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Review article

Hugs and kisses – The role of motor preferences and emotional lateralization for hemispheric asymmetries in human social touch



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ABSTRACT

Social touch is an important aspect of human social interaction - across all cultures, humans engage in kissing, cradling and embracing. These behaviors are necessarily asymmetric, but the factors that determine their lateralization are not well-understood. Because the hands are often involved in social touch, motor preferences may give rise to asymmetric behavior. However, social touch often occurs in emotional contexts, suggesting that biases might be modulated by asymmetries in emotional processing. Social touch may therefore provide unique insights into lateralized brain networks that link emotion and action. Here, we review the literature on lateralization of cradling, kissing and embracing with respect to motor and emotive bias theories. Lateral biases in all three forms of social touch are influenced, but not fully determined by handedness. Thus, motor bias theory partly explains side biases in social touch. However, emotional context also affects side biases, most strongly for embracing. Taken together, literature analysis reveals that side biases in social touch are most likely determined by a combination of motor and emotive biases.

1. Introduction

Humans often touch each other to seek or offer physical and emotional support, but also to communicate emotional states and intentions. Several types of social or affective touch, e.g. handshakes, high fives, kissing, embracing and cradling can be used to convey meaning (McGlone et al., 2014). From a laterality perspective, the various modes of social touch (e.g., embracing, kissing, and cradling) sit at the intersection of two lateralized systems: one that mediates motor behavior, particularly involving the hands, and the other that mediates emotional valence (positive/negative).

Thus, two hypotheses can be conceived about the laterality of social touch. On the one hand, about 90% of individuals are right-handed and 10% are left-handed (Corballis, 2012, 2009; Güntürkün and Ocklenburg, 2017; Schmitz et al., 2017). Laterality of social touch could therefore be determined by hand preference, given that the hands/arms are integral to most types of social touch. If so, populations should on average show a rightward preference for social touch, and that preference should be significantly correlated to handedness.

On the other hand, social touch often occurs in emotional situations, e.g. when kissing a loved one or embracing a mourning friend at a funeral to console them. Thus, it is conceivable that the lateralization of social touch should be determined (or at least modulated) by emotional lateralization. If this emotive hypothesis were correct, lateralization of social touch should be predicted by one of the major hypotheses for emotional lateralization. From a laterality perspective, lateralization of social touch is particularly interesting because most of the empirical evidence on emotional lateralization concerns emotion perception, but much less so emotional expression. Given that emotions are adaptive because they motivate action, social touch provides a nice way to test hypotheses about lateralization of emotional expression or emotional action.

There are three major predictions that can be made based upon these models for the role of emotional context for lateralization of social touch (Demaree et al., 2005). The right hemisphere model assumes that the right hemisphere is dominant for emotional processing, irrespective of emotional valence. Therefore, this model would assume a leftward bias for social touch in both positive and negative emotional situations,

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compared to emotionally neutral situations. Evidence supporting the role of the right hemisphere in emotional perception is vast. Visual halffield experiments have demonstrated an advantage of the left visual field in discrimination tasks using emotional faces as stimuli (Landis et al., 1979; Ley and Bryden, 1979) and dichotic listening studies similarly show a left ear advantage for the discrimination of emotional prosody (Bryden and MacRae, 1988; Godfrey and Grimshaw, 2015; Grimshaw et al., 2009). These effects have been replicated in patients with lesions in the right hemisphere who demonstrate inferior discrimination performance compared to left-hemispheric lesion patients (Adolphs et al., 1996). Additionally, patients with lesions to the right hemisphere are also impaired in identifying emotions in facial, prosodic and lexical perception tasks (Borod et al., 1998). Similar results have been observed using functional imaging during emotional face perception (Narumoto et al., 2001; Sato et al., 2004) and the processing of emotional prosody (Wildgruber et al., 2006).

The valence model assumes that the right hemisphere is dominant for processing of negative emotions while the left hemisphere is dominant for processing of positive emotions (Ahern and Schwartz, 1979; Heller et al., 1998; Silberman and Weingartner, 1986). This model therefore predicts differential lateralization of human social touch depending on emotional valence, with positive emotional situations inducing a rightward bias and negative situations inducing a leftward bias. There is a large body of evidence supporting valencespecific processing by the cerebral hemispheres. Participants evaluate the underlying emotionality of chimeric faces more positively when they are presented in the right visual field (Natale et al., 1983). Additionally, the expression of negative emotions is stronger in the left hemi-face compared to the right hemi-face (Sackeim et al., 1978; Sackeim and Gur, 1978). Negative emotional faces can also be more easily discriminated when presented on the left side, and positive emotional faces achieve higher discriminability when presented on the right side (Jansari et al., 2000).

The most pervasive evidence for the valence model stems from EEG studies indicating stronger activity of the left hemisphere during positive emotional processing and stronger activity of the right hemisphere during negative emotional processing (Davidson and Fox, 1982; Ekman and Davidson, 1993; Fox and Davidson, 1988; Waldstein et al., 2000). Functional neuroimaging studies have also supported the valence hypothesis. For example, it has been shown in some, but not all studies that overall brain reactivity is lateralized to the left while viewing positive stimuli and lateralized to the right for negative stimuli (Canli et al., 1998). However, this finding has been contradicted by later research (e.g., Beraha et al., 2012) and today the most compelling evidence for the valence model stems from EEG studies of alpha power lateralization over frontal cortex. Although EEG alpha asymmetries have been predominantly associated with trait affect, EEG asymmetries also shift with state affect, with greater activity over the left hemisphere during positive emotional processing and greater activity over the right during negative emotional processing (Reznik and Allen, 2018).

Importantly, there is also evidence from studies in non-human animals supporting the valence model. For example, research on dogs' behavioral lateralization in response to stimuli with different valence suggests that hemispheric specialization in the control of emotions is conserved across different taxa (reviewed in Siniscalchi et al., 2017). In a key study, Quaranta et al., (2007) showed that stimuli with a positive emotional valence (e.g., seeing the dog's owner) were associated with more rightward tail-wagging, indicating more left-hemispheric brain activation. In contrast, stimuli with a negative emotional valence (e.g. seeing a dominant unfamiliar dog) were associated with more leftward tail-wagging, indicating more right-hemispheric brain activation.

The third prediction actually derives from two theories of emotional lateralization that make the same prediction for social touch. These two theories are the approach/withdrawal model (also often called the motivational direction model) and the "Behavioral Inhibition System and the Behavioral Activation System" (BIS/BAS) model. The approach/withdrawal model proposes a functional lateralization of the hemispheres for approach and avoidance behavior, with the left hemisphere implementing approach and the right hemisphere implementing withdrawal (Davidson, 1998). As most positive emotional states are associated with approach and most negative emotional states involve withdrawal, there is strong overlap in the predictions of the valence model and the approach/withdrawal model. For example, the dog study by Quaranta et al., (2007) would be in line with both models. However, specific evidence for the approach/withdrawal can be found when looking at the emotion of anger (Harmon-Jones et al., 2010, 2002; Harmon-Jones and Allen, 1998; Harmon-Jones and Sigelman, 2001). Here, anger is associated with left-hemispheric activation even though it is a negatively connoted affective state.

The BIS/BAS model provides another account that could explain anger being lateralized to the left hemisphere. This model proposes left hemispheric processing for behavioral activation and right hemispheric processing for behavioral inhibition (Sutton and Davidson, 2007). EEG recordings also offer evidence supporting this model, namely that people with greater BAS sensitivity (sensitivity to conditioned reward, non-punishment and escape from punishment) demonstrated higher left-frontal activity (Harmon-Jones and Allen, 1997). As social touch always involves both approach motivation and behavioral activation, both the approach/withdrawal model and the BIS/BAS model make the same prediction. Here, the direction change would be more rightward biased in accordance to higher left hemispheric activation, with the strength of the bias correlating with the strength of the motivation.

Thus, there are essentially three versions of the emotive bias theory (see Fig. 1). The motor and the emotive bias hypotheses are not mutually exclusive and it could also be conceived that in emotionally neutral situations (e.g. when using an embrace to greet a person who one does not know very well), motor preferences determine lateralization of social touch, while in emotional situations this motor bias might be modulated be the valence or motivational value provided by the context.

The aim of this review article is to systematically integrate the literature on lateralization of human social touch in order to determine which theoretical account is best suited to explain the empirical data. To this end, literature on lateralization of cradling, embracing, and kissing is reviewed. In addition, open questions and future research directions are discussed.

2. Cradling

Historically, the first form of lateralized social touch to be investigated is cradling, i.e., holding and supporting an infant in one's arms (see Fig. 2A).

In 1960, Lee Salk from the City Hospital at Elmhurst, New York City, published a paper on the effects of the sound of a mother's heartbeat on the behavior of her infant, and its implications for mental health (Salk, 1960). Salk observed 287 mothers cradling their babies at the hospital he was working at. He found that mothers showed a pronounced tendency to use their left arm to cradle their babies irrespective of handedness. Among 32 left-handed mothers, 78.1% held their babies with the left hand, and 21.9% with their right hand. The results for 255 right-handed mothers looked similar. Here, 83.1% held their babies with the left hand and 16.9% with the right hand. This general leftward cradling bias has been well replicated by several more recent studies (Almerigi et al., 2002; Dagenbach et al., 1988; Fleva and Khan, 2015; Harris and Fitzgerald, 1985; Manning and Denman, 1994; Matheson and Turnbull, 1998; Saling and Tyson, 1981; Souza-Godeli, 1996; Turnbull and Lucas, 1991; van der Meer and Husby, 2006; Vauclair and Donnot, 2005). Moreover, it does not seem to be limited to humans, as it has been shown that several species of marine and terrestrial mammals show leftward lateralization in mother-infant interactions, indicating right hemisphere dominance for social processing (Karenina et al., 2017). Interestingly, there is recent research in animals that

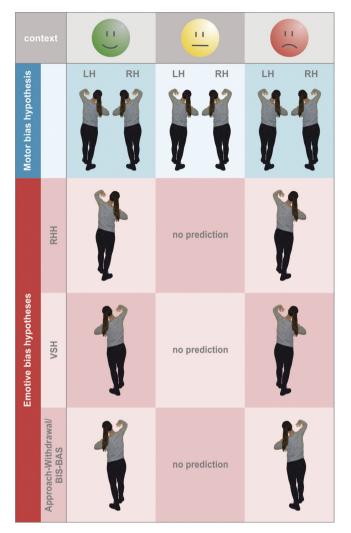


Fig. 1. The different possible theories on the role of emotional context for the lateralization of human social touch exemplified for hugging. The column with the green smiley shows the prediction of the respective model for situations with a positive emotional valence, the column with the yellow smiley shows the prediction of the respective model for situations with a neutral emotional valence and the column with the red smiley shows the prediction of the respective model for situations with a positive emotional valence. The blue row shows the predictions of the motor bias hypothesis for left-handers (LH) and right-handers (RH). The red rows show the predictions for the different versions of the emotive bias hypothesis (RHH: right hemisphere hypothesis; VSH: valence specific hypothesis; approach-withdrawal hypothesis).

indicates that lateralization in mother-infant interactions should not be automatically attributed only to the behavior of the mother. Instead, the infant is also an active member of the dyad and could be driving the effect with its own behavior. For example, it has recently been shown in the chicken (*Gallus gallus*), that already in newborn chicks there is a link between structural brain asymmetry and behavioral left/right preferences (Rugani et al., 2015), implying that preferences are innate to the infant and not necessarily determined by the mother's behavior.

Salk concluded that from an evolutionary perspective, mothers have a tendency to hold their babies close to their hearts on the left side of the body, irrespective of handedness (Salk, 1960). However, this heartbeat hypothesis has not been confirmed by a single-case study on the cradling preference of a dextro-cardiac mother (Todd and Butterworth, 1998). While the hypothesis would suggest that someone with their heart on the right side would cradle a baby with the right arm, this mother used her left arm to cradle her baby, just like the general population. However, as is not clear to what extent heart position and cradling bias are driven by the same ontogenetic processes. Thus, the cradling bias could have been evolved because it is adaptive for left-hearted mothers, and be inherited also by dextro-cardiac mothers. In addition, as the work by Todd and Butterworth (1998) was only a single-case study, more research is needed before any final conclusions can be drawn.

Regarding the motor bias hypothesis, the initial evidence for cradling was somewhat mixed. Salk (1960) did not report any statistical measures, but the absolute cradling bias percentages for the left or the right side were very similar for left- and right-handed mothers in his sample. This putatively indicates no systematic effect of handedness on cradling. Huheey (1977) suggested that from an evolutionary perspective, a leftward cradling bias might be one of the reasons why more people are more often right-handed than left-handed. The existence of the leftward cradling bias would lead to a selection pressure for righthandedness as right-handedness would allow mothers to better manipulate objects while cradling their babies and this ability to dual-task would increase evolutionary fitness. Dagenbach et al. (1988) showed a weaker leftward cradling bias in left- than right-handed mothers, but since they only observed five left-handed mothers, the generalizability of this result is somewhat limited. However, a recent systematic largescale investigation strongly supports the motor bias theory (van der Meer and Husby, 2006). In this study, 765 participants, of whom 64.3% were right-handed, 24.7% mixed-handed, and 11.0% left-handed, were asked to cradle a baby doll. Overall, 71.5% of participants used their left hand to cradle the baby doll, while 28.5% used their right hand. However, when taking handedness into account, this pattern changed dramatically. While 79.1% of right-handers cradled in the left arm, this number was reduced to 66.1% in mixed-handed participants, and even further reduced to 39.3% in left-handers. Moreover, an analysis of lateralization quotient data for handedness revealed that a higher

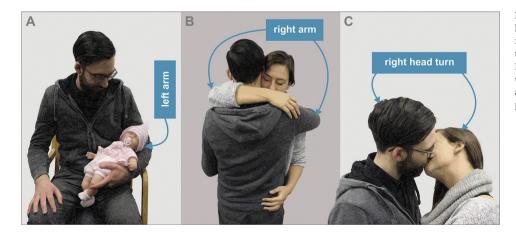


Fig. 2. The different forms of lateralized human social touch: A) An adult cradling an infant. Most adults show a preference for using the left arm for cradling B) Two adults hugging. Here, most individuals show a preference to use the right arm as the leading arm. C) Two adults kissing. Here, most individuals show a preference to turn their heads to the right side.

lateralization quotient, indicating a stronger rightward hand preference, was related to a higher likelihood of left arm cradling. (van der Meer and Husby, 2006) concluded that participants show a clear tendency to cradle infants with their non-dominant arm, as this allows performance of other fine motor tasks more accurately with their dominant hand.

With regard to the emotive bias theory, several authors have suggested that lateralization for emotion processing affects the side bias in cradling. A number of theorists have suggested that a left-sided cradling bias reflects a parent's desire to keep the infant in their left visual field, or in the left side of space, so its face is projected to the emotionallydominant right hemisphere (Manning and Chamberlain, 1991). One line of evidence to support this claim comes from studies using chimeric faces to assess lateralization of emotion perception. For example, (Bourne and Todd, 2004) conducted a study to test the hypothesis that cradling preferences could be explained by hemispheric specialization for the perception of facial emotional expression. The authors assessed cradling bias by asking 32 students to cradle a doll, and also by determining the dominant hemisphere for processing facial emotion by using the chimeric faces task (Levy et al., 1983). For male participants, there were no differences in the lateralization quotient in the chimeric faces task between left- and right-cradlers. However, for female participants, left-cradlers on average had a positive lateralization quotient in the chimeric faces task, indicating right-hemispheric facial emotion processing dominance. In contrast, right-cradlers on average had a negative lateralization quotient in the chimeric faces task, indicating left-hemispheric facial emotion processing dominance. Bourne and Todd (2004) concluded that women cradle babies on the side of the body that is contralateral to the hemisphere dominant for facial emotion processing.

The chimeric faces task was also used in a subsequent study on cradling bias and emotional asymmetries (Vauclair and Donnot, 2005). Here, the authors assessed cradling bias in 210 undergraduate students and additionally tested them with two different version of the chimeric faces task, one with happy and neutral faces to determine the hemisphere dominant for emotion processing, and another one with left and right mirror image chimeric faces. This task was used in order to test which side of the faces in the pictures the participants thought to be more emotionally expressive. They found the participants with a leftsided cradling preference also preferred the left visual field in the chimeric faces task, while participants with a right-sided cradling preference did not show any significant preference. However, this correlation was not replicated in a recent study by Harris et al., (2018). In the chimeric mirror faces task, there was no difference between left- and right-cradlers. The authors concluded that their data yielded further support for the idea of Manning and Chamberlain (1991) that mothers prefer to hold their babies with their left arm in order to facilitate communication between the left visual field and the right hemisphere, which is also supported by the animal literature (Karenina et al., 2017). Interestingly, this effect seems to be modulated by the infant's age, with the strongest leftward bias in mothers being found directly after the birth of the baby (Todd and Butterworth, 1998). This bias declines at week 12, consistent with the idea that when the baby is born, mothers might show a stronger emotionally-driven left side bias. However, as babies age, mothers start to multitask, and other factors might become more important (e.g., handedness). In addition to studies supporting the motor bias or emotive bias theory, a recent study on cradling bias in humans suggests that this bias may arise as a consequence of the left visual field advantage for face processing (Forrester et al., 2018).

Taken together, the cradling results yield support for both the motor bias hypothesis and the emotive bias hypothesis. The results in regard to the role of emotional lateralization seem to mainly support the right hemisphere hypothesis, but it has to be pointed out that valence has not yet been specifically assessed empirically. This would, however, be interesting for future studies, e.g. to determine to which extent side biases are moderated by the emotional state of either infant or mother.

3. Embracing

Embracing (or hugging) refers to the act of holding another person closely, while putting one's arms around their neck or back (see Fig. 2B). On average, embraces last about 3 s but can vary in length due to cultural or other factors (Nagy, 2011). An embrace is commonly performed by two people, but can in principle be performed by an infinite number of individuals (a so-called "group hug"). While embraces have been observed in almost all human cultures, there are gender and cultural differences in embracing. It has been reported that in Western societies, men on average feel more psychological discomfort when embracing other men than when embracing women (Rabinowitz, 1991). Moreover, men also engage less often in social touch overall (Andersen and Leibowitz, 1978; Major et al., 1990). With regard to cultural differences, embraces occur more frequently in Mediterranean societies compared to Northern Europe or the US, and there also seem to be cultural differences in embracing duration (Shuter, 2009). Individuals born in Asian countries display the least amount of social touch, including embraces (McDaniel and Andersen, 1998)

Lateralization of human embraces was first investigated by (Turnbull et al., 1995). These authors conducted two experiments, one natural observation study and one laboratory study. In the natural observation study, adults were observed embracing in the arrivals lounge of an international airport. Overall, 321 embraces were observed, of which 114 were between two females, 174 between a female and a male, and 33 between two males. The authors reported significant rightward biases (as indicated by the arm that was leading the embrace) in the female/female and the female/male group, but no significant asymmetry in the male/male group. However, since this group was decidedly smaller than the other two, this result might potentially be due to low statistical power. Thus, overall the results of the natural observation study by Turnbull et al. (1995) indicate a rightward bias for embraces in human adults.

In the laboratory study of Turnbull et al. (1995), biology students were asked to embrace their neighbor in a laboratory practical. Overall, 51 embraces were recorded, 14 between two females, 24 between a male and a female, and 13 between two males. The authors found a significant rightward bias in the female/female group, but not in the other two groups. Here, the absolute number of rightward embraces was higher than that of leftward embraces, but the comparisons failed to reach significance. However, since the sample sizes were very small, these results have to be interpreted with caution. In addition, Turnbull et al. (1995) tested the relation between handedness and embracing side bias in the female/female subgroup of their laboratory study and failed to find a significant effect. However, there were only two lefthanders in the sample and the overall sample size was small, so these findings must also be interpreted with keeping this power issue in mind.

More recently, Packheiser et al., (2018) investigated the lateralization of human embraces in a well-powered sample, also taking into account the effect of emotional context on the embracing bias. Similarly to Turnbull et al., (1995), the study consisted of both a field and a laboratory experiment. Both were designed to investigate if and how the affective state modulated embracing lateralization. Therefore, each study was divided into a negative, neutral and positive condition to identify specific modulation in accordance with theories of emotional lateralization. In the field observation, the positive and negative conditions were measured in a large German airport's arrival and departure areas, respectively. The rationale behind this was the likely underlying emotional context of reunion (positive) and farewell (negative). The neutral condition was observed using YouTube videos of people blindfolding themselves in public and asking random strangers to embrace them, which ensures a neutral relationship between the embracing pair. Overall, 2530 embraces were evaluated (1063 for arrival, 938 for departure, and 529 for the blindfold condition). Across conditions, there was a strong right bias in the population (83.04% right-side embraces). Additionally, neutral embraces were significantly more right lateralized than both positive and negative embraces, with 91.68% right-side embraces in the neutral condition, but only 80.21% in the positive and 81.56% in the negative condition. To validate these findings and gain further insights into the relationship to the motor phenotypes of handedness or footedness, the second experiment was conducted in a laboratory setting using mannequins as embracing partners. The affective state was induced via short stories presented over headphones prior to the embrace. Overall, there was a rightward asymmetry in all conditions. Interestingly, they were significantly higher in the neutral condition than both in positive and negative emotional contexts, indicating a left-shift induced by emotional context. Thus, the results are best explained by a combination of the motor bias hypothesis and the emotive bias hypothesis. The general rightward bias in all conditions could be explained using motor phenotypes as predictors, indicating that handedness and footedness play a significant role in the determination of the embracing side. Furthermore, the findings also support the right hemisphere hypothesis, as the general left-shift in emotional contexts can be explained under the assumption that neural networks involved in emotional and motor processing are intertwined. Since the right hemisphere exhibits motor control of the contralateral body-half, a general activation of right-hemispheric networks through affective state provides the most persuasive explanation for these results.

While Turnbull et al., (1995) and Packheiser et al., (2018) are the only two published studies on lateralization of embracing in humans, the topic has also been investigated in non-human primates. Boeving et al., (2017) investigated lateralization of embraces in the Colombian spider monkey (Ateles fusciceps rufiventris). The authors observed two types of embraces in 15 monkeys. Normal embraces resembled embraces in humans and the arms were used to embrace the other animal. Additionally, so-called "face-embraces" were observed in which the animals contacted each other with their cheeks, but without use of the arms. In contrast to what has been found for humans, the monkeys showed a significant leftward bias for both normal embraces and faceembraces. The authors concluded that this result might be explained by right-hemispheric dominance for processing of social stimuli as has been suggested for several animal species (Rogers and Vallortigara, 2015). In this context it has to be noted that it has been shown that spider monkeys do not show a population-level side bias for handedness (Nelson et al., 2015). Thus, their motor preferences should affect the embracing bias considerably less than they might do in humans, resulting in the observed results pattern. These findings demonstrate that more comparative research on embracing is needed in order to fully understand the similarities and differences between human and animal embraces.

4. Kissing

One type of social touch that frequently co-occurs with embracing is kissing. Kissing refers to the act of pressing one's lips against another person (commonly against their lips, but other body parts can be involved as well) or an object (see Fig. 2C). It is commonly used to display love or affection, but can also be used as a formal greeting or in a ritualized context. In heterosexual married couples, there seems to be a sex difference in the initiation of kisses, as men tend to initiate kisses significantly more often (in 79% of the cases) than women (Karim et al., 2017).

Despite the fact that kissing is a very common human behavior, scientific research on its neuronal foundation is sparse. Pehrs et al., (2014) used fMRI to analyze participants' brain activations to viewing kissing scenes from romantic comedies. They found that perception of kissing scenes leads to activations in the primary and secondary visual cortices, the fusiform gyrus, the amygdala, hippocampus, and medial prefrontal cortex. Thus, viewing of kissing scenes seemed to mainly activate areas related to visual perception and the processing of emotions. Unfortunately, the authors did not analyze lateralization of

activation, leaving it unclear whether viewing of kissing scenes lead to lateralized activity in the brain. Moreover, as of yet, no fMRI study on actual kissing or imagination of kissing has been performed, leaving it uncertain which brain activations are related to the act of kissing, and whether they are lateralized. This is unfortunate since while it might be difficult to perform actual partner kisses in an MRI machine due to the fact that the head coil would potentially be in the way, performing kisses with closed eyes while imagining a partner would be a feasible paradigm for a first exploratory study.

In contrast to the lack of imaging studies, several authors have investigated the laterality of kissing on the behavioral level. In the first study investigating lateralization of kissing, Güntürkün (2003) observed 124 kissing couples in public places like international airports, large railway stations, beaches, or parks in different countries (the United States, Germany, and Turkey). The author found a significant rightward asymmetry, with 64.5% of couples showing rightward head-turning preference during kissing and 35.5% of couples showing a leftward head-turning preference.

A rightward head-turning asymmetry has been replicated by several other authors. For example, Barrett et al., (2006) observed 125 kissing couples in public places in Belfast and found that 80.8% showed a rightward head-turning preference when kissing. In addition, they asked 240 students at Stranmillis University College, Belfast, to kiss a symmetrical doll on the cheek or lips in order to assess individual kissing preference without the impact of a kissing partner. Here, the authors found that 77.5% of the volunteers turned their head to the right when kissing, a percentage that was not significantly different from what had been found in the observational study. Using a similar technique with a symmetrical doll, Ocklenburg and Güntürkün, (2009) showed that out of 150 students, 62% kissed to the right and 38% to the left, resulting in significant rightward asymmetry. Similar results were also observed by van der Kamp and Canal-Bruland, (2011) who found that out of 57 participants, 71.9% showed a rightward head-turning preference when kissing, whereas 28.1% showed a leftward head turning preference.

While all of these studies were performed in Western participants, a recent study in a non-W.E.I.R.D. (Western, educated, and from industrialized, rich, and democratic countries) sample (48 Bangladeshi heterosexual married couples) also found a rightward bias (Karim et al., 2017). In this sample, 72.92% of kiss initiators and 75% of kiss recipients showed a rightward head-turning preference when kissing. This shows that the rightward bias when kissing is not caused by Western cultural norms, but seems to be a cross-cultural phenomenon. Nonetheless, more research in diverse samples has to be conducted to draw any final conclusions.

Several authors have tested the motor bias hypothesis with regard to kissing, e.g., whether handedness can predict the direction of the head turn when kissing. The first study to investigate the relation of handedness and head turning preference during kissing was conducted by Barrett et al., (2006). They had 240 volunteers kiss a symmetrical doll's face, with 176 participants (77.5%) kissing to the right and 64 (22.5%) kissing to the left. There was no significant difference in handedness of right- and left-kissers: 88.6% of the right-kissers and 84.4% of left-kissers were right-handers.

In contrast, a later study by Ocklenburg and Güntürkün, (2009) supported the motor bias hypothesis. The authors assessed head turning preference while kissing, as well as handedness, footedness, and eye preference with questionnaires. Unlike Barrett et al. (2006), these authors did not compare the frequency of left- and right-handedness between left- and right-kissers but used lateralization quotients as a continuous measure of both lateralization strength and direction instead. Right-kissers had a significantly higher (more rightward) average lateralization quotient than left-kissers for both handedness and footedness, but not for eye-preference. These findings indicated stronger rightward motor asymmetries in right- than left-kissers. Moreover, Ocklenburg and Güntürkün, (2009) also reported a somewhat higher

percentage of right-handers for right-kissers (~96%) than for left-kissers (~86%). Subsequently, one study failed to replicate this finding (van der Kamp and Canal-Bruland, 2011), while another did replicate it (Karim et al., 2017). Unrelated to kissing, a head-turning study investigating the relation between head turning preferences and handedness in children with congenitial torticollis also found a significant relationship between these two preferences (Ocklenburg et al., 2010).

Taken together, half of the studies investigating the role of motor biases on head-turning preference during kissing reported a significant relation, while the other half failed to find such an association. This indicates that the relation might exist, but may be rather weak, so that large sample sizes are needed in order for the effect to reach significance. Therefore, the motor bias theory could explain a small part of the kissing results, but clearly does not yield the sole explanation for the observed data pattern.

Regarding the role of emotional context, Barrett et al., (2006) noted that they expected a difference in lateralization between the emotional kisses exchanged within couples in the observational part of their study and the more neutral kisses that participants gave the doll. As there was no significant difference in the proportions of left- and right-kissers for doll and partner kisses, (Barrett et al., 2006) concluded that emotional lateralization is unlikely to explain kissing laterality.

Another study investigating the role of emotional context during kissing was performed by Sedgewick and Elias, (2016), who conducted an archival analysis of head turning bias in images of romantic kissing (wives kissing husbands) compared to parental kissing (mothers or fathers kissing sons or daughters). They found a strong effect of emotional context: For romantic kissing, couples showed a right-turn bias, just as previous studies on romantic kissing had indicated (Sedgewick and Elias, 2016). In contrast, there was a left-turn bias for parental kissing. The authors explained this unexpected finding by assuming that there might have been a learning effect, with leftward cradling bias (see above) influencing the direction of the kiss towards an infant.

Evidence for learning effects on kissing side preference also comes from a study on the role of social pressures on the side preference during cheek kissing as a greeting (Chapelain et al., 2016, 2015). These authors observed cheek kisses in public places in ten cities in France. Interestingly, they found that within cities, there were population-level side biases for cheek kissing, with the majority of individuals within each city showing a consistent bias. However, whether this direction was left or right depended on the city. The authors concluded that social pressures (e.g., a need for alignment of cheek kissing direction with other individuals in the same city) can play a large role when determining the side preference during kissing. Notably, this idea is in line with animal works showing that laterality on the population level can arise as an evolutionarily stable strategy when organisms showing lateralized behavioral preferences must coordinate with other organisms that also show asymmetric behavior (Ghirlanda et al., 2009).

Unfortunately, no study has yet conducted a valence-specific analysis for emotional context on kissing laterality by comparing kissing laterality for emotionally positive kisses, e.g., in a romantic context with emotionally negative kisses, e.g., when feeling social pressure to kiss a family member with bad breath. Thus, it is somewhat difficult to assess to what extent the emotive bias theory can explain kissing side biases. However, the studies by Sedgewick and Elias, (2016) and Chapelain and co-workers (Chapelain et al., 2016, 2015) clearly show that context can modulate kissing side bias. More research specifically addressing the role of valence is thus needed before any conclusions can be drawn.

5. Open questions and future research directions

Given the fact that social touch represents an important part of human everyday life and has been linked to psychological health and well-being, reduced stress, and better cholesterol levels (Floyd et al., 2009; Light et al., 2005), the lack of neuroscientific studies investigating it is striking. This is insofar understandable as it might be difficult to perform kisses or embraces in the MRI scanner, but recent advances in EEG technology provide the ability to capture brain activity during actual physical contact of freely moving participants. For example, recently more and more lightweight and ultraportable EEG systems have become available that would allow for the recording of EEG oscillations while participants perform actual embraces, kisses or cradling. Using these, hemispheric asymmetries in frontal EEG alpha oscillations during social touch could be assessed, a commonly used marker for emotional lateralization (Reznik and Allen, 2018), providing a way to estimate valence specific brain activity during social touch. Given that emotions are adaptive because they guide actions, paradigms that allow us to study the integration of emotional and motor systems will create better understanding of how these two lateralized networks interact.

In addition, more research specifically manipulating the emotional valence component is needed for all forms of social touch to fully test the different emotive bias theories. This is particularly important for kissing and cradling, as it has not been investigated for these behaviors at all, but also for hugging more research in larger samples and independent replication of published findings are essential. Another open question in this context is to what extent different forms of social touch are correlated, i.e., whether they represent separate forms of behavioral laterality, and whether they are modulated by the emotional valence in the same way and to the same degree. To this end, studies investigating laterality of all forms of social touch in the same sample are needed.

Another question that should be investigated in greater depth is the extent to which the need for social coordination between individuals within a social group drives the existence of population-level lateralized behaviors. Notably, an association between social coordination and population-level lateralization has been observed in several vertebrate species, ranging from different fish species (Bisazza et al., 2000), to amphibians such as toad tadpoles (Dadda et al., 2003) and mammals like elephants (Karenina et al., 2018). Importantly, this relation has also repeatedly been observed in animal species that are phylogenetically very distant from humans, such as insects (Niven and Bell, 2018); for example in ants (Frasnelli et al., 2012) and honey bees (Rogers et al., 2013). Thus, it likely represents a general functional principle of asymmetric nervous system organization in bilateral organisms that might also affect behavioral preferences in humans. In fact, social touch is one of those circumstances where the advantage of being lateralized in the same direction as the social partners might be particularly evident in humans. For example, if kissing on the cheek is used as a form of greeting, having a different head-turning bias than the social partner could result in an unwanted kiss on the mouth or a head bump that could lead to negative social consequences. Such social constraints are supported by findings that population-level side preferences during cheek kissing as a greeting vary by city (Chapelain et al., 2016, 2015). While it might be difficult to disentangle the extent to which such associations are driven by innate individual preferences or by enculturation within the given social group, it would nevertheless be important to conduct similar research on hugging as has been reported for kissing.

Last, but not least, kissing, cradling and embracing are not the only forms of social touch in which humans partake. Others forms of social touch, such as stroking (Morrison, 2016), shoulder patting, high-fiving, hand-shaking, hand-holding, or tickling have not yet been investigated regarding their laterality and could yield additional interesting insights.

6. Conclusion

Kissing, embracing, and cradling represent three forms of social touch that are integral parts of human interaction in almost all societies around the world. For these three forms of social touch, the literature has clearly indicated a population-level side bias: to the left for cradling and to the right for kissing and embracing. For all three forms of social touch, the empirical evidence suggests that the motor bias hypothesis might explain some of the inter-individual variability in side preference. However, it clearly cannot yield a satisfying explanation on its own. For all three forms of human social touch there is evidence that emotional lateralization might have an impact. Within the framework provided by emotive bias theories, it seems to be specifically the right hemisphere theory that can explain the observed data patterns. Taken together, lateralization of human social touch seems to be determined by an interaction between motor and emotive biases.

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