eScholarship International Journal of Comparative Psychology

Title

Bringing Touch Back to the Study of Emotions in Human and Non-Human Primates: A Theoretical Exploration

Permalink https://escholarship.org/uc/item/4gf475c2

Journal International Journal of Comparative Psychology, 31(0)

ISSN 0889-3675

Author Botero, Maria

Publication Date 2018

DOI 10.46867/ijcp.2018.31.02.05

Copyright Information

Copyright 2018 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <u>https://creativecommons.org/licenses/by/4.0/</u>

Peer reviewed



Bringing Touch Back to the Study of Emotions in Human and Non-Human Primates: A Theoretical Exploration

Maria Botero

Sam Houston State University, Huntsville, Texas

This paper provides a theoretical exploration of how comparative research on the expression of emotions has traditionally focused on the visual mode and argues that, given the neurophysiological, developmental, and behavioral evidence that links touch with social interactions, focusing on touch can become an ideal mode to understand the communication of emotions in human and nonhuman primates. This evidence shows that touch is intrinsically linked with social cognition because it motivates human and nonhuman animals from birth to form social bonds. It will be shown that touch is one of the modes of interaction used by the mother-infant or caregiver-infant dyad that facilitates the expression of emotions by the infant (and later the expression of emotions by the adult that the infant has become) in ways that are understood by other members of the group.

Keywords: expression of emotions, development of emotions, touch, apes, monkeys

This paper provides a theoretical exploration of how comparative research on emotions has traditionally focused on the visual mode to understand the perception of emotions and how that research has ignored the role played by other modes of interaction, such as touch, in the perception of emotions. The general aim of this paper is to argue that, given the neurophysiological, developmental, and behavioral evidence that links touch with social interactions, focusing on touch can become an ideal mode to understand the communication of emotions in human and non-human primates.¹ This evidence shows that one of the distinctive characteristics of touch is that touch rewards social interactions. Moreover, this evidence shows that touch requires an intentional movement towards the object or social partner (as opposed to facial expressions that can sometimes be expressed as a reflex and can be produced in the absence of social partners). It will be shown that touch is one of the modes of interaction used by the mother-infant² or caregiver-infant dyad that facilitates the expression of emotions by the infant (and later the expression of emotions by the adult that the infant has become) in ways that are understood by other members of the group. It is important to clarify that the argument does not defend touch as the only mode that must be considered. Rather, touch will serve as an

Please send correspondence to Dr. Maria Botero, Sam Houston State University (Email: mbotero@shsu.edu)

* Dr. H. M. Hill acted as action editor on this paper for the special issue

¹ Most of the examples reviewed in this paper will focus on apes, in particular chimpanzees, and on monkeys, in particular macaques. It is plausible that the ideas presented can be extended to other primate species. However, I will focus on these species because most of the work in touch has focused on these two species.

² Female parental care is common in more than 300 species of nonhuman primates, with the exception of a few species of marmosets, tamarins, and human primates, in which the care of the infant can be provided and shared by both genders. From this point, every time I refer to "mother" or "maternal care," I am using it as a convenient name for caregiving practices performed by the main caregiver of an infant. The aim is to highlight the continuity of caregiving practices among human and nonhuman primates, but those practices are not specific to the gender of the caregiver in humans.

example of how a mode of interaction other than visual can be incorporated in a comparative the study of emotions.

To demonstrate the hypothesis, first, one of the best known approaches that have been adopted to study the expression of emotions in non-human animals will be examined: an adaptation of Paul Ekman's Facial Scoring System (FACS) (Ekman & Friesen, 1978) to measure facial expressions of nonhuman emotions. Then, criticisms of using only one mode of communication or one behavioral feature to understand emotions in apes will be examined. Two different forms of evidence will be reviewed to argue for the inclusion of touch in the study of emotions. First, it will be argued that if we focus only on visually oriented forms, then we may not be able to include the ways in which nonhuman primates interact or to include the ways that mothers and infants interact in non-western rural cultures. Second, based on the neurophysiology of touch, it will be argued that touch is the ideal mode of interaction to show how emotions are intrinsically linked with social cognition and that this system motivates human and nonhuman animals from birth to form social bonds. Next, the importance of focusing on one element common to all primates (caregiver-infant or mother-infant interaction) will be demonstrated. It will be described how it is through this interaction that primate infants acquire the ability to communicate in ways that are understood by others and in ways that are adaptive. Finally, it will shown that one of the reasons the mother-infant interaction is so important for the development of emotions is that maternal touch can help primates to regulate their emotions, which, in turn, facilitates social interactions.

Understanding Emotions Through Visual Modes of Communication

Emotions have been studied in apes since the 1950s. D. O. Hebb (1946a, 1946b, 1949) argued for similarities in the recognition of emotions in humans and chimpanzees and for the need to classify emotions in distinctive patterns using neurophysiology and descriptions of behavioral patterns. These two aims continued to be found in later studies of emotions. Robert Plutchik (1962) argued for an evolutionary approach to emotions. He claimed that there are eight *primary* or *prototype* emotions (i.e., joy, sadness, acceptance, disgust, fear, anger, expectation, and surprise). All of these primary emotions are identifiable at a phylogenetic level and serve as communication and survival mechanisms for organisms. Based on this theory of primary emotions, Plutchik designed the Emotions Profile Index (EPI). This measurement is based on rates given by observers and through the combination of the eight primary emotions (i.e., adventurous, affectionate, brooding, cautious, gloomy, impulsive, obedient, quarrelsome, resentful, self-conscious, shy, and sociable).³ Silvan Tomkins (1962) also postulated a list of primary affects. He divided them into positive (i.e., interest-excitement, enjoyment-joy, and surprise-startle) and negative affects (e.g., distress-anguish, fear-terror, angerrage, shame-humiliation, and contempt-disgust). All of these affects are expressed through facial expression to others and to the self. According to Tomkins, the face is an innate activator for each affect; thus, specific affects are related to specific facial muscles.

However, the most famous of these approaches that argues for a distinct set of basic emotions is the one given by Paul Ekman (1992, 1999; Ekman & Cordaro, 2011). He argued for the existence of six basic emotions (BE) (i.e., anger, disgust, fear, happiness, sadness, and surprise) that are characterized by patterned changes in both the expression and the physiology of an organism. These changes are distinctive for each emotion or family of emotion, which helps differentiate each basic emotion or family of emotions from other

³ These emotional traits have been applied to the Kasekela community of chimpanzees in Gombe national Park (Tanzania).

affective states. Emotional expression plays a fundamental role in Ekman's theory. First, he followed Darwin in arguing that natural selection shaped expressions. Having an evolutionary history entails that basic emotions have the following characteristics:

- 1. There are common elements in the contexts in which emotions are found and occur (Ekman,1999). For example, the antecedent of fear is physical or physiological harm, but what counts as harm varies among cultures.
- 2. Emotions are observable in non-human primates (Ekman, 1992, 1999; Ekman & Cordaro, 2011). Ekman (1992) argued that his findings were consistent with other reports of similarity of expression in primates.
- 3. Emotions have a quick onset way to mobilize us to respond quickly to events that have adaptive value (Ekman, 1999).

Second, he designed the Facial Scoring System (FACS; Ekman & Friesen, 1978) to measure facial expressions of emotions and how these expressions can be correlated to BE. He showed how facial expressions are used across diverse groups of humans (Ekman, Sorenson, & Friesen, 1969; Ekman & Cordaro, 1972). Ekman called this approach the *Facial Affect Program*; the basic idea is to link every primary emotion to a distinct set of neural impulses that are directed to facial muscles (Ekman, Friesen, & Ellsworth, 1972; Keltner & Ekman, 2000).

Given Ekman's evolutionary approach to the study of emotion, several researchers have chosen Ekman's FACS (Ekman & Friesen, 1978) to study facial expression of emotion in non-human primates. Some (Steiner & Glaser, 1984, 1995; Steiner, Glaser, Hawilo, & Berridge, 2001; Ueno, Ueno, & Tomonaga, 2004) have applied FACS to study the relationship between facial expressions and taste. Preuschoft and van Hooff (1995) used FACS in studying homology in silent bared-teeth displays in macaques. Parr and colleagues (Vick, Waller, Parr, Smith Pasqualini, & Bard, 2007) created the Chimpanzee Facial Action Coding System (ChimpFacs), based on Ekman's FACS, and have used it to validate the existing categories of chimpanzees' facial expressions (Parr, Waller, Vick, & Bard, 2007; Waller, Bard, Vick, & Smith Pasqualini, 2007). Caeiro and colleagues (2013) designed OrangFACS to study facial expression in orangutans.

These studies focus on emotions from the perspective of visual modes of communication. Their aim was to identify homologous behavioral traits in reflexive facial displays of primates. They identified homologies of stereotyped facial displays, the different components of individual facial actions, and homology of the muscle substrate that are involved in facial expressions in monkeys, great apes, and humans. This reliance on stereotyped forms of facial communication has neglected to consider other modes of communication used in emotions. In what continues, I will show the limitations of focusing only on the visual mode.

Methodological Question: Is the Visual Mode the Best Way of Understanding Emotions in Primates?

As noted earlier, Hebb was one of the pioneers of the study of emotions in chimpanzees. Hebb (1946a, 1946b) argued, similar to Ekman's BE approach, that research of emotions in chimpanzees must find the distinctive features of the behavior associated with the emotion. However, he argued that this distinctive feature should not be the focus when understanding the expression of emotions in chimpanzees because one specific behavior can be used for different emotions. For example, piloerection can be associated with rage, fear,

submission, and sexual presentations. Instead, Hebb argued that these distinctive features must be understood in the context of an overall pattern of behavior. A similar suggestion was made by Plutchik (1962) who argued that to be considered a primary emotion, the emotional expression must not depend exclusively on a particular neurophysiological or body parts description for its definition.

This suggestion is in line with the way behavior is observed in apes and monkeys. The definitions of behaviors offered in different ethograms do not focus on one particular behavior but rather on a pattern of different behaviors; it is assumed that only some of these behaviors may be observed at a time and that some may be absent at certain times, absent in certain individuals, or absent in certain communities. For example, to define grooming in chimpanzees, there is a distinctive behavior that helps us recognize grooming (i.e., picking through hair and searching for/removing debris and/or parasites), but there are also a series of other behaviors that, even though they are included in the ethogram, may (or may not) appear during grooming, such as using the mouth, smacking lips, or teeth clacking. Thus, it seems contrary to the way behavior is traditionally observed to focus exclusively on one behavior (i.e., a particular facial expression) to identify an emotion such as fear or anger.

Moreover, Hebb argued that it is important to understand how these patterns of behavior appear in an individual. He argued that a short observation of a single moment is not useful for identifying emotions, such as an isolated facial expression produced by an individual. Rather, he argued for focusing on long-term observations to understand how these patterns of behavior are exhibited by the individual through time. This requires, as both Hebb (1946a) and Yerkes (1943) have suggested, that researchers become familiar with the behavior of individual chimpanzees to enable them to discriminate between these emotional states. For example, Hebb argued that to understand whether the behavior of a chimpanzee can be understood as expressing fear towards a person, it is helpful to have observed previously whether the chimpanzee consistently avoids all people or only unfamiliar people. This would allow researchers to differentiate among emotions and other states (i.e., fear, nervousness, and shyness) in that individual.

This methodological suggestion is in accordance with current observational practices in the field. To fully understand a behavior, researchers need to become familiar with the history of the individuals observed. Consider, for example, the case of grooming. To understand grooming in male chimpanzees, several factors such as rank of the focal, rank of the grooming partners, body mass, and past coalitions must be observed (Foster et al., 2009). Rank, in turn, entails becoming familiar with the rates and duration of aggressive displays of the individuals observed. Thus, understanding the past history of an individual (e.g., current status as an alpha) allows researchers to understand the grooming patterns of this individual.

In a similar way, familiarity with the individual would allow researchers to establish a baseline behavior for the individual and to understand, as Hebb suggested, emotional behavior. Becoming familiar with an individual also allows researchers to recognize individual behaviors that are not immediately related to the emotion (e.g., scratching itself, head movements, vocalizations) but that are part of the emotional pattern of behavior for that specific individual. These individual behaviors facilitate predicting specific emotions in the individual.

If we accept this criticism, it becomes evident that the study of the expression of emotions in apes must go beyond one feature (i.e., facial expression) and include diverse patterns of behavior including long-term observation of such patterns for an individual. There are several kinds of behavior beyond facial expressions (e.g., avoidance, proximity, piloerection, vocalization), several individual patterns of behavior that have an effect in the expression of emotions (e.g., rank), and diverse modes of communication that can be used to express emotions (i.e., tactile, auditory) that must be considered to understand emotional patterns of behaviors. In this paper, the focus will be on only one of these aspects: the use of touch as a mode of communication. Moreover, a developmental perspective will be adopted to show the importance of touch for our understanding of emotions in comparative psychology.

Touch

Touch, because of its links to pro-social behavior, is one of the best candidates to explore the role that other modes of communication play in human and nonhuman emotions. It has been shown that there is a link between behaviors that include touch and social bonding in nonhuman primates, for example, grooming in macaques (Majolo, Schino, & Aureli, 2012) and chimpanzees (Newton-Fisher & Lee, 2011), and contact in the form of embrace after aggressive encounters (Fraser, Stahl, & Aureli, 2008), as well as links between touch and pro-social behavior in the evolution of human primates (see, for example, Boone & Buck, 2003; Botero, 2016). I will focus on touch (as opposed to behaviors that include touch), to understand the role it plays in the development of emotions in humans and apes.⁴

Touch in Mother-Infant Interaction in Apes and Across Human Cultures

Facial expression helps us understand homologies in the expression of emotions in primates; however, it can also limit what can be observed in apes and humans in non-Western cultures.

Not-in-your-face apes. In the wild, even when the opportunity for face-to-face interaction arises, such as in breastfeeding, little gazing occurs between mother and infant in primates. Shortly after birth, chimpanzee mothers pay little visual attention to their babies with the exception of watching when they are grooming and cleaning their babies or licking the umbilical cords (Plooij, 1984; for a similar finding in monkeys, see Perry & Manson, 2008). It is only at 9 weeks of age that infant chimpanzees have been observed becoming interested in their mother's face (Plooij, 1984). Much later, when the infant is 4 months old, there is a clear indication that they start focusing on the mother's face for communication; for example, begging behaviors only appear at this age. Before then, the infant takes the food directly without looking at the mother (Plooij, 1984).⁵

⁴ Even though the focus is on apes, it is likely that these ideas are applicable to other species. Future research may include not only apes and monkeys but prosimians. Given that some of them are nocturnal, it is likely that a facial expression may not be important for them.

⁵ It may be objected that observations in captivity show that infant chimpanzees prefer face-to-face interaction. Tomonaga et al. (2004) and colleagues showed that infant chimpanzees presented "play-face" as a response to photographs of humans gazing at them. Moreover, they show a decline in cradling behaviors and increase in mutual engage in mutual gaze through development. These findings seem to contradict the observations done in the wild described earlier (Plooij, 1984). I would argue for caution when extrapolating the observation from captivity to a general species behavior because the ecological conditions found in captivity influence the way mother and infant pairs interact. I join others in arguing that the interactions between the human caregiver and the infant ape can modify the emergence of abilities in the social cognition of the ape (Russell, Bard, & Adamson, 1997).

Moreover, even though chimpanzees and humans share much of the same facial musculature (Waller et al., 2007), chimpanzees do not have some of the facial features that allow humans to easily detect facial expressions. As Parr and colleagues argued (Parr et al., 2007; Vick et al., 2007), because of skin pigmentation, reduced outer lip vermillion, and eye morphology, the chimpanzee face, unlike the human face, does not offer a salient contrast that facilitates the detection of facial movement. Furthermore, chimpanzees lack the contrast offered by the eye sclera, which, in humans, makes it easier to perceive eye movements (Kobayashi & Kohshima, 2001).

Not-in-your-face humans. An emphasis that privileges face-to-face interaction to understand the development of emotions in primates presents a problem for the understanding of the development of emotions in human primates across diverse cultures. One of the most widespread techniques of the mother-infant interaction across human cultures is the mother holding the baby close, providing the infant with constant contact (see Tronick, 1995, for an overview of the diversity of cultures in which touch has been recorded). For example, mothers who belong to the Gusii community in Kenya (LeVine, 2010) do not engage in face-to-face social communication with their infant, especially not in verbal exchanges, two cornerstone features of Western mother-infant social interaction; instead, Gusii mothers comfort infants through body contact day and night. Moreover, when researchers (LeVine, 1990; Tronick, 2005) asked Gusii mothers to engage in face-to-face play with their infants, they found (through video microanalyses) that when the infants made eve-to-eve contact and smiled, mothers looked away from their infants. As a response, infants looked away and stopped smiling. According to the authors, this is exactly opposite to the pattern observed in interactions of Western mothers and their infants. Another example can be found in the mother-infant pairs in Zincanteco, southern Mexico (Brazelton, 1972); in the first year of life, the infant is not often propped up to look around, not often stimulated by face-to-face contact and not often put on the floor to explore by themselves. However, these infants did not exhibit any significant cognitive and social differences compared with North American children as measured through the Neonatal Behavioral Assessment scale (NBAS).⁶

Meanwhile, face-to-face interaction seems to be the preferred mode in urban communities (but not in rural communities). Keller and colleagues (for a summary, see Keller & Kärtner, 2013) described two prototypical parenting styles that are adaptive: the distal and proximal styles. The distal style of parenting emphasizes face-to-face contact, object stimulation, and extensive verbal conversations. This parenting style predominantly occurs in middle-class families from urban areas of Western industrial and postindustrial societies (e.g., Berlin, Los Angeles or Athens). The proximal style of parenting emphasizes close bodily proximity and body/motor stimulation. This parenting style predominantly occurs in traditional subsistence-based communities (e.g., in sub-Saharan Africa or rural India).⁷ Thus, face-to-face interaction does not seem to have much explanatory power when used to describe the mother-infant interaction in diverse cultures.

⁶ For other examples of constant contact with their mothers that do not involve face-to-face interaction, see Bambara

babies (Mali) (Bril & Sabatier, 1986) and Ngas-speaking toddlers in Nigeria (Childers, Vaughan, & Burquest, 2007). ⁷ For other examples, see LeVine et al. (1994): Boston and Gusii community mothers; Carra et al. (2014): West African and Italian mothers; Konner (2005): Guatemala and Boston mothers.

Neurophysiology of Touch

Touch, because of its neurphysiological characteristics, can allow us to understand how emotions are connected to social interaction. To fully understand the unique characteristics of touch, it is necessary to understand how, from a neurophysiological perspective, it is possible to distinguish between two kinds of touch: discriminative (sensory) and emotional (affective), based on the area where touch is experienced (Ackerley, Saar, McGlone, & Backlund Wasling, 2014). Touch perceived through glabrous skin (i.e., palms of the hand) is linked to discriminative touch. Meanwhile, hairy skin (i.e., face, arms, etc.) contains C-tactile (CT) afferents, which are fundamental for affective touch and will preferentially signal an affective aspect of touch (Olausson, Wessberg, Morrison, McGlone, & Vallbo, 2010).

Several authors (Löken et al., 2009; McGlone, Vallbo, Olausson, Löken, & Wessberg, 2007) claim that CT afferents play an important role in the affective processing of interpersonal touch. Both the human psychophysical and animal genetic studies show that CT activation is associated with hedonic effects, suggesting an important role for CTs in social touch (Olausson et al., 2010). Anatomically, CTs and animal CLTMs C-fiber low-threshold mechanoreceptors (CLTMs) are associated with hairs: Both afferent types are only found in hairy skin (Liu et al., 2007; Li et al., 2011; Lou et al., 2013; Olausson, Wessberg, McGlone, & Vallbo, 2010; Vrontou, Wong, Rau, Koerber, & Anderson, 2013).

McGlone and colleagues developed the *affect touch hypothesis*, which predicts that the role of the CT system is to provide emotional and behavioral responses to skin-to-skin contact.⁸ Thus, it is not surprising that several studies have found that it is possible to communicate different emotions, such as fear, anger, disgust, love, gratitude, and sympathy, through touch (Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006).

There are several elements that can make touch pleasant and ideal for enhancing social bonds. First, the speed of touch can affect the perception of touch. There is an optimal velocity of touch: stroking in the range of 1-10 cm/s, with a peak about 3 cm/s. This kind of touch (a stroke as opposed to a tap) and velocity of touch is commonly perceived as the most pleasant kind of touch (Etzi, Carta, & Gallace, 2017). Moreover, most people, when asked to stroke their partner or a baby, are likely to spontaneously use this velocity of touch (Croy et al., 2016; Triscoli, Croy, Olausson, & Sailer, 2017). Second, Gentsch et al. (2015) found that active stroking elicits more pleasure when this kind of touch is given to another's skin rather than giving it to one's own skin. Moreover, they found a *social softness illusion* (SSI); the participants in this experiment judged another's skin softer than their own skin, even though the softness was a controlled variable (in other words, they found that participants always found the skin of other people softer than their own skin, regardless of the qualities of the skin). This SSI appeared when the neurophysiological system for touch, CT afferents, was activated in the receiver. The authors suggested that these findings could be interpreted as a mechanism for social bonding and affiliation.

In summary, based on the neurophysiology of touch, choosing touch as the mode of interaction when studying how we perceive emotions allows us to, first, use a mode of interaction that has a distinct neural system devoted exclusively for affective perceptions. Second, because of the neurophysiological make-up

⁸ Moreover, brain imaging studies have shown that the posterior insular cortex is the primary cortical target area for CT afferents (Björnsdotter et al., 2009; Morrison et al., 2011; Olausson et al., 2002).

present in human and nonhuman animals, the use of touch is linked to pleasant reactions. Thus, touch is a mode of interaction that motivates human and nonhuman animals to form social bonds with others.

It is important to notice that this emphasis on the neurophysiological aspect of touch is not advocating for an innate and reflexive mechanism that cannot be affected by the environment. Sailer and Ackerley (2017) found that individuals with low exposure to touch are comparable to those who receive regular exposure to touch in aspects such as tactile sensitivity and perceived intensity of the stimulation; however, such individuals differ in the hedonic evaluation of touch (i.e. they do not find more pleasant the kind of touch that is commonly perceived as the most pleasant kind of touch). Individuals with a low exposure to touch were exposed to moving touch at a CT (C-tactile afferents)-optimal velocity of touch (stroking in the range of 1-10 cm/s, with a peak about 3 cm/s). They reported this kind of touch (i.e., stroke at optimal velocity) less pleasant than controls. Furthermore, the curvature of pleasantness ratings for different velocities was flatter for these individuals; this means that they did not discriminate affective touch well. In summary, the results of this study show how experiences of social and interpersonal touch have a deep impact on human perception of affective touch; those who experience less frequent touch interactions, even though they perceive the emotion through touch, show decreases in affective touch processing.

The Development of Touch

When considering the development of perception in humans, newborn babies cannot focus their eyes well, and their visual acuity is limited (Slater, 2001)⁹; only later do they start using gaze to explore in more detail the objects around them (Ruff, 1984). Meanwhile, newborns can use touch to investigate their world. For example, newborn infants are capable of identifying different geometric shapes through the use of touch (Streri & Féron, 2005). Thus, the sensitivity of touch is developed from birth, and the infant is able to use this mode of perception to interact with the world from the moment of birth and engage in their first communicative interactions. To my knowledge, no similar studies have been conducted in apes. However, if we consider how chimpanzee infants travel in a ventral position where they are constantly required to grab their mother's hair and have limited visual information, it is conceivable that they can use touch from the moment of birth.

Thus, when we adopt touch as a mode of interaction to measure how we perceive emotions, we find that this is a mechanism that it is in place at the moment of birth (as opposed to vision) that allows the infant to start engaging in emotional and behavioral responses to skin-to-skin contact from the moment of birth. Moreover, there is an intentional element in touch that is present from the moment of birth that allows the infant to interact with the world. As opposed to other modes of interaction, such as vision or hearing, touch requires, as Streri and colleagues have demonstrated, that infants actively and intentionally use touch to engage with the world around them.

It may be argued that newborn human infants show a preference for face-to-face interaction, imitate facial expressions, and, at birth, are capable of following their mother's gaze (Meltzoff & Moore, 1977, 1994). However, even though the use of facial expressions is present from birth, it is not clear whether these facial

⁹ It may be argued that newborns are able to detect the difference between gaze and avert gaze (Farroni, Csibra, Simion, & Johnson, 2002). However, the point of my argument remains, the information that they can gather from the visual mode is still very limited at this stage.

expressions are just a reflex or are intentionally connected to an emotion. For example, it has been shown that infants are not capable of recognizing distinct facial expressions of emotions (Widen, 2013; Widen & Russell, 2008). Other primates also have this ability for following gaze; early imitation of facial features has been found in chimpanzees (Takeshita, Myowa-Yamakoshi, & Hirata, 2006) and monkeys (Ferrari & Fogassi, 2012). Similar questions can be asked regarding the comprehension of these facial features in these species.

Moreover, it seems that tactile modes of interaction not only develop earlier than vision but also help the development of visual modes of communication. Della Longa, Gliga, and Faroni (2017) showed that 4month-old infants had difficulties discriminating faces; however, they learned to discriminate faces when parents provided gentle stroking. Thus, touch seems to facilitate visual modes of communication.

Touch as the Way to Understand the Development of Communication of Emotions

An evolutionary perspective on the expression of emotions has to provide an explanation of how emotions are used as mode of communication; that is, how both human and nonhuman primates are capable of perceiving the emotions of their social partners. The neurophysiological and developmental characteristics described above show, first, that infants are ready from the moment of birth to use touch in their interactions with their caregivers. Second, that while facial expressions can be expressed as a reflex and can be produced in the absence of social partners, touch requires an intentional action to move towards the object or social partner. Touch requires an "other" and, as shown in the SSI illusion, touching an other (as opposed to themselves) is linked to pleasurable sensations.

How exactly is touch used as part of the development of emotions in the caregiver-infant interaction? Hertenstein (2002) showed how caregivers, through bodily changes such as skin temperature, respiratory patterns, perspiration, and pulse, can communicate the differences in emotional responses that they are experiencing. Hertenstein also argued that the caregiver does not need to be mindful of this communication; for example, a mother may be changing an infant's diaper, thinking about her stressful day, and not be aware she is communicating her anxious state to the infant. A similar argument can be made for great apes; consider for example, how in the wild, chimpanzee mothers touch their infants in different contexts, such as grooming, tickling, and playing, but most of the day is spent traveling. During that time, the mother spends long periods in contact with the infant. When the infant is traveling ventrally, mother and infant become a tight bundle, and this allows the infant to receive important information about the mother's emotional reactions to the external world. The infant can feel the mother's heartbeat speed up during an aggressive encounter; s/he can experience the mother's relaxed muscles when the mother is part of a grooming session; and, because of piloerection, the infant notices when his/her mother is aggressive or scared. Thus, the infant will start to comprehend through touch the reactions accepted in his/her mother's group.

Similarly, the mother gathers this same kind of information when she holds her infant during travel or touches her infant in other contexts. A chimpanzee mother is constantly monitoring her infant's behavioral state through touch (Goodall, 1986). She can sense when the infant is tense, relaxed, or experiencing piloerection and bring the infant to an adequate level of emotional response. Furthermore, through pulling their mother's hair or a tightening their grip, chimpanzee infants can start making a voluntary movement to express

an emotion such as fear or anger.¹⁰ Thus, when mother and infant touch, they process sensory information that is composed of each other's emotional responses, and they change their behavior accordingly.¹¹ In short, during the close contact interaction with the mother, the infant chimpanzee is first introduced to the mother's emotional responses, and this interaction is essential for the development of the infant's emotional responses. Moreover, it allows the infant to start expressing emotion in voluntary ways.

The importance that the mother-infant interaction has for the development of the expression of emotions - that can be understood by others - can be observed by the kinds of consequences that disrupting this interaction has for the infant's social development. One of the first things that fails to appear when the mother is missing (in both human and nonhuman primates) is the ability to communicate in ways that are understood by others. Experiments with macaques in the 1960s and 1970s (Harlow, Dodsworth, & Harlow, 1965; Harlow & Suomi, 1971) separated infants from their mothers and/or created "monster mothers" (i.e., replace mothers with wire constructions resembling a monkey that randomly threatened the infant by releasing spikes or high-pressure streams of air). The infants in these experiments exhibited abnormal behaviors that prevented them from engaging in social interactions: compulsive non-nutritional sucking, repetitive stereotyped movements, self-injurious behaviors, an inability to engage in social interaction (including sexual interactions), aggressiveness toward other members of the group, an inability to engage in cognitive tasks, and a lack of exploration, accompanied by rocking movements. Observations of the behavioral development of chimpanzee infants under new practices of enriched environments in captivity found similar, although milder, behavioral consequences for infants raised in groups that included peers. Some of these subjects also exhibited body rocking, mouthing, lack of initiative, lack of investigatory behavior, an inability to copulate, and an inability to nurse an infant (Brent, Lee, & Eichberg, 1991; van Ijzendoorn, Bard, Bakermans-Kranenburg, & Ivan, 2009). In wild chimpanzees, it has been shown that the absence of the mother, even in later stages of infancy, has profound effects on the infant's social behavior and levels of anxiety (Botero, MacDonald, & Miller, 2013).

The results of isolation in human infants have been observed in the case of the Romanian orphanages. In 1990, after the fall of the Ceauşescu regime, it was found that children in orphanages had been housed with minimal food, minimal clothing, minimal heat, and minimal caregiving. Several studies centered on these infants found difficulties in the children's attachment patterns and delays in cognitive and social functioning (Fisher, Ames, Chisholm, & Savoie, 1997; Kaler & Freeman, 1994; Marcovitch et al., 1997).

Similar effects have been observed in less extreme examples. High levels of stress interfere with maternal support of emotion regulations in the child (Belsky, 1984). Children who have been raised with mothers who suffer from depression are more likely to develop maladaptive emotional regulatory patterns (Cole, Zahn-Waxler, & Smith, 1994). For example, when sensitive adults attempted to interact with infants of depressed mothers, they found these infants to be difficult interactive partners (it was difficult for these adult to understand the infants' needs and to engage with their responses); the adults often described these interactions as negative (Field, 1995).

¹⁰ It is important to take in to account that a tighter grip or pull can also be a reflexive response to the sensation of falling. However, these reflexive responses can be identified and measured differently from the voluntary kinds of touch I am describing. For example, if this pull is done in the context of the mother being still in which there is no risk of falling down.

¹¹ To my knowledge, there are no current studies in apes that show a preferred body part of touch or an optimal speed and length of touch as in humans. However, specific body part preferences for touch have been shown in other species (see, for an example in dolphins, Dudzinski et al., 2012).

The evidence described above shows that the mother is an essential element for the infant's emotional development. The next question we need to answer is, how does the interaction with the mother facilitate the development of the capability of understanding emotions?

The Importance of Touch: How Maternal Touch Allows the Infant Regulate Its Emotions and How This Changes our Methodologies

Emotions in nonhuman animals are intrinsically linked with social cognition. As de Waal (2011) argued, it is fundamental to focus on this social aspect of emotions when determining whether animals have emotions. He claims about emotions in animals that, "Because of their effect on others, emotions bring individuals together by converging internal states such as fear, hunger, playfulness, and sleepiness. The study of this phenomenon is crucial for our understanding of social life" (p. 199). A similar argument has been made for human primates: Ekman (1999) argued that one of the roles of BEs is to allow the human and nonhuman animal to communicate with other members of their communities. Thus, understanding emotions in human and nonhuman animals entails focusing on the mechanisms that animals use to understand the emotions that others in their social group are experiencing.

The reason why the interaction with their mother has significant effects for the social development of the infant has been explained from different perspectives in human and nonhuman primates (see, for example, attachment theory, Suomi, 2005). I would like to focus on one aspect that has not received much attention: stress. Infants experience several stressors (i.e., hunger, change in temperature, pain, loud noises). These stressors activate reflexive emotional responses such as fear or anger. The mother is able to help the infant bring these emotions to a comfortable level where they can be used as a mode of communication with others. That is why, if the mother is absent (or interacts with the infant in way that does not facilitate this regulation), the infant is unable to bring these emotions to a comfortable level and, as shown, this renders the infant unable to engage in social interactions.

Several studies have shown how touch (in particular, maternal touch) has a soothing effect that is so powerful that it may be used to overcome psychologically or physically stressful conditions. For example, Mason and Berkson (1962) showed that chimpanzee infants who received electric shocks emitted fewer stress vocalizations when held by humans than when left by themselves on a table. Studies have shown that maternal touch has an effect on an infant's level of comfort, learning, exploration, and attachment and on the amount of crying or fussing (for a review on the effects of touch for well-being, see Field, 2011). Benefits of touch have also been observed in preterm infants, who, when they are held for longer periods of time, exhibit respiratory regularity, weight gain with the same intake as control groups, high activity levels, better sleep/wake organization, and shorter hospitalization than other preterm infants who receive less touch (Tribotti, 1990). This effect of touch has also been observed in cross-cultural studies. NBAS scores of Asian and Native-American babies reveal that they are less irritable than urban North American babies. Mothers in these cultures often encourage their babies' calm dispositions through swaddling, close physical contact, and nursing at the first sign of discomfort (Chisholm, 1989; Freedman & Freedman, 1969; Murett-Wagstaff & Moore, 1989). Maternal care that includes touch (i.e., carrying the baby all day) has been observed to change poor NBAS scores of undernourished infants in Zambia, changing unresponsive newborns into alert, contented 1-weekolds (Brazelton, Koslowski, & Tronick, 1976). Moreover, infants also use touch as a way to regulate their

emotions in various contexts such as maternal unavailability and new environments (Moszowski et al., 2009; Stack & LePage, 1996; Stack & Muir, 1992).

These findings show how maternal touch helps the infant to self-regulate its emotions. There are several definitions of self-regulation, but they converge on the idea that, in self-regulation, individuals use different strategies to adjust their emotions, drives, urges, appetites, actions, lack of action, beliefs, and values to comfortable levels (Thompson, 1994). Organisms who are unable to regulate the intensity and duration of their emotional responses tend to become under- or over-aroused and are unable to attend to information in social encounters, thus impairing their ability to interact with others.¹² If the mother is missing, infants will be unable to self-regulate their emotions and will exhibit, as described in the previous section, stress-related behaviors and become unable to engage in social interactions.

In short, these studies have shown us that if the BEs approach is right, and human and nonhuman primates are born with a reflexive ability to experience BEs, the infant (and, later, the adult) will not be able to use emotions as a communicative mode unless they undergo interaction with their caregiver/mother. Tactile forms of interaction allow the infant to self-regulate their emotions in ways that are conducive to interact with the members of their own group. This knowledge entails a change in the way we conduct observations of the development of emotions: Instead of understanding the expression of emotions as individual reflexive processes (as postulated in the facial expression of BEs), we move towards understanding the development of emotions in the context of mother-infant interaction. More specifically, this change in approach suggests that touch, together with other modes of communication, must be adopted to understand the different ways in which mother and infant interact in the context of their social community (for the methodological implications of adopting this approach to the observation of mother-infant interaction, see Botero, 2014).

Even though this is just a theoretical suggestion, it is possible to translate these ideas into future studies. Stack and colleagues have designed different methodologies to measure how touch takes place between human mother and infant pairs (see Stack, 2010 for an overview). These coding mechanisms can potentially be adapted to nonhuman primates, allowing us to observe how touch takes place in different mother and infant dyads. Moreover, based on previous studies that found that touch is used in a distinct manner by different mother-infant dyads (see, for example, Mantis, Mercuri, Stack, & Field, 2018, on how touch is used by mothers who suffer from depression), the study of touch could potentially allow us to observe differences among nonhuman primate mothers and understand whether these are related to the development of social behaviors in the infant.

Conclusion

The general aim of this paper is to argue for the adoption of touch as one of the modes of communication used in mother-infant interaction in primates to understand the development of emotions in human and nonhuman primates (as opposed to approaches that focus entirely in visual/facial modes of expression). It is argued that including touch as one of the fundamental modes of interaction between mother and infant allows us to understand emotions in human and apes. Focusing on touch, because of its

¹² Another way of arguing for the importance of touch in the development of self-regulation of emotions can be done through the neural perspective. Such a review goes beyond the scope of this paper, but, for a summary, see Weller and Feldman (2003).

developmental and neurophysiological characteristics, allows us to understand how infants are ready from the moment of birth to make social connections to engage with others.

Acknowledgments

I am thankful to the audience of the ECOM fifth annual workshop "Emotions and Expressions" at the University of Connecticut where a previous draft of this paper was presented.

References

- Ackerley, R., Saar, K., McGlone, F., & Backlund Wasling, H. (2014). Quantifying the sensory and emotional perception of touch: Differences between glabrous and hairy skin. *Frontiers in Behavioral Neuroscience*, *8*, 34.
- Belsky, J. (1984). The determinants of parenting: A process model. Child Development, 55, 83-96.
- Boone, R. T., & Buck, R. (2003). Emotional expressivity and trustworthiness: The role of nonverbal behavior in the evolution of cooperation. *Journal of Nonverbal Behavior*, 27, 163-182.
- Botero, M. (2014). How primate mothers and infants communicate, characterizing interaction in mother-infant studies across species. In M. Pina & N. Gontier (Eds.), *The evolution of social communication in primates: A multidisciplinary approach* (pp. 83-100). Heidelberg, German: Springer.
- Botero, M. (2016). Tactless scientists, ignoring touch in the study of joint attention. *Philosophical Psychology*, 29, 1200–1214.
- Botero, M., MacDonald, S., & Miller, R. (2013). Anxiety-related behavior of orphan chimpanzees (*Pan troglodytes schweinfurthii*) at Gombe National Park, Tanzania. *Primates*, 54, 21–26
- Brazelton, T. B. (1972). Implications of infant development among the Mayan Indians of Mexico. *Human Development*, 15, 90-111.
- Brazelton, T. B., Koslowski, B., & Tronick, E. (1976). Neonatal behavior among urban Zambians and Americans. *Journal* of the American Academy of Child Psychiatry, 15, 97–107.
- Brent, L., Lee, D. R., & Eichberg, J. W. (1991). Evaluation of chimpanzee enrichment enclosure. *Journal of Medical Primatology*, 20, 29–34.
- Bril, B. & Sabatier, C. (1986). The cultural context of motor development: Postural manipulations in the daily life of Bambara babies (Mali). *International Journal of Behavioral Development*, *9*, 439–453.
- Caeiro, C., Waller, B. M., Zimmermann, E., Burrows, A. M., & Davila-Ross, M. (2013). OrangFACS: A muscle-based facial movement coding system for orangutans (Pongo spp.) *International Journal of Primatology*, 34, 115–129.
- Carra, C., Lavelli, M., & Keller, H. (2014). Differences in practices of body stimulation during the first 3 months: Ethnotheories and behaviors of Italian mothers and West African immigrant mothers. *Infant Behavior & Development*, *37*, 5–15.
- Childers, J. B., Vaughan, J., & Burquest, D. A. (2007). Joint attention and word learning in Ngas-speaking toddlers in Nigeria. *Journal of Child Language*, 34, 199–225.
- Chisholm, J. S. (1989). Biology culture and the development of temperament: A Navajo example. In J. K. Nugent, B. M. Lester, & T. B. Brazelton (Eds.), *The cultural context of infancy* (pp. 341–364). Norwood, NJ: Ablex.
- Cole, P. M., Zahn-Waxler, C., & Smith, K. D. (1994). Expressive control during a disappointment: Variations related to preschoolers' behavior problems. *Developmental Psychology*, *30*, 835–846.
- Croy, I., Luong, A., Triscoli, C., Hofmann, E., Olausson, H., & Sailer, U. (2016). Interpersonal stroking touch is targeted to C tactile afferent activation. *Behavioural Brain Research*, 297, 37–40.
- de Waal, F. B. M. (2011). What is an animal emotion? Annals of the New York Academy of Sciences, 1224, 191-206.
- Etzi, R., Carta, C., & Gallace, A. (2017). Stroking and tapping the skin: Behavioral and electrodermal effects. *Experimental Brain Research*, 236, 1–9.

- Ekman, P. (1992). Are there basic emotions?. Psychological Review, 99, 550-553.
- Ekman, P. (1999). Basic emotions. In Dalgleish, T, & Power, M. J. (Eds.), Handbook of cognition and emotion (pp. 45– 60). Chichester, England: Wiley.
- Ekman, P., & Cordaro, J. (1972). Universals and cultural differences in facial expressions of emotion. In *Nebraska symposium on motivation* (pp. 207–284). Lincoln, NE: University of Nebraska Press.
- Ekman, P., & Cordaro, D. (2011). What is meant by calling emotions basic. Emotion Review, 3, 364–370.
- Ekman, P., & Friesen, W. V. (1978). Facial action coding system. Palo Alto, CA: Consulting Psychology Press.
- Ekman, P., Friesen, W. V., & Ellsworth, P. (1972). *Emotion in the human face: Guide-lines for research and an integration of findings*. New York: Pergamon.
- Ekman, P., Sorenson, E. R., & Friesen, W. V. (1969). Pan-Cultural elements in facial displays of emotion. *Science*, *164*, 86–88.
- Ferrari, P. & Fogassi, L. (2012). The mirror neuron system in monkeys and its implications for social cognitive functions. In de Waal, F. B., & Ferrari, P. F. (Eds.), *The primate mind* (pp. 13–31). Cambridge, Mass: Harvard University Press.
- Field, T. (1995). Infants of depressed mothers. Infant Behavior & Development. 18, 1–13.
- Field, T. (2011). Touch for socioemotional and physical well-being: A review. Developmental Review, 30, 367–383.
- Fisher, L., Ames, E. W., Chisholm, K., & Savoie, L. (1997). Problems reported by parents of Romanian orphans adopted to British Columbia. *International Journal of Behavioral Development*, 20, 67–82.
- Foster, M. W., Gilby, I. C., Murray, C. M., Johnson, A., Wroblewski, E. E., & Pusey, A. E. (2009). Alpha male chimpanzee grooming patterns: implications for dominance "style". *American Journal of Primatology: Official Journal of the American Society of Primatologists*, 71, 136–144.
- Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. Proceedings of the National Academy of Sciences, 105, 8557–8562.
- Freedman, D. G., & Freedman, N. C. (1969). Behavioural differences between Chinese–American and European– American newborns. *Nature* 224, 1227.
- Gentsch, A., Panagiotopoulou, E., & Fotopoulou, A. (2015) Active interpersonal touch gives rise to the social softness illusion. *Current Biology*, 25, 2392–2397.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Belknap Press of Harvard University Press.
- Harlow, H., Dodsworth, R., & Harlow, M. (1965). Total isolation in monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, 54, 90–97.
- Harlow, H. F., & Suomi, S. J. (1971). Social recovery by isolation-reared monkeys. *Proceedings of the National Academy* of Sciences, 68, 1534–1538.
- Hebb, D. O. (1946a). On the nature of fear. Psychological Review, 53, 259-276.
- Hebb, D. O. (1946b). Emotion in man and animal: An analysis of the intuitive processes of recognition. *Psychological Review*, *53*, 88–106.
- Hebb, D. O. (1949). Temperament in chimpanzees: I. Method of analysis. *Journal of Comparative Psychology*, 42, 192–206.
- Hertenstein, M. (2002). Touch: Its communicative functions in infancy. Human Development, 45, 70-94.
- Hertenstein, M. J., Keltner, D., App, B., Bulleit, B. A., & Jaskolka, A. R. (2006). Touch communicates distinct emotions. *Emotion*, *6*, 528–533.
- Kaler, S., & Freeman, B. J. (1994). Analysis of environmental deprivation: Cognitive and social development in Romanian orphans. *Journal of Child Psychology and Psychiatry*, 35, 769–781.
- Keller, H., & Kärtner, J. (2013). Development—The cultural solution of universal developmental tasks. In M. Gelfand, C. Chiu, & Y. Hong (Eds.), Advances in culture and psychology (pp. 63-116). New York, NY: Oxford University Press.
- Keltner, D. & Ekman, P. (2000). Facial expression of emotion. In Lewis, M. & Haviland-Jones, J. (Eds.), Handbook of emotions, 2nd edition (pp. 236–249). New York, NY: Guilford Publications, Inc.
- Kobayashi, H. & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the primate eye. *Journal of Human Evolution*, 40, 419–435.

- LeVine, R. A. (1990). Enculturation: A biosocial perspective on the development of self. In D. Cicchetti & M. Beeghly, (Eds.), *The self in transition: Infancy to childhood* (pp. 99–117). Chicago, IL: University of Chicago Press.
- LeVine, R. (2010). Protective environments in Africa and elsewhere. In B. Lester & J. Sparrow (Eds.), *Nurturing children and families: Building on the legacy of T. Berry Brazelton.* Chichester; Malden, MA: Wiley-Blackwell.
- LeVine, R. A., Dixon, S., LeVine, S., Richman, A., Leiderman, P. H., Keefer, C. H. & Brazelton, T. B. (1994). *Child care and culture: Lessons from Africa*. New York, NY: Cambridge University Press.
- Li, L., Rutlin, M., Abraira, V.E., Cassidy, C., Kus, L., Gong, S., Jankowski, M. P., Luo, W., Heintz, N., Koerber, H.R. & Woodbury, C. J. (2011). The functional organization of cutaneous low-threshold mechanosensory neurons. *Cell*, 147, 1615–1627.
- Liu, Q., Vrontou, S., Rice, F. L., Zylka, M. J., Dong, X., & Anderson, D. J. (2007). Molecular genetic visualization of a rare subset of unmyelinated sensory neurons that may detect gentle touch. *Nature Neuroscience*, 10, 946–948.
- Löken, L.cS., Wessberg, S., Morrison, I., McGlone, F., & Olausson, H. (2009). Coding of pleasant touch by unmyelinated afferents in humans. *Nature Neuroscience*, 12, 547–548.
- Della Longa, L., Gliga, T., & Farroni, T. (2017). Tune to touch: Affective touch enhances learning of face identity in 4month-old infants. *Infancy*, 4, 451–473.
- Majolo, B., Schino, G., & Aureli, F. (2012). The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. *Animal Behaviour*, 83, 763–771.
- Mantis, I., Mercuri, M., Stack, D.M., & Field, T. M. (2018). Depressed and non-depressed mothers' touching during social interactions with their infants. *Developmental Cognitive Neuroscience*. https://doi.org/10.1016/j.dcn.2018.01.005
- Marcovitch, S., Goldberg, S., Gold, A., Washington, J., Wasson, C., Krekewich, K., & Handley-derry, M. (1997). Determinants of behavioural problems in Romanian children adopted in Ontario. *International Journal of Behavioral Development*, 20, 17–31.
- Mason, W. A., & Berkson, G. (1962). Conditions influencing vocal responsiveness of infant chimpanzees. *Science*, *137*, 127–128.
- McGlone, F., Vallbo, A. B., Olausson, H., Löken, L. S., Wessberg, J. (2007). Discriminative touch and emotional touch. Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale, 61, 173–183.
- Meltzoff, A. N., & Moore, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science*, *198*, 75–78.
- Meltzoff, A., & Moore, M. (1994). Imitation, memory, and the representation of persons. *Infant Behavior & Development*, 17, 83-99.
- Murett-Wagstaff, S., & Moore, S. G. (1989). The Hmong in America: Infant behavior and rearing practices. In J. K. Nugent, B. M. Lester, & T. B. Brazelton, (Eds.), *The cultural context of infancy* (pp. 319–340). Norwood, NJ: Ablex.
- Newton-Fisher, N. E., & Lee, P. C. (2011). Grooming reciprocity in wild male chimpanzees. *Animal Behaviour*, 81, 439–446.
- Olausson, H., Wessberg, J., Morrison, I., McGlone, F., & Vallbo, A. (2010). The neurophysiology of unmyelinated tactile afferents. *Neuroscience & Biobehavioral Reviews*, 34, 185–191.
- Parr, L. A., Waller, B., Vick, S. J., & Bard, K. A. (2007). Classifying chimpanzee facial displays by muscle action. *Emotion*, 7, 172–181.
- Perry, S., & Manson, J. H. (2008). *Manipulative monkeys: The capuchins of Lomas Barbudal*. Cambridge, Mass.: Harvard University Press.
- Plooij, F. (1984). *The behavioural development of free living chimpanzee babies and infants.* New Jersey: Ablex Publishing Corporation.
- Plutchik, R. 1962. The emotions: Facts, theories and a new model, New York: Random House.
- Preuschoft, S., & van Hooff, J. (1995). Homologizing primate facial displays: A critical review of methods. *Folia Primatologica*, 65, 121–137.
- Ruff, H.A. (1984). Infants' manipulative exploration of objects: Effects of age and object characteristics. *Developmental Psychology*, 20, 9–20.

- Sailer, U., & Ackerley, R. (2017). Exposure shapes the perception of affective touch. *Developmental Cognitive Neuroscience*, 17, 30032-4.
- Slater, A. (2001). Visual perception. In G. Bremner & A. Fogel, (Eds.), Blackwell handbook of infant development: Handbooks of developmental psychology (pp. 5–34). Malden, MA: Blackwell.
- Steiner, J. E., & Glaser, D. (1984). Differential behavioural responses to taste stimuli in non-human primates. *Journal of Human Evolution*, 13, 709–723.
- Steiner, J. E., & Glaser, D. (1995). Taste-induced facial expressions in apes and humans. Human Evolution, 10, 97–105.
- Steiner, J. E., Glaser, D., Hawilo, M. E., & Berridge, K. C. (2001).Comparative expression of hedonic impact: Affective reactions to taste by human infants and other primates. *Neuroscience and Biobehavioural Reviews*, 25, 53–74.
- Stack D. M. (2010). Touch and physical contact during infancy: Discovering the richness of the forgotten sense (pp. 532-567). In J. G. Bremner & T. D. Wachs (Eds.), *The Wiley-Blackwell handbook of infant development* (2nd edition). Chichester, West Sussex: Wiley-Blackwell.
- Stack, D. M., & Muir, D. W. (1992). Adult tactile stimulation during face-to-face interactions modulates five-month-olds' affect and attention. *Child Development*, 63, 1509–1525.
- Stack, D. M., & LePage, D. E. (1996). Infants' sensitivity to manipulations of maternal touch during face-to-face interactions. Social Development, 5, 41–55
- Streri, A., & Féron, J. (2005). The development of haptic abilities in very young infants: From perception to cognition. *Infant Behavior & Development*, 28, 290304.
- Suomi, S. J. (2005). Mother-infant attachment, peer relationships, and the development of social networks in rhesus monkeys. *Human Development*, 48, 67–79.
- Takeshita, H., Myowa-Yamakoshi, M., & Hirata, S. (2006). A new comparative perspective on prenatal motor behaviors: Preliminary research with four-dimensional ultrasonography. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), Cognitive development in chimpanzees (pp. 37–47). Tokyo: Springer.
- Thompson, R. A. (1994). Emotion regulation: A theme in search of definition. *Monographs of the Society for Research in Child Development*, 59, 25-52.
- Tomkins, S. S. (1962). Affect, imagery, consciousness. Vol. 1. The positive affects, New York, NY: Springer
- Tribotti, S. T. (1990). Effects of gentle touch on the premature infant. In N. G. Gunzenhauser (Ed.), Pediatric Round Tables Series 14: Advances in touch. New implications for human development. Skillman, NJ: Johnson & Johnson Consumer Products, Inc.
- Triscoli, C., Croy, I., Olausson, H., & Sailer, U. (2017). Touch between romantic partners: Being stroked is more pleasant than stroking and decelerates heart rate. *Physiology & Behavior*, 177, 169–175.
- Tronick, E. (1995). Touch in mother-infant interaction. In T. F. Field (Ed.), *Touch in early development* (pp. 53–66). Mahwah, NJ: Lawrence Erlbaum Associates.
- Tronick, E. (2005). Why is connection with others so critical? The formation of dyadic states of consciousness and the expansion of individuals' states of consciousness: Coherence governed selection and the co-creation of meaning out of messy meaning making. In J. Nadel & D. Muir (Eds.), *Emotional development: Recent research advances* (pp. 293–315). Oxford, England: Oxford University Press.
- Ueno, A., Ueno, Y., & Tomonaga, M. (2004). Facial responses to four basic tastes in newborn rhesus macaques (Macaca mulatta) and chimpanzees (Pan troglodytes). Behavioural Brain Research, 154, 261-271.
- van Ijzendoorn, M. H., Bard, K. A., Bakermans-Kranenburg, M. J., Ivan, K. (2009). Enhancement of attachment and cognitive development of young nursery-reared chimpanzees in responsive versus standard care. *Developmental Psychobiology*, 51, 173–185.
- Vrontou, S., Wong, A. M., Rau, K. K., Koerber, H. R., & Anderson, D. J. (2013). Genetic identification of C fibres that detect massage-like stroking of hairy skin in vivo. *Nature*, 493, 669–673.
- Vick, S-J, Waller, B., Parr, L., Smith Pasqualini, M., & Bard, K.A. (2007). A cross species comparison of facial morphology and movement in humans and chimpanzees using FACS. *Journal of Nonverbal Behavior*, 31, 1-20.
- Waller, B., Bard, K. A., Vick, S-J., & Smith Pasqualini, M. (2007). Perceived differences between chimpanzee (Pan troglodytes) and human (Homo sapiens) facial expressions are related to emotional interpretation. Journal of Comparative Psychology, 121, 398–404.
- Widen, S. C. (2013). Children's interpretation of children's interpretation of facial expressions: The long path from valence-based to specific discrete categories. *Emotion Review*, *5*, 72–77.

Widen, S. C., & Russell, J. A. (2008). Young children's understanding of other's emotions. In M. Lewis & J. M. Haviland-Jones (Eds.), *Handbook of emotions* (pp. 348–363). New York, NY: Guilford.
Varlag, B. M. (1942). *Chima and a scheme testing and and the scheme based on York*. New York, NY: Guilford.

Yerkes, R. M. (1943). Chimpanzees: A laboratory colony. New Haven, London: Yale University Press.

Financial conflict of interest: No stated conflicts.

Conflict of interest: No stated conflicts.

Submitted: August 28th, 2018 Resubmitted: September 23rd, 2018 Accepted: October 22nd, 2018