A., 2010. Beyond WEIRD: towards a broad-based behavioral science. Behav. Brain Sci. 33, 111–135.
Hummel, T., Sekinger, B., Wolf, S.R., Pauli, E., Kobal, G., 1997. 'Sniffin' sticks': olfactory performance assessed by the combined testing of odor identification, odor discrimination and olfactory threshold. Chem. Senses 22, 39–52.
Jansz, J., 2000. Masculine identity and restrictive emotionality. In: Fischer, A.H. (Ed.), Gender and Emotion: Social Psychological Perspectives. University Press, Cambridge, pp. 166–186.
Kamiloğlu, R.G., Smeets, M.A.M., de Groot, J.H.B., Semin, G.R., 2018. Fear odor facilitates the detection of fear expressions over other negative expressions. Chem. Senses 43, 419–426.
Kennedy, D., Norman, C., 2005. So much more to know. Science 309, 78–102.
Kitayama, S., Markus, H.R., Kurokawa, M., 2000. Culture, emotion, and well-being: good feelings in Japan and the United States. Cogn. Emot. 14, 93–124.
Klineberg, O., 1938. Emotional expression in Chinese literature. J. Abnorm. Soc. Psych. 33, 517–520.
Kuhn, F., Natsch, A., 2008. Body odour of monozygotic human twins: a common pattern of odorant carboxylic acids released by a bacterial aminoacylase from axilla secretions contributing to an inherited body odour type. J. R. Soc. Interface 6, 377–392.
Le Guérer, A., 2002. Olfaction and cognition: a philosophical and psychoanalytic view. In: Rouby, C., Schaal, B., Dubois, D., Gervais, R., Holley, A. (Eds.), Olfaction, Taste and Cognition. Cambridge University Press, UK, pp. 3–15.
Levenson, R.W., Soto, J.A., Pole, N., 2007. Emotion, biology, and culture. In: Kitayama, S., Cohen, D. (Eds.), Handbook of Cultural Psychology. Guilford, New York, pp. 780–796.
Low, A., Lang, P.J., Smith, J.C., Bradley, M.M., 2008. Both predator and prey: emotional arousal in threat and reward. Psychol. Sci. 19, 865–873.
Martin, A., Saathoff, M., Kuhn, F., Max, H., Terstegen, L., Natsch, A., 2010. A functional ABCC11 allele is essential in the biochemical formation of human axillary odor. J. Invest. Dermatol. 130, 529–540.
McGann, J.P., 2017. Poor human olfaction is a 19th-century myth. Science 356 eaam7263.
Mujica-Parodi, L.R., Strey, H.H., Frederick, B., Savoy, R., Cox, D., Botanov, Y., Tolkunov, D., Rubin, D., Weber, J., 2009. Chemosensory cues to conspecific emotional stress activate amygdala in humans. PLoS ONE 4, e6415.
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.
Olsson, M.J., Lundstrom, J.N., Kimball, B.A., Gordon, A.R., Karshikoff, B., Hosseini, N., Sorjonen, K., Hoglund, C.O., Solares, C., Soop, A., Axelsson, J., Lekander, M., 2014. The scent of disease: human body odor contains an early chemosensory cue of sickness. Psychol. Sci. 25, 817–823.
Pause, B.M., Ohrt, A., Prehn, A., Ferstl, R., 2004. Positive emotional priming of facial affect perception in females is diminished by chemosensory anxiety signals. Chem. Senses 29, 797–805.
Pelli, D.G., 1997. The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat. Vision 10, 437–442.
Penn, D.J., Oberzaucher, E., Grammer, K., Fischer, G., Soini, H.A., Wiesler, D., Novotny, M.V., Dixon, S.J., Xu, Y., Brereton, R.G., 2007. Individual and gender fingerprints in human body odour. J. R. Soc. Interface 4, 331–340.
Pierce, K.A., Kirkpatrick, D.R., 1992. Do men lie on fear surveys? Behav. Res. Ther. 30, 415–418.
Russell, J.A., 1980. A circumplex model of affect. J. Pers. Soc. Psychol. 39, 1161–1178.
Russell, J.A., Weiss, A., Mendelsohn, G.A., 1989. Affect grid: a single-item scale of pleasure and arousal. J. Pers. Soc. Psychol. 57, 493–502.
Soto, J.A., Levenson, R.W., Ebling, R., 2005. Cultures of moderation and expression: emotional experience, behavior, and physiology in Chinese Americans and Mexican Americans. Emotion 5, 154–165.
Steptoe, A., Wardle, J., Marmot, M., 2005. Positive affect and health-related neuroendocrine, cardiovascular, and inflammatory processes. Proc. Nat. Acad. Sci. USA 102, 6508–6512.
Stevenson, R.J., 2010. An initial evaluation of the functions of human olfaction. Chem. Senses 35, 3–20.
Susskind, J.M., Lee, D.H., Cusi, A., Feiman, R., Grabski, W., Anderson, A.K., 2008. Expressing fear enhances sensory acquisition. Nat. Neurosci. 11, 843–850.
Tsai, J.L., Levenson, R.W., 1997. Cultural influences on emotional responding Chinese American and European American dating couples during interpersonal conflict. J. Cross. Psychol. 28, 600–625.
Tsai, J.L., Levenson, R.W., McCoy, K., 2006. Cultural and temperamental variation in emotional response. Emotion 6, 484–497.
Tsuchiya, N., Koch, C., 2005. Continuous flash suppression reduces negative afterimages. Nat. Neurosci. 8, 1096–1101.
Wolfensberger, M., Schnieper, I., Welge-Lüssen, A., 2000. Sniffin'Sticks: a new olfactory test battery. Acta Otolaryngol. 120, 303–306.
Wudarczyk, O.A., Kohn, N., Bergs, R., Goerlich, K.S., Gur, R.E., Turetsky, B., Schneider, F., Habel, U., 2016. Chemosensory anxiety cues enhance the perception of fearful faces–An fMRI study. NeuroImage 143, 214–222.
Yoshiura, K.I., Kinoshita, A., Ishida, T., Ninokata, A., Ishikawa, T., Kaname, T., et al., 2006. A SNP in the ABCC11 gene is the determinant of human earwax type. Nat. Genet. 38, 324–330.
Zhou, W., Chen, D., 2009. Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. Psychol. Sci. 20, 177–183.
Zhou, W., Jiang, Y., He, S., Chen, D., 2010. Olfaction modulates visual perception in binocular rivalry. Curr. Biol. 20, 1356–1358.
Zhou, W., Zhang, X., Chen, J., Wang, L., Chen, D., 2012. Nostril-specific olfactory modulation of visual perception in binocular rivalry. J. Neurosci. 32, 17225–17229.