

SOCIO-SEXUAL COMMUNICATION: A REVIEW OF THE SENSORY MODALITIES USED BY NON-HUMAN PRIMATES

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ABSTRACT

As social animals, primates use signals to transmit information about social and sexual status to conspecifics. When these signals lead receivers to change their behavior, we can consider that communication between the individuals has occurred. Primates can produce and use four sensory modalities to communicate between conspecifics: acoustic, chemical, visual and tactile. The use of each modality depends on the social and physical environment, the receiver's sensory system and the context. In this review, the authors present behavioural evidence of each sensory modality used in socio-sexual contexts and compare this evidence for Old World and New World monkeys in an attempt to guide future studies on the evolution of communication.

Keywords: Primate communication; sensory modalities; socio-sexual signals; Old World monkeys; New World monkeys.

INTRODUCTION

Communication is generally defined as the interaction between at least two individuals, a sender and a receiver, with the transmission of information and its subsequent use to change the receiver's behavior (Bradbury & Vehrencamp 2011). It can be considered in terms of three components: signal production (the type of signals), usage (producing signals in an appropriate context) and comprehension (responding appropriately to other signals) (Seyfarth & Cheney 2010).

Most primates, as social animals, need to communicate with conspecifics and individuals of other species in different contexts, such as: agonistic interactions, territorial defense, mating rituals, foraging and group cohesion. Primate communication has been the object of studies for a long time and the meaning of the signals is still being unraveled (Hauser *et al.* 2002, Zuberbuhler 2000a, 200b, Di Bitetti 2005, Slocombe & Zuberbuhler 2005 a, b, Arnold & Zuberbuhler 2006a, 2006b, Heymann 2010).

Among the major modalities of communication used by vertebrates (acoustic, visual, chemical, tactile, electrical), primates can produce and receive signals from four of these: acoustic, chemical, visual and tactile (Maryanski 1997). Acoustic communication involves

sound production consisting of vibrations that propagate in a medium over short and long distances, but can be modified by boundaries such as the ground, forest canopy or surface of the water (Bradbury & Vehrencamp 2011). Sound undergoes spreading loss as it propagates rapidly away from the sender, characterizing its low persistence, but providing directionality to the signal (Bradbury & Vehrencamp 1998). Chemical signals used for communication between conspecifics are usually called pheromones, organic compounds that differ in size, shape and composition (Snowdon *et al.* 2006) Primates disseminate chemical signals by rubbing sebaceous glands onto a surface, object or food, in addition to depositing urine and feces with secretions from sex accessory glands or the anal gland (Kleiman 1966). Their transmission is mainly via diffusion, with high persistence, low directional information and low propagation speed (Bradbury & Vehrencamp 2011). Primates use reflected light from the sun to produce visual signals. These signals can be characterized by brightness or intensity, spectral composition or color, spatial characteristics (size, shape, surface features and color pattern of color patches) and temporal variability in intensity, color and spatial properties (Dusenbery 1992). Since visible light travels in straight lines, visual communication between two animals must

be direct, without large or opaque objects situated directly between them, making it highly directional (Dusenbery 1992). Ultimately, tactile signals are highly directional and immediately perceived, given the direct contact between individuals, especially conspecifics, and their variable persistence (McGregor 2008).

Context plays an important role in communication and receivers may integrate the information received in the context (Tomasello & Carpenter 2007). Recipients may even take the nature of previous interactions into account when perceiving the meaning of signals, such as the relative rank of the signaler and recipient (Cartmill & Maestriperi 2012, Roberts *et al.* 2012). Social and sexual contexts demand interaction between individuals and the exchange of information about the animal's quality, rank status and sexual availability.

Animal communication, like any other behavior, can be studied from four different perspectives: mechanistic, ontogenetic, functional and phylogenetic (Tinbergen 1963). Accordingly, this review presents functional perspectives by indicating some behavioral data for all four sensory modalities exploited by primates in socio-sexual contexts. Our aim was not to review all studies on the four modalities, but rather to review the core modalities of communications used by primates. Furthermore, we compare evidence for Old World monkeys (Catarrhini) and New World monkeys (Platyrrhini) as a means of understanding the evolution of primate communication.

ACOUSTIC COMMUNICATION

The emission of acoustic signals is an important communication modality for most primates. The wide use of acoustic signals is related to social and physical environments, and as primates are usually arboreal, it is more difficult to see conspecifics (Fedurek & Slocombe 2011). Furthermore, as members of a group can sometimes be separated as they travel and forage over large distances, acoustic signals can disseminate long distances and deviate from obstacles, making them useful for primate communication (Fedurek & Slocombe 2011).

Unlike human oral language, which is formed by different phonemes and semantic structures, nonhuman animal acoustic communication is simpler (Fedurek & Slocombe 2011), albeit sufficient to transmit messages about predators, food sources, conspecific

reproductive state and social condition.

In socio-reproductive contexts, primates can produce acoustic signals. Several nonhuman primate females can produce loud and distinct sounds immediately before, during and/or after copulation, although the causes that explain this behavior are not well known (Maestriperi & Roney 2005, Pradhan *et al.* 2006). Pfefferle *et al.* (2008a) sought to explain the function and information contained in calls produced by Barbary macaque females (*Macaca sylvanus*) during coupling. The authors tested two hypotheses: first, calls are produced to indicate the female fertile period; second, these calls might influence male ejaculation. Correlations between acoustic analyses of calls and hormone measures were undertaken and a temporal association was made between coupling and call emission. The authors found that calls produced by females during coupling influence male ejaculation, but do not signal their fertile period. In another study using playbacks, Pfefferle *et al.* (2008b) recorded female calls produced during coupling with and without ejaculation. Males exposed to playbacks of females calls during coupling with ejaculation gazed longer at other females and approached them at a higher frequency when compared to exposure to playbacks of female calls during coupling without ejaculation. The authors hypothesize that female calls might be signals to their partner, enhancing the probability of ejaculation and fertilization, and to other males of the group to announce successful couplings, thereby increasing interest in future coupling. Thus, the emission of calls during coupling might induce spermatic competition.

In 2011, Engelhardt *et al.* showed for the first time for primates that females of long-tailed macaques (*Macaca fascicularis*) signal if they are paired or not, by the structure and frequency of their calls during coupling. Moreover, these vocalizations can signal coupling accessibility and the social hierarchy of their partners. This study, together with others using nonhuman primates [*Cercocebus torquatus atys* and *Macaca nemestrina* (Gouzoules *et al.* 1998), *Papio cynocephalus ursinus* (Fischer *et al.* 2004), *Macaca nigra* (Neumann *et al.* 2010)], shows that differences in vocalizations depend mainly on social organization and the reproductive strategy adopted by each species.

To date, few studies have investigated New World monkey vocalization in socio-reproductive contexts. However, a large number [e.g., *Leontopithecus rosalia* (Benz *et al.* 1990), *Callithrix*

jacchus (Norcross & Newman 1993), *Cebuella pygmaea* (Elowson *et al.* 1991, Elowson & Snowdon 1993, Snowdon & de la Torre 2002), *Saguinus oedipus* (McConnel & Snowdon 1986, Scott *et al.* 2005), *Callithrix kuhlii* (Smith *et al.* 2009), *Brachyteles hypoxanthus* (Arnedo *et al.* 2010), and *Brachyteles arachnoides* (Ades & Mendes 1997)] suggest that vocalizations vary according to sex and age in several species. This evidence indicates that even in species where sexual dimorphism is absent, there may be biological constraints, such as morphological differences (HersHKovitz 1977), imposing distinct vocalization repertoires on individuals of different sex and age. Bezerra & Souto (2008) described the calls of common marmosets (*C. jacchus*) for the first time in wild conditions, showing that, in addition to sex differences, the subject's age influences the type of calls present in their vocal repertoire. The authors conclude that juvenile calls reflect their social status, since they utter submission cries when watching conspecifics, possibly denoting an attempt to get closer to other group members or receive assistance from adults without being rejected (Bezerra & Souto 2008).

Changes in the social environment may constitute one of the critical features that influence vocal modification in some species. Rukstalis *et al.* (2003) studied vocalization change in Wied's black tufted-ear marmosets (*C. kuhlii*) when exposed to new neighbors. They showed that animals exposed to new social contexts undergo significant modifications in the parameters of *phee* calls, a call type uttered by marmosets on different occasions, such as, to make contact with conspecifics, in order to bring members together (Epple 1968, Winter 1977).

A New World primate genus, well known for its powerful long-distance roars, is the *Alouatta* spp., also known as the howler monkey (Whitehead 1995). Males have an enlarged hyoid bone, which surrounds a hyolaryngeal apparatus that functions as a resonance chamber (Kelemen & Sade 1960), amplifying their roars. It is known that these vocalizations are used in intergroup communication (Whitehead 1987, Chiarello 1995, Kitchen 2004), but it is still unclear how they use these signals to communicate in their own groups. Hence, Holzmann *et al.* (2012) tested three hypotheses to evaluate the ultimate function of roaring (howling) behavior: i) roars are used to gain exclusive access to food; ii) roars ensure exclusive access to mates; iii) roaring behavior serves to avoid male takeovers and

infanticide. The authors recorded the roaring behavior of two groups of *Alouatta caraya* and *Alouatta guariba clamitans* over a 12-month period. The results did not support the food defense or infanticide avoidance hypothesis, but did corroborate the mate defense theory.

In summary, acoustic signals might be very important for primate communication, particularly in arboreal species, given that their social and physical environments require a signal that can deviate from obstacles and exhibit directionality. The study of acoustic communication in socio-sexual contexts in primates has involved numerous species of Old World monkeys and a few of New World monkeys. The focus on New World monkey communication has been on the physical structure of calls, but their function is still poorly known.

CHEMICAL COMMUNICATION

The general consensus regarding primates is that they are "visual" animals (Laska *et al.* 2000). Apes and Old World monkeys use more visual communication such as color vision and facial expressions as well as tactile and vocal communication (Epple 1974, Laska *et al.* 2000) rather than chemical communication. However, New World monkeys are known to primarily use chemical signals to communicate (Epple 1976, Epple 1973, Epple 1986).

As described by Johnson (1973), scent marking is the behavior by which glandular secretions are deposited on the ground or onto objects in an animal's environment. Moreover, the deposition of urine and feces can also constitute marking behavior (Ewer 1968, Rails 1971) and is part of an animal's olfactory communication system.

In an attempt to explain the difference between Old World and New World monkeys in the use of chemical communication, Gilad *et al.* (2004) found that Old World monkeys and the howler monkey, a New World primate, have a significantly higher proportion of olfactory receptor pseudogenes (genes that have lost their coding ability or are no longer expressed in the cell) than other New World monkeys or the lemur, a prosimian. The authors suggest that the deterioration of the olfactory repertoire occurred concomitantly with the acquisition of full trichromatic color vision in Old World primates and the howler monkey and might be an exchange in the importance of these two senses in

primate evolution. Contradicting this hypothesis, Dong *et al.* (2009) concluded that the reduced olfaction ability in apes and Old World monkeys cannot be explained by the higher number of pseudogenes or by fewer functional olfactory genes because of the extensive birth-and-death processes (whose gene families expand by duplication and contract by deletion), and that such variations in number of pseudogenes did not cause a significant difference in the number of intact and functional olfactory receptor genes in individual primate genomes.

Despite the discussion about the possible trade-off between the gain and loss of these two senses, some studies suggest a broader role for scent communication in Old World monkeys than is currently recognized, especially concerning socio-sexual contexts. Setchel *et al.* (2010) compared scent profiles of mandrills (*Mandrillus sphinx*) with the features of signalers and found that scents can transmit variable information such as age and male dominance as well as fixed information such as sex. However, the authors could not find scent signals for either female cycle or rank, suggesting that chemical signals have different importance between males and female mandrills. Other evidence that olfactory cues are important to Catarrhines was reported by Freeman *et al.* (2012), who studied chest rubbing behavior in vervet monkeys (*Chlorocebus aethiops*). They found that chest rubbing behavior is associated with higher ranking males, who are more likely to engage in such behavior during the breeding season in areas where territorial encounters occur, indicating that this behavior may be involved in intrasexual competition. The authors report that, although they could not perform histological analysis of skin from the chest region or analysis of any substance transferred onto tree trunks via chest rubbing, this behavior very likely represents scent marking.

In New World monkeys, the presence of scent glands in the sternal and anogenital regions (Epple & Lorenz 1967, Perkins 1975, Zeller *et al.* 1988), a functional vomeronasal organ (Maier 1982), in addition to behavioral evidence, suggests that chemical signals are widely used for socio-sexual communication. Indeed, several endocrinological, behavioral and chemical composition studies have provided evidence for chemical communication in a number of species [*C. jacchus* and *S. oedipus* (Abbott *et al.* 1993), *C. pygmaea* (Converse *et al.* 1995), *C. jacchus* (Smith

& Abbott 1998), *S. oedipus* (Ziegler *et al.* 1993a, 1993b, 2005), *L. rosalia* (Miller *et al.* 2003)].

Ziegler *et al.* (1993a) found that male cotton-top tamarins (*S. oedipus*) responded to ovulatory signals when presented with the scents of a novel, ovulating female, with behavioral arousal indicating reception of these signals. This contradicted the long-held idea that ovulation was concealed. In 2004, Ziegler *et al.* reported changes in male urinary androgens that occurred simultaneously with the follicular phase, resulting in an increase in male fertility. Moreover, this is the period when estrogens are elevated and female scent-marking increases (Ziegler *et al.* 1993b). Ziegler *et al.* (2004) report that, due to high offspring mortality, a high reproductive rate is important for this species and requires a clear signaling process to indicate fertility. Furthermore, since a large number of breeding males participate in infant care when females are ovulating after parturition, the former will be in close enough proximity to respond to such signals (Ziegler *et al.* 2004).

Interestingly, Ziegler *et al.* (2005) found that single and pair-housed male marmosets demonstrated behavioral arousal when presented with the scents of novel periovulatory females and a significant elevation in serum testosterone levels related to vehicle control scents. However, an additional group of males who were fathers at the time of testing did not respond behaviorally and showed a minimal hormonal response to the scents of novel, periovulatory females, demonstrating that something about being a father affected the response to the scent (Ziegler *et al.* 2005). Additionally, studies with functional imaging of the brain have revealed activation of specific brain areas when female sexual scents are presented to male common marmosets (*C. jacchus*) (Ferris *et al.* 2001, Ferris *et al.* 2006).

Smith & Abbott (1998) also demonstrated that male common marmosets (*C. jacchus*) discriminated between scents of periovulatory and anovulatory female marmosets. Furthermore, Snowdon *et al.* (2011) showed that male common marmosets (*C. jacchus*) were capable of associating a novel and arbitrary olfactory cue with access to a periovulatory female. These results suggest that the scents of ovulating females are not pheromones (scents that release innate behavioral responses in recipients) and that marmoset males may learn specific characteristics of female scents, providing a possible basis for mate identification.

Chemical signals are also used to regulate social and reproductive process dominance in New World primates (Epple 1972, French & Cleveland 1984, Dobroruka 1972, Epple & Lorenz 1967, Homburg 1989, Abbot *et al.* 1993, Lazaro-Perea 1999, White *et al.* 2000, Miller *et al.* 2003), since dominant individuals scent mark at higher rates than social/reproductive subordinates (Epple 1972, Dobroruka 1972, Epple & Lorenz 1967, Homburg 1989, White *et al.* 2000).

Reproductively dominant females can suppress subordinate ovulation using scent marks (Abbott *et al.* 1993). Intrasexual dominance in golden lion-tamarin (*L. rosalia*) is communicated through scent marking by males but not by females outside intergroup encounters (Miller *et al.* 2003). Reproducing adult female aripana marmosets (*Mico intermedius*) scent marked more than subordinates (Rylands 1982). However, in *C. jacchus* and *Callithrix flaviceps* no differences were recorded between overall rates of scent marking by dominant and subordinate males and females (Lazaro-Perea *et al.* 1999, Guimaraes 1998). Nor was a pattern found in *Saguinus mystax*, since in some groups there were differences between scent marking rates while in others there were none (Heymann 1998). However, intersex differences are observed in *C. jacchus* (Sousa *et al.* 2006) and *Saguinus labiatus* (Smith & Gordon 2002), where females scent mark more frequently than males.

The study of chemical communication in Old World monkeys has been neglected. However, new evidence shows that this communication modality is important in some groups (Setchell *et al.* 2010, Freeman *et al.* 2012). Thus, the gap in this sensory modality needs to be filled. On the other hand, the use of chemical signals by New World monkeys is widely known, but information from wild populations is scarce.

VISUAL COMMUNICATION

Charles Darwin was the first to document human facial expressions and their similarities with other primates in a book entitled "The Expression of Emotions in Man and Animals", published in 1872. Darwin was trying to show how human facial expressions have parallels with the expressions of other animals, providing a behavioral argument for evolutionary continuity. Darwin's theory has been corroborated by a number of behavioral studies showing that facial expressions, as well as gestures and body posture, are used by animals

to communicate (De Waal 2003, Pollick & De Waal 2007, Van Hoof 1967).

A facial expression alone does not indicate whether an individual is aggressive, fearful, or friendly, and such judgments are derived from concomitant behavioral observations (De Waal 2003). Behavioral records are necessary to interpret visual communication, paying attention to the signals, sender and receiver behaviors and the consequences during social interactions. A general assumption about facial expressions is that they can transmit a variety of information about an individual's emotion, motivation or intention (van Hooff 1967, Ekman 1997, Parr *et al.* 2002).

Jan van Hooff (1967), in one of his first studies, showed that when a female pigtail monkey (*M. nemestrina*) is in heat, a male may smell her genital region, which is highly swollen. It then exhibits a facial gesture, mainly characterized by protruding lips, and maintains the facial posture for a short time, followed by copulations (Van Hoof 1967). Rhesus macaques (*Macaca mulatta*) also show facial expressions. This species lives in a social system known to be strict, with a linear dominance hierarchy. Subordinates display bared-teeth behavior (retraction of the lips to expose both rows of teeth) to higher ranking individuals (De Waal and Luttrell 1985). However, the bared-teeth behavior does not have the same meaning in other species (van Hooff 1967, Preuschoft & van Hooff 1995), which use these displays, sometimes mutually between individuals, to increase social attraction and communicate that there is no risk of aggression (van Hooff 1967, 1976, Waller & Dunbar 2005). It can also occur during affiliative contexts, such as grooming, sexual solicitation and reconciliations (van Hooff 1973, Preuschoft & van Hooff 1997, Parr *et al.* 2002, Waller & Dunbar 2005).

Some authors propose that the bared-teeth displayed by different species is homologous with the human smile, which means that this behavior can be traced to a common ancestor (van Hooff 1972, Preuschoft & van Hooff 1997, Waller & Dunbar 2005). This conclusion is based on the physical similarity between the bared-teeth display and the human smile, as well as on the similar social function of these expressions, indicating appeasement, reassurance, increased social bonding, and its consequent important role in facilitating social cohesion among primates (Preuschoft & van Hooff 1997).

Compared to Old World monkeys, their New World counterparts are considered to display poorly developed facial expressions (Moynihan 1976, Hershkovitz 1977). Indeed, they do have a rich repertoire of visual signals, but these may be less noticeable due to their small size (Stevenson & Poole 1976, Snowdon & Soini 1988). For example, in the context of sexual behavior, tamarins (*Saguinus* sp.) and common marmosets (*C. jacchus*) display rapid tongue-flicking, which appears more frequently during the periovulatory period (Stevenson & Poole 1976, Snowdon & Soini 1988). However, tongue-flicking can also be seen during agonistic encounters (Stevenson & Poole 1976). A common behavior exhibited in intragroup and intergroup agonistic encounters in *C. jacchus* is the 'raised tail' behavior pattern (Stevenson & Poole 1976). Another visual signal usually displayed by New World monkeys is piloerection, used as a response to the introduction of another individual into a group or to the presence of a potential predator (Mason 1968, Moynihan 1963, 1964, 1970, Stevenson & Poole 1976), whereby the individual appears larger than it actually is, and then intimidates its adversary (Stevenson & Poole 1976).

A marked singularity between humans and other primates is the use of manual gestures to communicate (Maestriperi 1996, 1997, 2005, De Waal 2003). This consists of intentional hand movements without the use of objects or substrate (Pollick & De Waal 2007). The intentional use of manual gestures to influence others has been reported in all great ape species (Tomasello & Call 1997). There is clear evidence of flexibility, which means that some gestures can be used across a number of different contexts (Pika & Tomasello 2002, Liebal *et al.* 2004, 2006, Pollick & de Waal 2007, Genty *et al.* 2009, Hobaiter & Byrne 2011, Roberts *et al.* 2012). This flexibility is greater than in vocal communication, because it involves fewer evolutionarily urgent activities (Pika *et al.* 2005). A consistent association between a given type of gesture and a particular behavioral change may be used to infer the meaning of different gestures, or of the same gesture used in different contexts (Seyfarth *et al.* 2010). Nonhuman primates communicate using manual gestures mainly in relatively intimate social contexts such as play, grooming, nursing and sexual and agonistic encounters (Pika *et al.* 2005).

Facial expressions, gestures and body posture are not the only signals used by primates for visual

communication. Females of many primate species signal sexual receptivity, which occurs more frequently around the periovulatory phase of the cycle (Bielert 1986, Aujard *et al.* 1998, Deschner *et al.* 2004), with changes in the size, shape, turgidity, color and luminance of their perineal skin (Rowell 1972, Dixson 1983).

One of the most notable visual signals is perineal swelling of the skin in the anogenital region and rump around the time of ovulation in many species (Zinner *et al.* 2004). This exaggerated swelling is an estrogen-dependent edema of the tissue, with primarily extracellular water retention and some intracellular retention (Krohn & Zuckermann 1937, Aykroyd & Zuckermann 1938). Primates of different radiations, such as Callitrichids (Sicchar & Heymann 1992), howler monkeys (Glander 1980), tarsiers (Wright *et al.* 1986), patas monkeys (Dixson 1983) and white handed gibbons (Dahl & Nadler 1992), show sexual swelling. Domb & Pagel (2001) studied a population of wild olive baboons (*Papio cynocephalus anubis*) and found that males use the size of sexual swelling to determine their mating effort, fighting more aggressively to consort females with larger swelling, since they live in a multi-male breeding system where there is intense competition for access to females. A study with Barbary macaques (*M. sylvanus*) showed a significant correlation between sexual swelling sizes and female estrogen levels (Brauch *et al.* 2007). However, no relation was found with sexual behaviors. The results clearly show that female sexual swelling is a sign of the fertile phase (Brauch *et al.* 2007).

Color variability has long been thought to be a product of sexual selection and to play an important role in animal communication (Zahavi 1977, 1991, Dawkins & Krebs 1978, Krebs & Dawkins 1984, Andersson 1994). Among mammals, primates exhibit striking examples of skin and pelage color variation (Bradley & Mundy 2008). In many cases, these characteristics convey information about a signaler to a receiver. Such information can be either to a member of the opposite sex, characterizing an intersex competition or mate choice, or to a member of the same sex, that is, intrasex competition. Facial color patterns can also play a role in society and species recognition, as described by Santana *et al.* (2012) in a recent study in Neotropical primates. The authors found that species living in smaller groups where social interactions are less frequent and in sympatry with a higher number of species from the same genus have

evolved more complex patterns of facial colors.

A number of authors have proposed that chromatic variations are associated with male competition and struggles for social position (Vandenburgh 1965; Henzi 1985; Gerald 2001). Changizi *et al.* (2006) argues that skin color assumes an important role in signalization, since it is related to fundamental blood characteristics that are common to all primates. Coloration may play an important role in communication between male vervet monkeys (*Cercopithecus aethiops*), gelada (*Theropithecus gelada*) mandrills (*M. sphinx*) and green monkeys (*C. aethiops sabaesus*) (Gartlan & Brain 1968, Dunbar 1984, Setchell & Dixson 2001, Gerald 2001, Setchell & Wickings 2005). Signals of status can benefit individuals because they can regulate the degree of costly conflict and even avoid agonistic encounters with the absence of direct interaction (Gerald 2001). In addition to communication between males, male color differences can influence communication between sexes (Cooper & Hosey 2003, Waitt *et al.* 2003, Setchell 2005). Contradicting this assertion, Gerald *et al.* (2007) conducted an experiment modifying scrotal coloration in male vervet monkeys (*C. aethiops*) and introducing females to these males. The authors found that females pay attention to male coloration, but do not bias their interactions toward males solely on the basis of natural male coloration. In the red-fronted lemur (*Eulemur fulvus rufus*), a prosimian species, facial hair coloration is related to male quality, but no relation was found for reproductive success or dominance rank.

Chromatic variations in female sexual skin are regulated by ovarian estrogen (Czaja *et al.* 1975, Herbert 1966), which increases vascular blood flow under the skin surface, thereby signaling the fertile phase in many species of Old World monkeys. It has long been thought that color variation in sexual skin plays a role in stimulating male sexual interest. However, few studies have tested this hypothesis. In 1989, Bielert *et al.* showed for the first time that female red swelling elicited a significant male masturbatory response in chacma baboon males (*Papio ursinus*). In 2006, Waitt *et al.* demonstrated that rhesus macaque male (*M. mulatta*) visual preferences are influenced by the color of the anogenital skin, but not female facial color, indicating that displays of red coloration in non facial skin alone are not sufficient to elicit the attention of males.

However, sexual skin color of the face and hindquarters has been associated with intrasexual communication and this clue can be used to monitor another female reproductive status or cyclic phase for competitive purposes (Gerald *et al.* 2007), or even to convey social intentions toward other females (Gerald *et al.* 2009). In some primate species, females exhibit chromatic variation during pregnancy in their faces and anogenital regions, as documented in *Lophocebus albigena* (Rowell & Chalmers 1970), *Theropithecus gelada* (Dunbar 1977) and *Papio cynocephalus* (Altmann 1973). Gerald *et al.* (2009) demonstrated for the first time that pregnancy coloration in rhesus macaques (*M. mulatta*) contains information about reproductive status and might be an attention-grabbing stimulus to males and a warning stimulus to both male and female rhesus macaques.

To date, only one study has investigated socio-sexual communication by chromatic signals in a New World primate. Oliveira (2009) studied common marmosets (*C. jacchus*) and found a relation between chromatic variation on female skin and fecal progesterone. Using color vision models (Vorobyev & Osorio 1998), he suggests that these chromatic signals can be detected by males. A possible reason for the negligence of this type of study in Platyrrhini is that the bodies of the vast majority of New World monkeys are covered with hair, and that bare skin should be a premise to perceiving skin color variation (Changizi *et al.* 2006). However, this should be reviewed, given that New World primates have a few hairless areas on their bodies. Moreover, New World monkeys have different color vision than their Old World counterparts. The former typically have polymorphic color vision, which provides individuals with any of several distinct types of color vision, including both trichromatic and dichromatic variants (Jacobs 2007), while Old World monkeys are routine trichromats (Jacobs & Deegan 1999).

Luminance, a visual signal that has been neglected, may be used as a socio-sexual signal. Highman *et al.* (2010) used vision models and found luminance changes outside the fertile period in female rhesus macaques (*M. mulatta*) that could lead to paternity confusion. The authors highlight the importance of considering receiver perception instead of using field data collected by digital photography, since the latter can be misleading when values are unrelated to the visual system of the beholder. Thus, studies on chromatic and

luminance variation in New World monkeys are needed to improve knowledge of primate visual communication and understand the difference in color vision between New World and Old World primates.

TACTILE COMMUNICATION

Compared to other sensory modalities, the study of tactile communication in humans and nonhuman primates has been neglected, favoring other modalities, mainly vision. Furthermore, the methodologies used to study it are quite difficult and sometimes even inaccessible to researchers (Hertenstein *et al.* 2006). However, researchers should give more attention to tactile communication since it has two primacies: phylogenetic primacy, whereby nonverbal communication, such as touch, preceded language in a species' evolutionary history (Dew & Jensen 1977, Dunbar 1996); and ontogenetic primacy, which states that in the beginning of life, the importance of nonverbal communication, particularly tactile stimulation, supersedes that of verbal communication (Field 2001). The role of tactile communication in primates has been studied with an emphasis on attachment in the mother-infant relationship, contact in post-conflict events and as a social mechanism (Hertenstein *et al.* 2006).

Grooming, which consists of removing lice, parasites and other objects from the fur with the hands or mouth, is a tactile behavior exhibited by most primates (Hutchins & Barash 1976, Sparks 1967). The evolutionary origin of this behavior was self-cleaning or even to help conspecifics by cleaning their bodies in places they could not reach (Hutchins & Barash 1976, McKenna, 1978). In addition to its cleaning function, grooming plays an important role in the maintenance or establishment of social relationships. For this reason, primates may engage in social grooming (allogrooming), self-grooming or even both (Tanaka & Takefushi 1993).

The social factors involved in allogrooming are multifaceted, and include sex, rank and time available for the activity (Hertenstein *et al.* 2006). In 1977, Seyfarth proposed a model that integrates rank, attractiveness, preference for close relations and time available for grooming, to determine which grooming interactions are most likely. According to the model, higher ranked females may receive more grooming than their lower ranking counterparts. This indeed occurs with most Old World primate species and some New World monkeys (Gouzales & Gouzoules 1987,

Seyfarth 1977, 1980). However, the model cannot be extrapolated, especially to females. Each species may have its own grooming pattern related to its specific needs (Sambrook *et al.* 1995). For example, in some species, such as the brown capuchin (*Cebus apella*), blue monkey (*Cercopithecus mitis stuhlmanni*), northern plains gray langur (*Semnopithecus entellus*), wedge-capped capuchin (*Cebus olivaceus*), rhesus monkey (*M. mullata*) and common marmoset (*C. jacchus*), allogrooming pattern can be from higher to lower rank, lower to higher or even between females of the same hierarchy status (Borries *et al.* 1994, Di Bitetti 2000, O'Brien 1993, Parr *et al.* 1997, Rowell *et al.* 1991, Lindburg 1973, Lazaro-Perea *et al.* 2004).

Grooming between males is much more uncommon than between females, because there is generally only one male per group, since groups are usually bound through female lineages and males leave their troops at a young age (Drickamer, 1976). However, in groups with more than one male, the dominant individual is most often groomed (Borries *et al.* 1994, Terry 1970). Grooming between males can also occur in order to avoid aggression when there is competition for dominance, as occurs in chimpanzees (*Pan troglodytes*) (Goodall 1986).

During sexual interactions, the increased contact, grooming and proximity behaviors between males and females influence the likelihood of reproduction (Epple 1977, Sousa *et al.* 1977, Maestriperi & Wallen 1997). Females tend to choose males that give reciprocal attention in grooming (Goodall 1986, Michel *et al.* 1976, Smuts 1987, Tutin 1979). In common marmosets (*C. jacchus*), the higher grooming rates between the breeding pair, associated to coordinated behaviors, such as piloerection, are important indicators of the existence of pair bonding between males and females (Silva & Souza 1997).

Primate societies form permanent associations between individuals. The existence of these associations means that conflicts must be regulated so that they do not weaken relationships (De Waal & Aureli 1996). Conflicts can be regulated by reconciliation and consolation, such as post-conflict contacts that serve to repair social relationships and reassure distressed individuals. Physical contacts during reconciliation include grooming, mounting, and clasping (Thierry 1984). These promote physical and emotional homeostasis (De Waal 1993) by reducing the uncertainty that new aggressions between

conspecifics will occur (Silk 2002). Reconciliation contacts have been evidenced in over 20 primate species (Aureli & De Waal 2000).

Another way to regulate post-conflict stress is consolation, consisting of affective contact between recipients of aggression and non-opponent third parties (bystanders) (De Waal & Aureli 1997). This phenomenon is rare in the animal kingdom and among primates it has been documented in chimpanzees (*Pan troglodytes*; De Waal & Van Roosmalen 1979, Fraser *et al.* 2008, Romero & De Waal 2010, Romero *et al.* 2011) bonobos (*Pan paniscus*; Palagi *et al.* 2004, Clay & De Waal 2013) and gorillas (*Gorilla gorilla*; Cordoni *et al.* 2006, Mallavarapu *et al.* 2006). Consolation behaviors, which can be affiliative, include expressions of empathy such as touching, embracing, and kissing (Romero *et al.* 2010).

Finally, an inherent characteristic of mammals is the relationship between mother and infant, given that during intrauterine development and after birth they are physically closely related. Tactile communication plays an important role in the attachment between them, as first described by Harlow & Harlow (1962), who demonstrated that infant rhesus macaques (*M. mulatta*) find contact comfort more appealing than feeding alone, indicating that touch may be the primary mechanism of attachment. Recently, Clay and De Waal (2013) studied post-conflict interactions in bonobos, and found that mother-reared individuals are significantly more involved in post-conflict interactions than orphans. The authors conclude that maternal care in infancy is critical for the development of secure and organized attachment styles as well as for cognitive and socio-emotional development. Moreover, contact behaviors are also important in the development of parental care in common marmosets (*C. jacchus*), since they are related to an increase in plasma prolactin in parents that carry their offspring (Dixson & George 1982, Mota & Sousa 2000).

Touch seems to be very important in primate communication. It is used in different contexts and plays an important role in primate development. Therefore, future studies on this modality are necessary, since it is an important key to understanding human and nonhuman communication.

CONCLUSIONS

As presented in this review, primates use different modalities to communicate with conspecifics in socio-

sexual contexts and evidence was found elucidating all four sensory modalities (acoustic, chemical, visual and tactile). We observed gaps in the study of each modality, mainly because of the much larger number of studies on Old World primates compared to their New World counterparts for each sensory modality.

The use of each sense depends on the social and physical environment, the receiver's sensory system and the context. Because of these limitations, primates usually use more than one modality to transmit information. Thus, we cannot affirm that one sensory modality is more important than another, since the animal may use more than one type of signal to communicate.

In addition to acquiring knowledge *per se*, studying the way nonhuman primates use various signals to communicate and the shared modalities between the species helps us understand human communication and how nonhuman primates are closely related to humans, sharing anatomic, physiological and behavioral characteristics. The study of the evolution of language represents an exciting and rapidly growing field, and comparative data will continue to play a fundamental role on it.

Finally, by understanding how primate species perceive the world and communicate among themselves, researchers can design and refine experiments, housing, husbandry systems and enrichment strategies, in order to ensure their well-being and improve conservation programs.

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