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ORIGINAL ARTICLE

Embracing your emotions: affective state impacts lateralisation of human embraces

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Abstract

Humans are highly social animals that show a wide variety of verbal and non-verbal behaviours to communicate social intent. One of the most frequently used non-verbal social behaviours is embracing, commonly used as an expression of love and affection. However, it can also occur in a large variety of social situations entailing negative (fear or sadness) or neutral emotionality (formal greetings). Embracing is also experienced from birth onwards in mother–infant interactions and is thus accompanying human social interaction across the whole lifespan. Despite the importance of embraces for human social interactions, their underlying neurophysiology is unknown. Here, we demonstrated in a well-powered sample of more than 2500 adults that humans show a significant rightward bias during embracing. Additionally, we showed that this general motor preference is strongly modulated by emotional contexts: the induction of positive or negative affect shifted the rightward bias significantly to the left, indicating a stronger involvement of right-hemispheric neural networks during emotional embraces. In a second laboratory study, we were able to replicate both of these findings and furthermore demonstrated that the motor preferences during embracing correlate with handedness. Our studies therefore not only show that embracing is controlled by an interaction of motor and affective networks, they also demonstrate that emotional factors seem to activate right-hemispheric systems in valence-invariant ways.

Introduction

Human social interaction can be conducted either verbally or non-verbally, for example, by gestures, facial expressions or touch (Forsell, & Åström, 2012). Tactile forms of human social interaction include kisses, handshakes, high fives and embraces. Embraces are particularly interesting as they are used in a wide variety of social situations, the main one being the expression of love or affection. In addition, they are also used in situations such as neutral greetings, embracing people out of joy, as well as offering consolation to other persons in times of sadness, disappointment or fear. It can therefore be observed in diverse emotional contexts covering the whole spectrum from extremely negative to exceptionally positive mental states.

Since embraces are commonly used in emotional situations, it can be assumed that the neuronal circuits involved in processing of emotion might also be involved in embracing. The processing of emotional content is lateralised within the brain, albeit not nearly as strongly as speech or handedness (Corballis, 2014; Friederici, 2011; Ocklenburg, & Güntürkün, 2017). In neuroscientific research, four major theories have emerged regarding the lateralisation of emotion processing, namely the "Right-Hemisphere hypothesis (RHH)", the "Valence-Specific hypothesis (VSH)", the "Approach Withdrawal hypothesis (AWH)" and the "Behavioral Inhibition System and Behavioral Activation System model (BIS/BAS)". As embraces always involve approach and behavioural activation, no differential predictions can be made using the AWH and BIS/BAS models to investigate lateralised emotional processing in the brain. We will

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therefore focus on the RHH and VSH in particular as specific predictions can be derived from both of these models. The RHH postulates a general rightward lateralisation of emotional processing within the brain, regardless whether the emotion has positive or negative valence (Demaree, Everhart, Youngstrom, & Harrison, 2005). Evidence supporting this approach stems from behavioural (Adolphs, Damasio, Tranel, & Damasio, 1996; Ley, & Bryden, 1979), electrophysiological (Kestenbaum, & Nelson, 1992; Laurian, Bader, Lanares, & Oros, 1991) and neuroimaging studies (Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004). The VSH hypothesis proposed a differential processing pattern of the two hemispheres within the human brain. Specifically, it assumes that the left hemisphere is responsible for positive emotions, whereas the right hemisphere computes negative emotions (Ahern, & Schwartz, 1979). As for the RHH, there is also a large body of evidence supporting the VSH (Davidson, & Fox, 1982; Dolcos, LaBar, & Cabeza, 2004; Silberman, & Weingartner, 1986). At their core, these theories are mutually exclusive and the investigation of lateralised embracing can shed light on the accuracy of these theories as they make different predictions under the assumption that the lateralisation of embracing is influenced by its emotional context. This idea is supported by the fact that other motor behaviours are influenced by the emotional context in which they occur. These behaviours include posing for pictures. It has been found that English academics who wish to be perceived as emotional show a stronger leftward cheek bias when posing for pictures than academics in the sciences who wish to be perceived as non-emotional rationalists (Churches et al., 2012). Moreover, it has been shown that for kissing, subjects show a right-turn bias for romantic kissing, but a left-turn bias for non-romantic parental kissing (Sedgewick, & Elias, 2016). Context dependent effects have also been observed for laterality in seat choice (Harms, Reese, & Elias, 2014; Harms, Poon, Smith, & Elias, 2015). Based on these findings, it can be predicted that embracing direction may also depend on the emotional context. In this case, the RHH would predict a general shift of embracing towards the left side in emotional conditions compared to a neutral context. The VSH on the other hand would predict a differential pattern based on the type of affect. In positive situations, embraces would be more right-side oriented, whereas negative situations would demonstrate a more left-sided bias compared to the neutral embrace. As motor lateralisation and other cognitive functions including emotions are deeply intertwined, it raises the question if the emotional context can influence the choice side of an embrace in accordance to either of the stated theories.

As embracing involves a coordinated motor response from the arms (one arm encloses the other person first), it could be potentially determined by handedness, a phenotype that is lateralised on the population level (Ocklenburg, Beste, & Güntürkün, 2013). Therefore, embracing could also be a lateralised behaviour, driven by an asymmetrical motor bias. In humans, Turnbull, Stein, and Lucas (1995) investigated human embracing in both a natural observation study and a laboratory study. In the natural observation study, the authors observed 321 embraces in the arrivals lounge of an international airport. They found a significant rightward bias for female–female embraces ($n = 114$) and female–male embraces ($n = 174$), but not for male–male embraces ($n = 33$). However, since the sample size in this condition was significantly smaller than in the other two conditions, these results are somewhat difficult to interpret. Moreover, Turnbull at al. (1995) conducted a laboratory study in which they asked biology first year students to embrace their neighbour in a laboratory practical. Overall, they observed 41 embraces (14 female–female, 14 female–male and 13 male–male). They found a significant rightward bias in the female–female condition, but not in the other two. Furthermore, they did not find an association of handedness and embracing laterality in their laboratory sample. These nonsignificant results might potentially be, however, due to small sample sizes and therefore low statistical power. Thus, the study of Turnbull et al. (1995) at least partly supports the idea that there might be a rightward bias in human embracing. Due to the small sample size, particularly in the laboratory study, replication in a larger sample is needed before any final conclusions can be drawn. Additionally, the study did not systematically assess emotional valence of embraces, which might be a critical factor when taking the aforementioned literature on the effects of emotional context on motor laterality into account. Lateralisation of embraces has also been investigated in non-human primates. Boeving, Belnap, and Nelson (2017) investigated embraces, face-embraces (a face only embrace using no hands to touch the other conspecific) and grooming behaviour in spider monkeys (*Ateles fusciceps rufiventris)* and discovered a significant left-side lateralisation both for embraces and face-embraces.

Moreover, another form of physical social behaviour has been shown to be lateralised, namely kissing. Güntürkün (2003) reported that 64.5% of the subjects favoured a right-sided kiss between partners, a ratio that does not reflect the distribution of handedness in the population indicating potential emotional influence. A follow-up study by Ocklenburg and Güntürkün (2009) found that head-turning biases were roughly the same with 62% of the participants kissing to the right when kissing a mannequin. Importantly, kissing laterality is modulated by emotional context, as subjects show a right-turn bias for romantic kissing but a left-turn bias for non-romantic parental kissing (Sedgewick, & Elias, 2016). As kissing and hugging are two behaviours that often occur together, this finding argues strongly for the idea that also embracing lateralisation might be influenced

by emotional context. Additionally to kissing, mother–infant social behaviour has also shown to be lateralised in humans, but also in various other mammalian species. Karenina, Giljov, Ingram, Rowntree, and Malashichev (2017) showed that there is a consistent leftward bias in mother–infant interactions, indicating right hemisphere dominance for social processing in mother–infant situations.

To examine the role of emotional context in human embracing interaction and to dissociate between the RHH and VSH, we devised two consecutive experiments, a field and a laboratory study, in which we observed embraces when people were subjected to either neutral, negative or positive emotions. Based on the literature on handedness and emotional lateralisation, three different predictions can be made for the outcome of our experiments: (1) if handedness is determining embracing preference, participants should show a rightward embracing preference in all three emotional contexts and emotionality should have no effect. (2) The RHH of emotional lateralisation predicts that participants should show a more leftward bias in positive and negative emotional contexts compared to an emotionally neutral context. (3) If the VSH of emotional lateralisation could explain the effect of emotional context on embracing preferences, participants should show a more rightward bias for positive and a more leftward bias for negative contexts compared to an emotionally neutral context.

Experiment 1: field experiment

Methods experiment 1

Participants

In the field experiment, 2530 participants were observed during embraces in public places. The sample size was determined based on a field study investigating lateralisation of cheek kissing in major French cities (Chapelain, Pimbert, Aube, Perrocheau, Debunne, Bellido, & Blois-Heulin, 2015). In this study, the authors used on average 550 participants per city to measure their desired effects. We therefore aimed to record similar amounts of observations per condition.

Procedure and materials

For the positive and negative emotional contexts, observations took place at a large German airport. We monitored embracing both at the gate entries for departure (938 observations) and the terminals for arrival (1063 observations). The departure of a familiar person to a different country is likely to induce a more negative connoted emotionality, whereas the arrival after a longer stay abroad can be assumed to be associated with positive emotions of reunion. For that reason, we focused on international flights in case of the arrival condition. For departure, this dissociation could not be made as there is no clear indication of travel destination at the gate entry. It is, however, still very likely that embraces occur much more often for emotional farewells rather than for short-distance travels. Furthermore, aviophobia is an extremely common phenomenon in the general population. Representative surveys have shown that up to 38% of people suffer from fear or discomfort during flying (Institute for Demoscopy Allensbach, 2003; Van Gerwen, Spinhoven, & Van Dyck, 1997; Van Gerwen, & Diekstra, 2000). This negative emotional state is not only present during the flight itself, but also prior to boarding (Ekeberg, Seeberg, & Ellertsen, 1989). After landing, as the passengers are on safe grounds again, the relief of the anxious state leads to a positive feeling as well. When combined, the emotional state of people both at arrival and departure can be estimated to be positive or negative, respectively.

For the neutral condition, we systematically analysed YouTube videos of people blindfolding themselves in public asking to be embraced by any pedestrian walking by. The following search terms were used on http://www.youtube.com to identify possibly relevant videos: “blindfold hug”, “blindfold embrace” and “blindfold trust experiment”. This resulted in more than 4000 hits. The experimenters then watched the videos starting with the initial hits and then continued using related links to similar videos. Data collection was aborted after a number of embraces had been collected that was sufficient for data analysis.

Overall, 29 videos were analysed by two observers yielding a number of 529 valid data points. The length of the videos varied between two and 30 min. Since the person in the YouTube videos was most likely unknown to the embracing pedestrians, a neutral emotional background for the embrace can be assumed. The rationale behind this method of data collection was that it allows for collection of emotionally neutral embracing data that are largely comparable to the emotional data collected at airports. In comparison to asking a single confederate to stand in a public space blindfolded to collect these data, we observed a larger variety of embracing individuals, minimising potential systematic bias that could be induced by position or physical features of a single person. Moreover, as the individuals in the videos were unaware of our hypothesis, systematic experimenter effects are effectively ruled out by this method of data collection.

As the dependent variable, we recorded the embrace’s leading hand (defined as the clear upper hand located above or next to the shoulder of the embracing partner). Since every embrace was conducted by two human subjects, we recorded the gender pairing as a further independent variable in addition to the emotional context. To be recorded as a valid embrace, it had to meet several criteria: clearly

identifiable leading hand, no large bags or handbags that could bias the decision, no children, no visible physical disabilities and no multiple embraces to either side.

Data analysis

As we only had one observation per participant, we compared the frequencies of left and right leading hand embraces in general and in relation to gender pairing and emotional context using Pearson's χ^2-test. For the analysis of the Youtube videos, the inter-rater reliability was determined based on a random sample of 25% of the videos. Inter-rater reliability was high (Cohen's $\kappa = 0.9$, $p < 0.001$).

Results experiment 1

Overall, embracing was strongly lateralised (83.04% right-side embraces). Right-sided embraces were observed significantly more often than left-sided embraces [$\chi^2(1, N = 2530) = 1104.97$, $p < 0.001$, $\varphi = 0.66$]. The factor "emotional condition" yielded a significant result as well [$\chi^2(2, N = 2530) = 36.25$, $p < 0.001$, $\varphi = 0.12$].

Comparing the positive and negative conditions revealed that there was no significant difference in the direction of embracing bias between them [80.21% positive right-side embraces, 81.56% negative right-side embraces, $\chi^2(1, N = 2001) = 0.72$, $p = 0.396$, $\varphi = 0.02$]. There was, however, a significant difference in the direction of embracing bias between positive and negative emotion conditions compared to the neutral condition. Overall, the direction of the embracing bias was more rightward in the neutral condition (91.68%) than in the positive and negative conditions [$\chi^2(1, N = 1467) = 27.51$, $p < 0.001$, $\varphi = 0.14$ for negative vs. neutral; $\chi^2(1, N = 1592) = 35.38$, $p < 0.001$, $\varphi = 0.15$ for positive vs. neutral].

Frequencies of embraces differed significantly in their amount across gender combinations [$\chi^2(2, N = 2530) = 348.69$, $p < 0.001$, $\varphi = 0.37$]. The gender specific results are shown in Fig. 1. Absolute numbers of male–male interactions ($n = 533$) occurred less frequently compared to both female–female [$n = 725$, $\chi^2(1, N = 1258) = 29.30$, $p < 0.001$, $\varphi = 0.15$] and female–male embraces [$n = 1272$, $\chi^2(1, N = 1805) = 302.36$, $p < 0.001$, $\varphi = 0.41$]. Overall, the factor "gender combination" did not have a significant impact on embracing [$\chi^2(2, N = 2530) = 3.28$, $p = 0.196$, $\varphi = 0.04$]. The investigation of the gender combination across emotional conditions, however, demonstrated significant asymmetries for male–male and female–male interactions [$\chi^2(2, N = 533) = 31.18$, $p < 0.001$, $\varphi = 0.24$ for male–male; $\chi^2(2, N = 1272) = 14.65$, $p = 0.001$, $\varphi = 0.11$ for female–male]. Across all emotional settings, this did not reach significance for female–female embracing [$\chi^2(2, N = 725) = 4.08$, $p = 0.13$, $\varphi = 0.08$]. Comparing the emotional contexts directly, no significant difference was found for the negative vs. neutral condition for female–female embraces [84.41% negative right-side embraces, 91.51% neutral right-side embraces, $\chi^2(1, N = 369) = 3.25$, $p = 0.07$, $\varphi = 0.09$]. However, a significantly stronger rightward bias in the neutral condition was found for male–male [71.43% negative right-side embraces, 92.66% neutral right-side embraces, $\chi^2(1, N = 365) = 29.61$, $p < 0.001$, $\varphi = 0.28$] and female–male interactions [82.95% negative right-side embraces, 90.73% neutral right-side embraces, $\chi^2(1, N = 733) = 7.06$, $p = 0.008$, $\varphi = 0.10$]. For positive vs. neutral, all three groups of gender

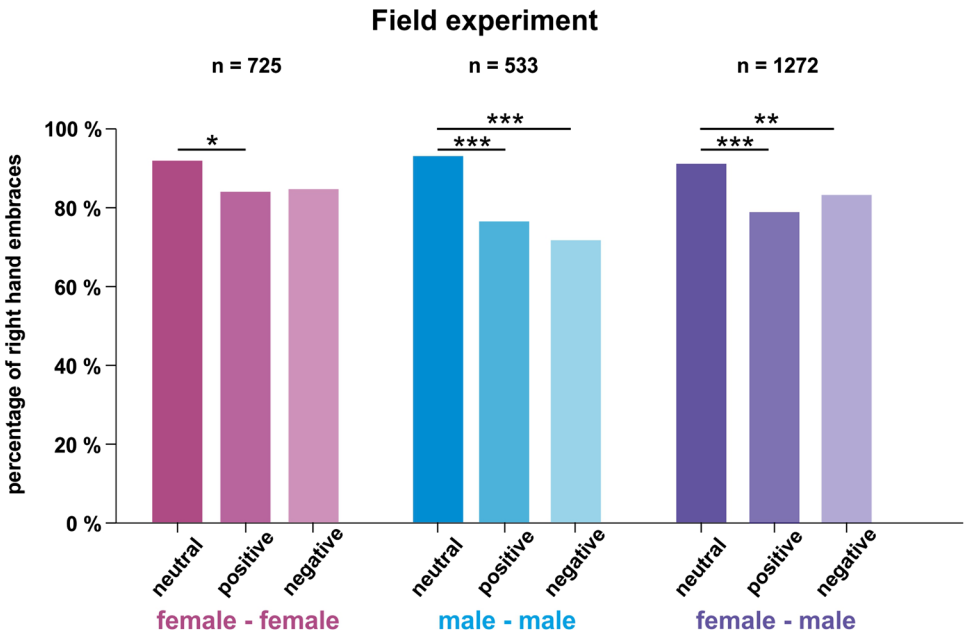

Fig. 1 Effects of condition and gender pair in the field experiment. Percentage of right-hand embraces in the field experiment is shown. Female–female embraces are depicted in pink, male–male embraces are depicted in blue and female–male embraces are depicted in purple. The significance levels for comparisons are depicted as follows: *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$. (Color figure online)

combinations reached significance, with less rightward bias in the positive than in the neural condition [female–female: 83.71% positive right-side embraces, $\chi^2(1, N=462)=4.01$, $p=0.045$, $\varphi=0.09$ female–male: 78.85% positive right-side embraces, $\chi^2(1, N=744)=14.28$, $p<0.001$, $\varphi=0.14$ male–male: 76.19% positive right-side embraces, $\chi^2(1, N=386)=20.75$, $p<0.001$, $\varphi=0.23$]. No significance was reached for any gender combination comparing the positive to the negative setting.

Experiment 2: laboratory study

Methods experiment 2

Participants

For the laboratory study, we tested 120 healthy adults (71 females) as subjects (mean age 24.06, range from 19 to 52 years). Ocklenburg and Güntürkün (2009) used a similar sample size to produce robust effects investigating the lateralisation of kissing. As there exist no studies investigating embracing directly, we referred to this comparable experiment performed in our lab to determine the sample size. All participants signed an informed consent form and all procedures were approved by the Ethics committee of the department of Psychology of the Ruhr University Bochum.

Procedure and materials

Testing of the participants took place individually. After consenting to participation in the study, subjects were instructed to position themselves onto marked spots in front of clothed mannequins (one male and one female mannequin, see Fig. 2). The mannequins were different in height (male = 185 cm, female = 175 cm) and had a symmetrical orientation. Standing on the mark (located around 50 cm away from the mannequin), participants listened to short stories (each with 2–5 min duration) via wireless headphones to induce an emotional context. The stories were specifically designed to end with the participant embracing the mannequin. As the participants were German, the stories were told in German (English translations can be found in supplements 1, German originals can be found in supplements 2).

Participants were instructed to directly look at the mannequins during presentation of the story to immerse the mannequin into the narrative. They were also told to immediately embrace the mannequin after the story had ended. Additionally, the stories always closed with the instruction to embrace either a man or a woman depending on the gender of the mannequin. Overall, subjects embraced the mannequins ten times divided into two neutral, four positive and four negative emotion trials. Each of the ten trials was associated with a unique story and gender of the mannequins was balanced across conditions. As in the first experiment, we recorded the leading hand during the embrace. Initially, the neutral condition was tested with both mannequins. After listening to the story associated either with the male or female mannequin, the participants were instructed to embrace it. To do so, subjects had to move towards the mannequin to reach it as the marked spot was located too far from it. The neutral stories were played first to exclude residual emotionality lasting from previous trials using either a positive or a negative priming. Afterwards, the emotional stories were presented in a randomised order following the same procedure. At the end of the testing procedure, the participants filled out questionnaires regarding handedness (Oldfield, 1971), footedness (Elias, Bryden, & Bulman-Fleming, 1998), eyedness (Reiss, & Reiss, 1997), an empathy rating and demographic data. The empathy scores ranged from 1 to 10 where a value of 1 signified a complete absence of emotion induction for the participants and a value of 10 signified that the subjects were highly affected by the emotionality of the story. Furthermore, the participants had to state their perceived handedness. The short stories were evaluated individually prior to the experiment using a rating score ranging from −5 to 5 where a negative value indicated negative valence and a positive value indicated positive valence. A value of 0 signified a neutral rating of the story. Additionally, all stories were given an individual empathy score during the pre-rating procedure to allow for a comparison between the effectiveness of the stories between the rating and the experimental sample. A repeated measures ANOVA revealed significant differences between the pooled data of all positive, negative and neutral stories [$F_{(2,8)}=105.9$, $p<0.001$, $\eta_p^2=0.93$]. The neutral stories with a mean score of 1.22 (SEM 0.32) had significantly lower ratings than the positive stories (mean score 3.58, SEM 0.38, $p=0.014$), but significantly higher ratings than the negative stories (mean score − 3.67, SEM 0.33, $p<0.001$). Empathy scores across stories were very high during the pre-rating for the stories (mean 7.41, SEM 0.27). The emotional valence had no effect on the empathy ratings ($F_{(2,8)}=0.47$, $p>0.250$, $\eta_p^2=0.05$).

Data analysis

We computed lateralisation quotients (LQs) for handedness, footedness, eyedness and for embraces in all three experimental conditions. The LQ can range between − 100 and + 100 where a value of + 100 reflects consistent right-side preference, whereas a value of − 100 indicates consistent left-side preference. Gender differences in LQs were tested using *t* tests. For perceived handedness, differences between males and females were evaluated using Pearson's χ^2 test. Embracing LQs were analysed with a three-factorial ANOVA using emotion, gender of

Fig. 2 Task procedure in the laboratory setting. **a** The location of the mannequins in relation to the marked spot for the participants. **b** A male and a female participant are listening to a story via wireless headphones. All participants had to keep eye contact to the mannequin during the presentation. **c** After the story had finished, participants of both genders had to embrace the male and female mannequins over the course of the experiment. The two embraces displayed on the left showcase a right embrace (right leading hand), the two embraces displayed on the right demonstrate a left embrace (left leading hand). Notice the step forward during embracing because of the distanced location of the mark

the participants and gender of the mannequins as factors. Post hoc tests were performed using Bonferroni correction. Additionally, multiple regression analysis was used to investigate the relationship between handedness, footedness and eyedness concerning the choice preference during embracing the mannequins. To check for correlations between these three factors, we computed Pearson correlation coefficients.

The measured empathy scores were tested for gender effects using a *t* test. Furthermore, a linear regression of the empathy score and embracing LQs was computed to investigate if immersion into the stories and their efficacy of emotional induction had an effect on the embracing.

Results experiment 2

Embracing bias

Overall, the LQ for embraces was 57.59 (SEM 4.99), indicating that, comparable to experiment 1, there was an overall rightward bias during embracing. There was a significant main effect of the emotional condition over all subjects ($F_{(2,236)} = 15.550$, $p < 0.001$ $\eta_p^2 = 0.116$), indicating that the average LQ was higher in the neutral condition with a mean LQ of 76.37 [SEM 4.78, confidence interval (CI) (66.90, 85, 83)] compared to the mean LQ of the negative condition {48.12 [SEM 6.03, CI (36.17, 60.06)]} and to the mean

LQ of the positive condition {49.64 [SEM 6.29, CI [37.18, 62.10)]}.

To identify both participant gender and mannequin gender effects, LQs were computed separately for each experimental combination of factors. The results of this analysis are shown in Fig. 3a for female and 3b male participants.

There were no significant main effects for gender of the participants ($F_{(1,118)} = 0.005$, $p > 0.250$, $\eta_p^2 = 0.000$) and gender of the mannequin ($F_{(1,118)} = 0.637$, $p > 0.250$, $\eta_p^2 = 0.005$). However, there was a significant interaction between all three investigated main factors ($F_{(2,236)} = 3.455$, $p = 0.033$, $\eta_p^2 = 0.028$). Post hoc pair-wise comparisons revealed the following effects: for female participants, all neutral condition embraces were more lateralised to the right compared to all emotional conditions, irrespective of gender of the mannequin ($p \leq 0.01$). This indicates that the mean LQs in the neutral condition for embracing both mannequins [female: 80.28, SEM 6.36, CI (67.68, 92.89); male: 80.28, SEM 7.79, CI (64.85, 95.71)] were significantly higher than during the induction of emotions. Here, quotients shifted in the positive condition towards the left {mean female mannequin 43.66 [SEM 9.25, CI (25.35, 61.97)], mean male mannequin 54.93 [SEM 8.76, CI (37.59, 72.27)]}. In the negative condition, embracing displayed a similar leftward-shift {mean female mannequin 44.13 [SEM 9.61, CI (25.11, 63.16)], mean male mannequin 46.95 (SEM 8.66, CI (29.80, 64.93)]}. For male participants, we found the same results, but only while embracing the female mannequin ($p < 0.001$ for neutral vs. both positive and negative). Here, LQs in the neutral emotional condition were again significantly higher {mean 83.67 [SEM 7.66, CI (68.50, 98.94)]} compared to LQs in the emotional conditions embracing both mannequins {mean positive female 45.58 [SEM 11.13, CI (23.54, 67.62)]; mean negative female 40.82 [SEM 11.57, CI (17.91, 63.72)]}. No significant differences between the emotional conditions could be observed during male–male interactions ($p > 0.10$), demonstrating that there was no difference between the neutral condition LQ {mean 61.22 [SEM 9.38, CI (42.65, 79.80)]} and the positive and negative conditions {mean positive male 45.58 [SEM 11.13, CI (27.42, 69.18)]; mean negative male 66.67 [SEM 10.42, CI (46.03, 87.30)]}.

Association between motor preferences and embracing bias

The mean LQs were 72.41 (SEM 5.29) for handedness, 56.60 (SEM 4.99) for footedness and 24.50 (SEM 7.84) for eyedness. There was no significant effect of gender for handedness ($t_{(118)} = 1.561$, $p = 0.121$, Cohen's $d = 0.29$), footedness ($t_{(118)} = 1.946$, $p = 0.06$, $d = 0.36$) or eyedness ($t_{(118)} = 0.961$, $p = 0.34$, $d = 0.18$). Perceived handedness of participants amounted to 106 right-handers (88%) and 14 left-handers (12%). Again, no effect of gender could be detected [$\chi^2(1, N = 120) = 1.74$, $p = 0.187$, $\varphi = 0.12$].

Handedness and footedness correlated significantly ($r_{(118)} = 0.394$, $p = 0.001$). Similar results were found for the

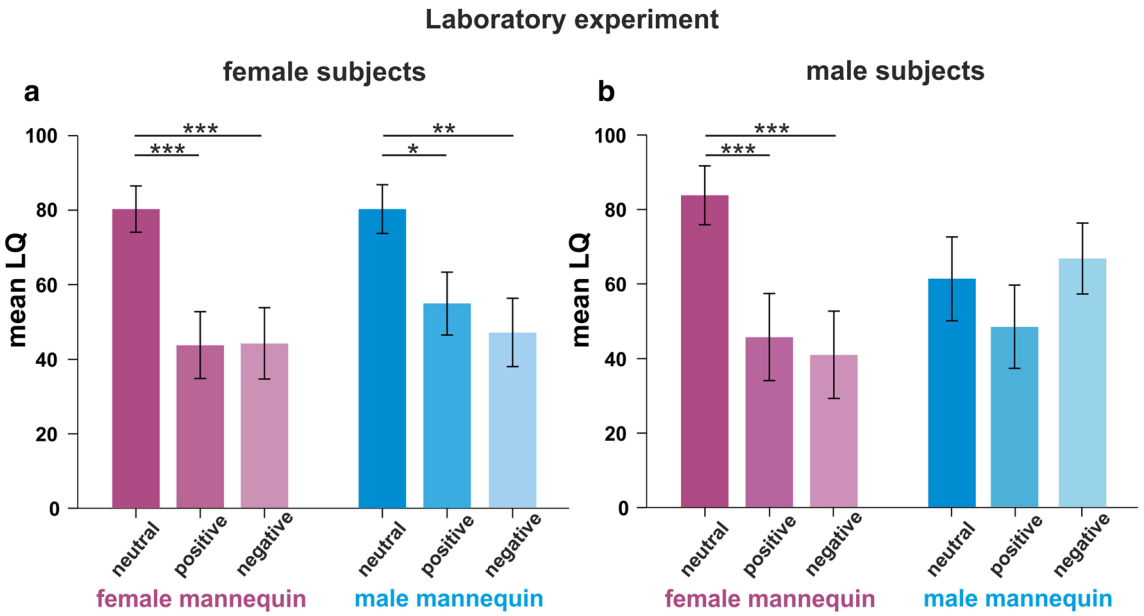

Fig. 3 Effects of condition, gender of the participant and gender of the mannequin in the laboratory experiment. Mean LQs for female subjects in the laboratory study are shown in **a**. Mean LQs for male subjects in the laboratory study are depicted in **b**. In both figures, mean LQs for embraces with the female mannequin are depicted in pink and mean LQs for embraces with the male mannequin are depicted in blue. The significance levels are depicted as follows: $^*p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$. Error bars represent SEM

correlation between handedness and eyedness ($r_{(118)} = 0.251$, $p = 0.006$). Only the correlation between eyedness and footedness did not reveal a significant result ($r_{(118)} = 0.179$, $p = 0.05$). To identify the relation between these factors and embracing, we performed multiple regression analysis with handedness, footedness and eyedness as predictors and embracing LQs as dependent variable. Overall, the model reached significance, indicating that individual motor preferences could to some extent predict individual embracing bias ($R^2 = 0.096$, $F_{(3,116)} = 4.115$, $p = 0.008$). Thus, about 9.6% of the variance in embracing side bias could be explained by individual motor preferences. Individual beta-weights failed to reach significance for all three factors, likely because of the high intercorrelation between them ($t_{(116)} = 1.675$, β-weight = 0.153, $p = 0.10$ for handedness; $t_{(116)} = 1.958$, β-weight = 0.189, $p = 0.05$ for footedness; $t_{(116)} = 0.873$, β-weight = 0.086, $p = 0.38$ for eyedness).

Association between empathy scores and embracing bias

Mean empathy scores were generally high and comparable to the empathy scores of the participants in the pre-rating (mean 7.03, SEM 0.15), indicating that the stories were successful in inducing emotions in the participants. Comparing males and females concerning empathy did not display a significant result ($t_{(118)} = 1.336$, $p = 0.19$, $d = 0.25$). Empathy scores did not correlate with lateralisation of the embrace in any experimental condition.

Discussion

In the present study, we investigated lateralisation of human embraces and how they are modulated by emotional contexts and individual motor preferences. Regarding the latter, embracing could potentially be determined by handedness. For emotional influence, two theories of emotional lateralisation were investigated as they made distinct predictions for the lateralisation of embraces due to the hemispheric control of motor output. The RHH predicted that embraces would be lateralised to the left in emotional vs. neutral conditions. The VSH, however, predicted a stronger lateralisation to the left in negatively connoted contexts, whereas positively evaluated contexts should lead to a more rightward bias during embracing in comparison to neutral conditions. We systematically pitched these models against one another using a combined approach of field and laboratory work.

First, we investigated human embraces in an observational study. Here, overall we found that embraces were right-lateralised on the population level using a well-powered sample of more than 2500 subjects. During observations, 83% of the subjects displayed a right-side preference for embracing. This finding is well in line with the results of an earlier study on embracing bias by Turnbull et al. (1995), who also conducted an observation study at an airport, but only in the arrivals lounge. Comparable to our results, these authors found a significant rightward bias for female–female embraces and female–male embraces. While they did not observe a significant rightward bias for male–male embraces, this might be due to low statistical power in this specific condition in the Turnbull et al. (1995) study and is not necessarily in contradiction to our findings in a much larger and well-powered sample. Importantly, we found that emotional context modulated the side bias in embracing. In the neutral condition, embracing was right-sided in more than 91% of the cases. However, in emotional contexts, subjects used their right leading hand less often with about 80% right-side embraces in the positive and 81% right-side embraces in the negative condition. Thus, both negative and positive emotional contexts lead to a left-shift of embracing side preferences, indicating a stronger involvement of the right hemisphere in emotional as compared to neutral embraces, a result which is in line with the RHH.

To gain more insights about this phenomenon, we conducted a follow-up laboratory study as a purely observational approach has limitations to answer questions such as the impact of handedness—and related motor phenotypes—and controlled emotional induction on embraces. In general, experiment 2 replicated the findings of experiment 1. Overall, participants showed a pronounced rightward side bias when embracing. Also in line with the findings of experiment 1, emotional context modulated the side bias when embracing: after positive and negative emotional inductions through specifically designed short stories, the participants again displayed an overall shift to the left in their embraces in comparison to the neutral condition. In conclusion, we found highly consistent results across the two experiments which we will discuss in more detail in the following.

Overall, we found that embraces display a high level of lateralisation as our results demonstrated a strong preference of right leading hand choices during embracing. This is in line with the findings of the laboratory study of Turnbull et al. (1995) for female–female embraces, but not the two other conditions of their experiment, in which no significant bias was observed. As for the observation part of the Turnbull et al. (1995) study, these nonsignificant results might potentially be due to small sample sizes in the other two conditions and thus low statistical power. Since our study has a substantially larger sample than the Turnbull et al. (1995) study, our results are more likely to reflect embracing bias in the population. In line with Turnbull et al. (1995), we also did not observe a significant correlation between handedness and embracing bias, as the beta-weight for handedness failed to reach significance. However, multiple regression analysis of handedness, footedness and eyedness revealed a significant effect of the combination of these factors. Interestingly, the strongest loading factor in this analysis was footedness

rather than handedness. Such a finding could be explained by the nature of embracing that is actually a full body motion. Embracing someone requires movement towards that person and a stable position (we simulated this process in the laboratory study through the location of the mark). Therefore, using the preferred foot to acquire a firm standing seems reasonable. Interestingly, footedness has been found to be a better predictor for emotional lateralisation than handedness which could also explain the stronger correlation between footedness and embracing (Elias et al., 1998). In addition to a correlation between handedness and head-turning preferences, Ocklenburg and Güntürkün (2009) also discovered a correlation between footedness and head-turning preferences during kissing that could be explained similarly.

The general shift of choice preference towards the left side during the negative and positive emotional condition could provide evidence for the RHH of emotional processing. The consistent results in both the laboratory and the field study provide support for this particular theory as we found this difference in embrace lateralisation during both experiments. The RHH has received empirical support from a large numbers of studies. Emotional content of speech for example is processed predominantly by the right hemisphere (Buchanan et al., 2000; Haggard, & Parkinson, 1971). Also facial processing of affect has been demonstrated to be lateralised in the right hemisphere (Landis, Assal, & Perret, 1979; Suberi & McKeever, 1977). The consistency in the result pattern also confirms that the assumption of a specific emotional state at the airport holds when measured across a very large sample. However, as our effects were generally smaller in the field study, there is also a strong indication that this did not affect every embrace during the observation probably leaving a substantial amount of neutral embraces in the sample. Moreover, it should be noted that the results of the field experiment could also be explained if people maintained a positive mindset in the departure condition (e.g. individuals were sad to say goodbye to a loved one, but still retained a generally positive attitude towards that individual) as the RHH would make the same prediction in this case.

Because the execution of embracing was considerably altered in terms of direction, intrahemispheric interactions between emotional and motor structures provide the most pervasive explanation for such a change. Evidence in favour of that interpretation can be drawn from various studies indicating that the left hemiface expresses emotions more intensely compared to the right hemiface (Borod, 1993). This differential processing of the left and right hemiface has been demonstrated in non-human primates as well indicating that this functional asymmetry is homologous across species (Fernández-Carriba, Loeches, Morcillo, & Hopkins, 2002). Even in dogs, emotional processing and its subsequent influence on behaviour have been shown to be lateralised: Siniscalchi et al. (2010) discovered that dogs turn preferentially to the left when presented with emotional instead of neutral stimuli. Since we did not find a lateralisation difference between positive and negative emotions, the results seem to reject the VSH. In contrast to the general view of the RHH and the VSH being mutually exclusive, Prete et al. (2015) proposed an integrative model of emotional processing stating that the VSH is the default state of the brain, whereas right-hemisphere dominance accounts hold true whenever decision-making is involved. As our participants had to choose a side for embracing the mannequin after listening to the stories or when embracing other humans in the field experiment, this "modified valence hypothesis" could still account for the right-hemispheric control in our task.

A gender related effect was found when men had to embrace the male mannequin. Here, men displayed a strong shift to the left comparable to the emotional conditions. This intriguing result could be explained by assuming that German men did associate negative emotions with embracing the male mannequin in general and not just after being emotionally primed through the short stories. Studies have demonstrated that US men engage less often in same-sex touch interaction and are far less comfortable during these occurrences compared to women (Andersen, & Leibowitz, 1978; Major, 1981). Also, Turnbull et al. (1995) remark in their paper on embracing bias that some of the male participants in the laboratory study refused to embrace other male participants. Therefore, a same-sex embrace might feel uncomfortable and thus more negative for the majority of men in some specific Western societies than for women. Rabinowitz (1991) noted that even in familiar environments, men feel psychological discomfort when embracing other men. Although we did not find the lateralisation difference in the field experiment, we did find that the amount of male–male interactions was significantly less prevalent compared to both female–female and female–male embracing. This disparity of the results can be explained in design differences between the two experiments: in the laboratory design, all male participants had to embrace the puppet to fulfil the participation requirements. Therefore, both males comfortable and uncomfortable with the situation engaged in the embracing process. In the field, however, only males comfortable with embracing could be sampled as the others simply did not engage in it (especially in the neutral condition as they would have just walked past the blindfolded person). This design difference reasonably explains both the significantly less observable embraces in male–male interactions in the field and the existing difference in the neutral vs. emotional conditions as the neutral condition for males was truly neutral in the field due to their lack of discomfort during the embrace. A secondary possible explanation for this result could be that the effect was indeed specific for embracing the male mannequin and not men altogether. However, in view of the reduced male–male interactions in

the field study and no effect for women embracing the male mannequin, it does not seem likely to be limited to the laboratory study.

Overall, our results provide evidence for a rightward bias in human embracing lateralisation in two large samples. While embracing lateralisation seems to be influenced by motor lateralisation, this is not the only factor determining the behavioural outcome, since emotional context also influences embracing lateralisation. Therefore, our findings suggest that an interaction between motor preferences and emotional context determines embracing bias. While handedness induces a motor constraint on embracing preference that leads to an overall rightward bias, this bias is moderated by the emotional context.

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Author contributions JP and NR analysed the data, wrote the manuscript and supervised the experiments. SO conceived the experiment, analysed the data, supervised the experiments and reviewed the manuscript. OG reviewed the manuscript and provided the laboratory setting to perform the experiments. ZD, JM and AW performed the data acquisition.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

Data access We have full access to our data and allow the journal to review the data if requested.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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