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► **To cite this version:**

Julia Sliwa, Marion Mallet, Maëlle Christiaens, Daniel y Takahashi. Neural basis of multi-sensory communication in primates. *Ethology Ecology and Evolution*, 2022, pp.1 - 22. 10.1080/03949370.2021.2024266 . hal-03549702

HAL Id: hal-03549702

<https://hal.science/hal-03549702>

Submitted on 31 Jan 2022

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Review

Neural basis of multi-sensory communication in primates

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Primates present a rich range of communication strategies in different modalities that evolved as signaling, perceiving and signaling back behaviors. This diversity benefits from specialized dedicated neural pathways for signaling and for perceiving communication signals. The brain areas for perceiving and producing communicative signals can be described separately, but form integrated neural loops, which coordinate perception and action in the signaler and receiver. Moreover, the different sensory modalities are initially processed separately by the brain but eventually share neural pathways for communication: a redundancy that might ensure proper signal transfer. Only a few primate species have been studied so far, including rhesus, long-tailed macaques, squirrel monkeys, marmosets, and humans. Yet, the evidence suggests that all primates possess specialized neural pathways coordinating a diverse range of communication systems for organizing their complex kin and friendship bonds.

KEY WORDS: vocalization, face, body, odor, touch, social interaction, brain.

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INTRODUCTION

From fast automatic attention-getters to complex and flexible referential signs: The range of communicative signals displayed by primates is wide. Many are multisensory and their efficiency, range and directedness vary with their modality. Tactile signals are primarily short range, instantaneous, and reciprocal. Olfactory signals are perceived at spatiotemporal distance and can be displaced from the body. Auditory signals are flexible, fast and transient but attenuate with distance while visual signals are easily occluded. All are used routinely by primates to make inferences about their social environment. How are the production and perception of these signals modulated by the brain?

NEURAL BASIS OF SIGNAL PRODUCTION

In this section, we consider neural bases for production of two well-studied behaviors in primates: vocalization and facial expression production, and we briefly discuss neural mechanisms of olfactory and haptic signals production. Production of communicative gestures has been investigated in chimpanzees and baboons (Tagliabue et al. 2006; Becker et al. 2021) and is described in detail in another article of this issue (Mederguitchian 2022).

Producing facial expressions

One of the most distinctive features of primate communication, compared to that of other mammals, is the importance of orofacial movements. Stereotyped facial movements and postures, which communicate primates behavioral state (Van Hooff 1967; Ekman et al. 1969), are produced by a conserved suite of facial muscles (Diogo et al. 2009). The facial muscles are controlled mainly by two cranial nerves: jaw muscles related to ingestion are primarily innervated by the trigeminal nerve (V), while the superficial ‘mimetic’ muscles are innervated by the facial nerve (VII). Both are under the common control of the facial nucleus, which (uniquely in anthropoids) receives projections directly from motor cortex (Sherwood et al. 2005).

Cortical governance of voluntary and automatic facial movements is dissociable (Hopf et al. 1992; Morecraft et al. 2004). Lesions in the motor area M1 cause “volitional” facial paralysis, whereby patients are impaired at voluntarily moving their facial muscles for example, to speak, but are spared when responding reflexively to emotionally provocative stimuli. Lesions of the anterior cingulate cortex (ACC), insula, thalamus, striatocapsular region, or pons, cause the opposite condition of “emotional” facial paralysis, in which a patient cease to produce spontaneous facial expressions on one side of the face, though they can voluntarily approximate them with effort. In particular, electrical stimulation of ACC can induce both affective facial expressions and vocalization in monkeys (Smith 1945), while lesions of ACC are associated with flattened facial affect and decreased spontaneous vocalization (Devinsky et al. 1995).

Because the ACC is also implicated in the processing of reward contingencies and social valuation (Paus 2001; Rudebeck et al. 2006; Rushworth et al. 2007; Behrens et al. 2009; Chang et al. 2013), it may transform perceived social risks and rewards into appropriately responsive facial displays, such as lip-smacking, fear grin or bared-teeth display in macaques (Morecraft et al. 2001; Shepherd & Freiwald 2018). The ACC is part of a wider network involved in governing adaptive behavior (Weinstein & Bender 1943), including the amygdala, which also initiates production of facial signals via its connections to the motor systems (Livneh et al. 2012).

Producing vocalizations

Primate facial expressions are often accompanied by vocalizations. Primate vocalization is the result of coordinated action of the diaphragm, chest muscles, ribs, lungs, larynx, and upper vocal cavity (Fig. 1A). Each of these effectors is governed by specific neural nuclei coordinated by two brainstem areas: The reticular formation which has connections to phonatory motor neurons, and the nucleus retroambiguus, a relay to respiratory centers (Hage & Jürgens 2006; Jürgens 2009). Both receive input from the periaqueductal

gray (PAG). Electrical stimulation of PAG in squirrel monkeys produces vocalizations resembling naturally produced species-specific calls, different from the artificially sounding vocalizations produced when the reticular formation alone is stimulated (Jürgens & Ploog 1970). PAG works as a vocal trigger rather than a vocal pattern generator (Hage & Jürgens 2006): More than half of its neurons increase their neural activity before vocal onset, and most of their neural activity is not correlated with the specific acoustic features of vocalizations (Düsterhöft et al. 2004). PAG is also a relay for sensory-motor interaction, and receives inputs from limbic structures, including the ACC, amygdala, or hypothalamus (Mantyh 1982; Dujardin & Jürgens 2005). Lesioning these limbic structures disrupts spontaneous vocal production, which can be rescued by direct stimulation of PAG (Jürgens & Pratt 1979). These structures are in turn modulated by activity in frontal cortex. However, this feedforward hierarchical view is an oversimplification, not least because somatosensory feedback, e.g. from the lungs, plays a crucial role for vocal production (Nakazawa et al. 1997).

Cortical centers contribute to the ability to modulate vocal signals (Tagliabata et al. 2008). Lesions to Broca’s area lead in humans to significant speech disorders, including mutism (Trupe et al. 2013), but lesions to ventro-lateral prefrontal cortex (VLPFC), a possible Broca’s area homologue, do not significantly alter vocal production in macaques (Kirzinger & Jürgens 1982). Interestingly though, correlate of volitional initiation of vocalizations have been found in the VLPFC through audio-vocal neurons (Hage & Nieder 2013; Gavrilov & Nieder 2021) and in the ventral premotor cortex (Coudé et al. 2011), and VLPFC stimulation produces orofacial and laryngeal movements (Petrides et al. 2005). Stimulation of orofacial regions of human primary motor cortex consistently induces vocalization, but attempts in monkeys failed (Robinson 1967; Jürgens & Ploog 1970). Stimulation of ACC in humans does not induce vocalization — although there are reports of momentary speech arrest and change in prosody (Pool 1954; Lewin & Whitty 1960; Talairach et al. 1973) — but it systematically induces vocalization in monkeys (Smith 1945; Robinson 1967; Jürgens & Ploog 1970). The cortex thus appears to exert different control over vocal signaling in humans but the precise nature of these differences remain elusive.

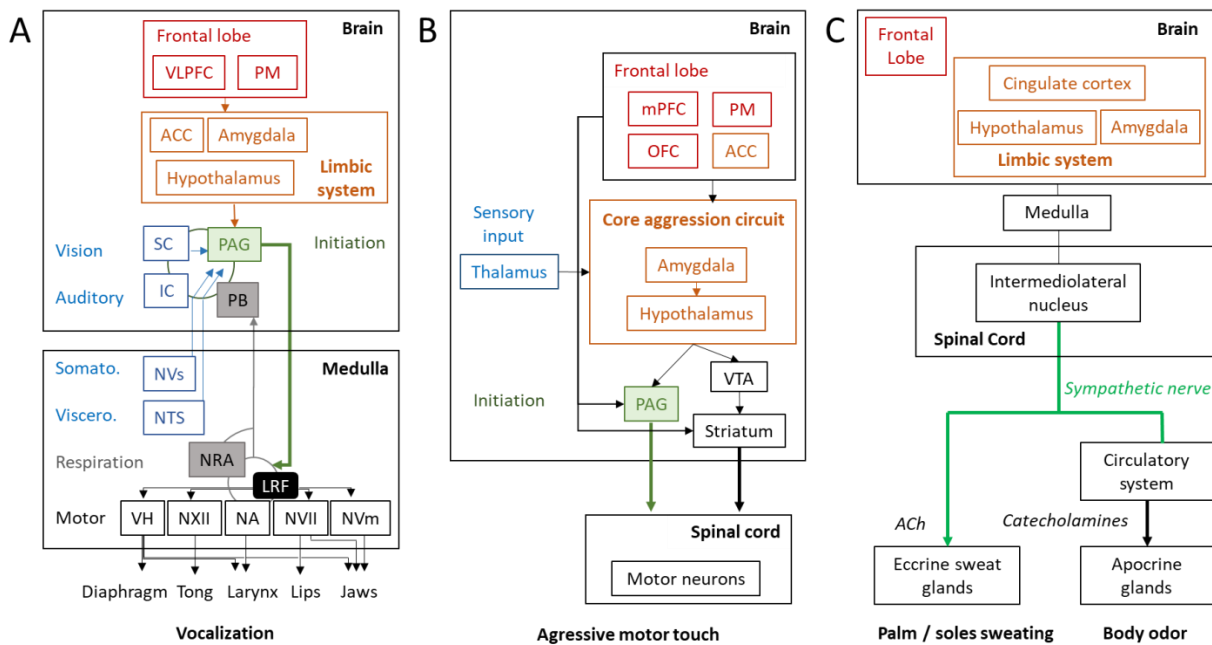


Fig. 1. — Schematic diagrams of the main neural connections in three primate signal production pathways. (A) Producing vocalizations: Descending executive control from the frontal cortex (red; VLPFC, ventrolateral prefrontal cortex; PM, Premotor cortex) and limbic system (orange; ACC, anterior cingulate

cortex) and incoming sensory input (blue, NTS, solitary nucleus; NV_s, sensory trigeminal nucleus; IC, inferior colliculus; SC, superior colliculus) project on the PAG. The periaqueductal gray (PAG, green) coordinates behavioral state and initiates affective vocalization, while the lateral reticular formation (LRF, solid black) coordinates the motor nuclei (black outline; VH, ventral horn of the medulla; N XII, hypoglossal nucleus; N A, nucleus ambiguus, N VII, facial nucleus; N V_m, trigeminal motor nucleus). Respiratory control centers (grey; PB, parabrachial region; NRA, nucleus retroambiguus). Note: is omitted uniquely anthropoid primates' direct connection from motor cortex to the motor nuclei governing face and jaw movements. (B) Producing aggressive touch: Top-down control of the frontal cortex (red; mPFC, medial prefrontal cortex; OFC, orbitofrontal cortex; ACC, anterior cingulate cortex) on the core aggression circuit (orange), initiates aggressive behavior through the periaqueductal gray (PAG, green) or ventral tegmental area (VTA) and striatum. Adapted from (Lischinsky & Lin 2020). (C). Producing body odor in response to emotional changes: The limbic system (orange) integrates information from emotional situations and triggers a response that circulates via efferent fibers through the medulla and intermediolateral nucleus and follows sympathetic nerves controlling apocrine glands through the release of Catecholamines in the circulatory system. Eccrine glands are mainly responsible for thermoregulatory sweating controlled by the hypothalamus, but palm and sole glands can react to emotional sweating as well. Adapted from (Harker 2013; Hu et al. 2018).

Producing touch

One of the first modes of communication between parent and infant in primates is touch (Simpson et al. 2019). Touch is usually initiated by the glabrous skin of the fingers – which is packed with Meissner's corpuscles (Hoffmann et al. 2004; Verendeev et al. 2015); and is sometimes referred to as the “tactile fovea”. Feeling with the glabrous skin of fingers is mediated by A-beta afferents (McGlone et al. 2012). It results in increased activations of the right cerebellum and left parietal cortex in humans (Gordon et al. 2013), and is dependent on previous tactile experiences (McGlone et al. 2012). Tactile experiences start with innate behaviors of nursing, mating and aggression, which engage the social behavior network of the amygdala, lateral septum, preoptic area, hypothalamus and PAG (Newman 1999; Gothard & Hoffman 2010; Lischinsky & Lin 2020; Wei et al. 2021) (Fig. 1B). This network engagement, together with the motor and parietal cortices, which contain ethological action maps in the macaque monkey, owl monkey, squirrel monkey or galago (Stepniewska et al. 2005; Kaas et al. 2013; Graziano 2016) can directly result in aggressive touch of kicking, biting, slapping, or clasping. But interpersonal touch also develop into affiliative behaviors of hugging, rough-and-tumble play, grooming (Dunbar 2010; Hobaiter & Byrne 2014), and in certain human and ape cultures, ontogenetically ritualized handshakes used as a greeting (van Leeuwen 2021). Social grooming in particular is a monkey social bonding ritual that plays an important role in reducing stress and cementing alliances (De Waal & Yoshihara 1983; Dunbar 1991, 2010; Schino 2001; Jablonski 2021). In this context approach for touching is motivated by social attachment and avoidance of social isolation through the μ -opioid receptor and oxytocin systems (Machin & Dunbar 2011; Chang et al. 2013; Loseth et al. 2014).

Producing odors

The most abundant olfactory cue that conveys information about the emitter is body odor. Skin glands first produce odorless fluids containing secondary metabolites that are later degraded into volatiles molecules by skin microflora (Saga 2002). Among skin glands, apocrine glands are associated with body odor, and secrete oily fluids containing secondary metabolites; while eccrine glands are mainly responsible for thermoregulatory sweating through secretion of water (Best & Kamilar 2018) (Fig. 1C). Those glands are supplied with sympathetic nerve fibers using catecholamines for apocrine glands, via a neuro-humoral system, and a cholinergic neurotransmitter for eccrine glands (Harker 2013). A loss of emotional sweating has been observed in a patient with bilateral amygdala lesion (Asahina et al. 2003). The condition improved

when the lesion regressed showing that the amygdala participates in emotional sweating regulation. In primates, amygdala ablation also leads to reduction of electrodermal activity, an indirect measure of emotional sweating (Laine et al. 2009). More generally, the entire limbic system is thought to impact emotional sweating (Asahina et al. 2011) via the amygdala, cingulate cortex and medulla, which then project into the intermediolateral nucleus (Asahina et al. 2015; Hu et al. 2018), and the frontal lobes albeit to a lesser extent (Mangina & Beuzeron-Mangina 1996).

NEURAL BASIS OF SIGNAL PERCEPTION

Signal processing pathways in primates' brain can be distinguished based on the modality of the signal but also on the depth of processing that appears different for reflexive vs flexible signal reception. While signals catching the receiver's attention and those triggering a reflexive response are modulated by subcortical structures, in-depth processing often relies on cortical areas dedicated to social perception.

Processing signals that influence attention

Attention-getters are abrupt sound or movement, such as a cleared throat or waved hand, or touch gesture, such as the 'poke at' or 'throw chips' gestures of chimpanzees, that indicate "where" a signal is sent from. Attention-getters trigger reflexive orienting behavior, computed in neural nodes that map between sensory and motor reference frames; the earliest are the inferior and superior colliculi (Jay & Sparks 1984; Groh & Sparks 1996) (Fig. 2). These pathways are used in social signal processing but are not specific to it. Socially dedicated subcortical systems also contribute to orienting responses to faces and eyes, through the superior colliculus in concert with the pulvinar nucleus of the thalamus and the amygdala (Vuilleumier et al. 2003; Johnson 2005).

Seeing another animal's body, head, eye, or hand direction can trigger sophisticated attention shift in the receiver. This flexible orientating behavior requires geometric computation of line-of-sight, and involves neuronal computation occurring in cortical networks. For gaze, this network includes the lateral intraparietal cortex, dorsal posterior inferotemporal cortex and the posterior Superior Temporal Sulcus (STS) of macaques (Shepherd et al. 2009; Roy et al. 2012; Marciniak et al. 2014) and their putative homologues in humans (Hoffman & Haxby 2000; Pelphrey & Morris 2006). This network both reads the orientation of the signaler and computes the orientation behavior to be undertaken by the receiver, a seeming 'mirror mechanism'.

Subcortical processing of communicative signals

Neural processing of phylogenetically conserved signals involves subcortical brain areas (Sewards & Sewards 2002). A large body of work has examined the involvement of the amygdala in automatic processing of fear and other emotions in human facial displays (Breiter et al. 1996; Morris et al. 1996; Costafreda et al. 2008), voice (Dolan et al. 2001; Sander & Scheich 2001), and body posture and movement (de Gelder et al. 2004) (Fig. 2). This pathway is broadly conserved in rhesus monkey (Gil-da-Costa et al. 2004; Gothard et al. 2007; Hoffman et al. 2007; Kuraoka & Nakamura 2007; Hadj-Bouziane et al. 2012).

One of the least understood communicative systems in primate brains is chemosensory. Social odors are processed by both the main olfactory pathway and the accessory olfactory pathway. Accessory olfaction is anatomically separated from main olfactory pathway as it employs the vomeronasal organ (VNO). Vomeronasal function is maintained within the strepsirrhines and tarsiers, reduced in platyrrhines, and mostly absent in the catarrhines including humans (Evans 2006). However, even in humans, in whom the VNO is entirely vestigial (Wyatt 2014), some hormone-like scents cause sex-differentiated hypothalamic activation (Savic et al. 2001). Similarly, in marmosets, sexually arousing odors of ovulating monkeys enhanced activity in the preoptic area and anterior hypothalamus (Ferris et al. 2001), striatum, septum, PAG, and cerebellum (Ferris et al. 2004) compared to the odors of ovariectomized monkeys.

Another less studied social perception system in primate brains is touch. Tactile interactions stimulate the C-tactile nerves present on the hairy skin of primates (Kumazawa & Perl 1977; Vallbo et al. 1993). These nerves are absent in the palms of hands and soles of feet. When C-tactile nerves are stimulated oxytocin, endorphins, dopamine and serotonin are released (Depue & Morrone-Strupinsky 2005; Dunbar 2010; Walker et al. 2017), explaining the rewarding feeling associated with gentle touch (Machin & Dunbar 2011; Tricoli et al. 2017). The C-tactile nerves are poorly spatially discriminative and mainly encode the affective aspect of touch (McGlone et al. 2007; Olausson et al. 2010), especially during grooming, cuddling and huddling (Morrison et al. 2009; von Mohr et al. 2018).

Cortical networks processing communicative signals

Cortical networks enable computation based on learned patterns and remembered experiences. In primates, this includes flexible analysis of “who” sent the signal and “why”, and “what” the signal means, i.e. “what is expressed” by a face, body or vocalization (Sliwa et al. 2016, 2018; Scott 2019). Cortical networks operate in parallel with subcortical pathways and advance hierarchically from primary sensory areas toward integrative neural representations in associative cortex (Rosa & Tweedale 2005).

Studies in the 1970s identified the existence of neurons preferentially active when macaques were seeing a face (Gross et al. 1972). These neurons were seemingly scattered throughout the temporal lobe, but are now known to cluster into specialized areas for face perception (Tsao et al. 2006; Bell et al. 2011). These areas have been imaged in humans (Haxby et al. 1994; Puce et al. 1995; Kanwisher et al. 1997), chimpanzees (Parr et al. 2009), macaques (Logothetis et al. 1999; Tsao et al. 2003; Ku et al. 2011) and marmosets (Hung et al. 2015; Schaeffer et al. 2020). In all of these species, they run through similar regions of the temporal lobe, suggesting they evolved prior to the split between New and Old World monkeys; and are abutted by areas specialized for body perception (Downing et al. 2001; Pinsk et al. 2005; Jastorff et al. 2012; Popivanov et al. 2014).

Brain areas for processing vocalizations parallel that for face processing, running dorsally through the temporal lobe in humans (Belin et al. 2000; Binder et al. 2000; von Kriegstein et al. 2003), chimpanzees (Tagliabata et al. 2008), macaques (Gil-da-Costa et al. 2004; Poremba et al. 2004; Petkov et al. 2008) and marmosets (Sadagopan et al. 2015). Vocalization-sensitive neurons were recorded in marmosets (Wang et al. 1995; Wang 2000; Wang & Kadia 2001), and in the macaque monkey (Rauschecker et al. 1995; Tian et al. 2001; Recanzone 2008; Russ et al. 2008; Kikuchi et al. 2010), principally clustered within superior temporal gyrus (Perrodin et al. 2011) but also in the insula, prefrontal and orbitofrontal cortex (Romanski & Goldman-Rakic 2002; Cohen et al. 2004; Rolls et al. 2006; Remedios et al. 2009). These areas also contribute to the perception of non-vocal auditory communicative signals: Macaque drumming (an auditory attention-getter) activates both the amygdala and cortical ‘voice’ areas in macaques (Remedios et al. 2009).

Chemosensory and tactile cortical pathways likely follow similar patterns for flexible odors and touch processing. Cortical processing of chemosensory signals occurs in piriform and insular cortex, extending into the anterior temporal and ventral frontal lobes (Gottfried 2010), where they may interact with the auditory and visual social processing streams for more nuanced processing of behavioral relevance (Ferris et al. 2004; Pause 2012). Cortical processing of touch to the hairy skin, arises in somatosensory cortex; while affective aspects of touch additionally activates the orbitofrontal cortex and insula (Keysers et al. 2010; Gazzola et al. 2012; Gordon et al. 2013), and the posterior STS and the medial prefrontal cortex (mPFC) (Gordon et al. 2013) —which are key nodes of the “social brain” (Brothers 1996; Sliwa & Freiwald 2017).

Finally, multisensory integration is a prominent feature of primate signal processing (Partan 2002; Ghazanfar & Santos 2004; Sliwa et al. 2011). This is evident from the grouping of similar functional processes in nearby brain regions irrespective of signal modality; and by the existence of large brain region, such as dorsal STS, maximally engaged when signals are presented in multiple modalities (Beauchamp et al. 2004; Chandrasekaran & Ghazanfar 2009; Dahl et al. 2009).

Perceiving traits: identity and status

Neurons from these networks code for social information present in faces, bodies and vocalizations about “who” is sending a signal. Individual facial identity is encoded in most anterior face areas in both humans and macaques (De Souza et al. 2005; Rotshtein et al. 2005; Leopold et al. 2006; Kriegeskorte et al. 2007; Freiwald & Tsao 2010). Individual vocal identity is also processed in most anterior vocalization areas in both humans and macaques (Imaizumi et al. 1997; Nakamura et al. 2001; Andics et al. 2010; Kikuchi et al. 2010; Perrodin et al. 2011). Familiarity of the signaler is encoded by adjacent mnemonic parahippocampal complex for faces (Leveroni et al. 2000; Denkova et al. 2006; Sliwa et al. 2014; Landi & Freiwald 2017; Landi et al. 2021) and vocalizations (Nakamura et al. 2001; von Kriegstein & Giraud 2004) (Fig. 2).

Other social characteristics of the signaler include gender, age, dominance status, kinship, sexual state, attractiveness, or health state. They are encoded in the mPFC (Mitchell et al. 2002; Marsh et al. 2009), posterior cingulate cortex (Schiller et al. 2009) and temporal pole (Zahn et al. 2007; Olson et al. 2013; Platonov et al. 2019). The orbitofrontal cortex, close to brain regions devoted to processing reward, in particular encodes face and body attractiveness (Nakamura et al. 1998; Ishai 2007; Kim et al. 2007; Sescousse et al. 2010), and stereotypes about gender and race in humans (Stolier & Freeman 2016); and age, gender and social status in macaques (Barat et al. 2018).

Perceiving states: actions and affect

Faces, bodies and vocalizations signal the “current internal state” of the signaler, perception of which engages not only the amygdala but also a large portion of the STS. Expressive body postures and movements activate the human amygdala, and body processing areas (de Gelder 2006; Vangeneugden et al. 2014); likewise, threat signals preferentially activate macaque body processing areas (de Gelder & Partan 2009). Facial movements including expressions, gaze and lip movements selectively activate the STS in humans (Puce et al. 1998; Allison et al. 2000; Hoffman & Haxby 2000; Pitcher et al. 2011; Harris et al. 2012; Furl et al. 2015; Pitcher & Ungerleider 2021). And facial movements activate homologue regions in the monkey upper STS (Fisher & Freiwald 2015). However, while neurophysiological recordings in macaques found that neurons in the upper STS encode facial expressions (Hasselmo et al. 1989; Sugase et al. 1999; Yang & Freiwald 2021), imaging studies of macaques have failed to constrain them to single cortical regions (Hadj-Bouziane et al. 2008, 2012; Furl et al. 2012; Zhu et al. 2013; Janssens et al. 2014; Morin et al. 2015; Taubert et al. 2020; Zhang et al. 2020).

Vocalizations also convey the signaler’s current state. The VLPFC has been found in macaques to host neurons categorizing the different types of vocalizations according to their complex acoustic characteristics (Cohen et al. 2004, 2006, 2007; Gifford et al. 2005; Russ et al. 2007, 2008), and prefrontal regions in humans were found to process emotional vocal sounds (Imaizumi et al. 1997). Importantly, prefrontal processing of emotional utterances in humans is segregated from the pathways processing non-emotional semantic signals and language (Vouloumanos et al. 2001; von Kriegstein et al. 2003; von Kriegstein & Giraud 2004).

Perceiving meaning: semantic and indexical signals

Language-related capacities are classically thought to arise through interactions between Wernicke’s area and Broca’s area. Wernicke’s area plays a role in speech perception via links to auditory cortex; Broca’s area in speech production via links to motor cortex; and the two are interconnected through the arcuate fasciculus (Geschwind 1970). A modern understanding stresses dissociable ventral and dorsal components of this network, with the ventral one processing conceptual relations and the dorsal one auditory-motor sequences (Hickok & Poeppel 2007) via a thalamo-cortico-striatal loop (Petkov & Jarvis 2012). This pathway is not specific of heard language: communicative gestures that are non-emotional also engage the human left inferior frontal regions where Broca’s area lies (Holle et al. 2008; Straube et al.

2011). Homologous brain regions in other primates might thus be involved in proto-syntactic signaling and processing (Petkov & Wilson 2012) and in processing communicative gestures (Ghazanfar & Takahashi 2014) (Fig. 2).

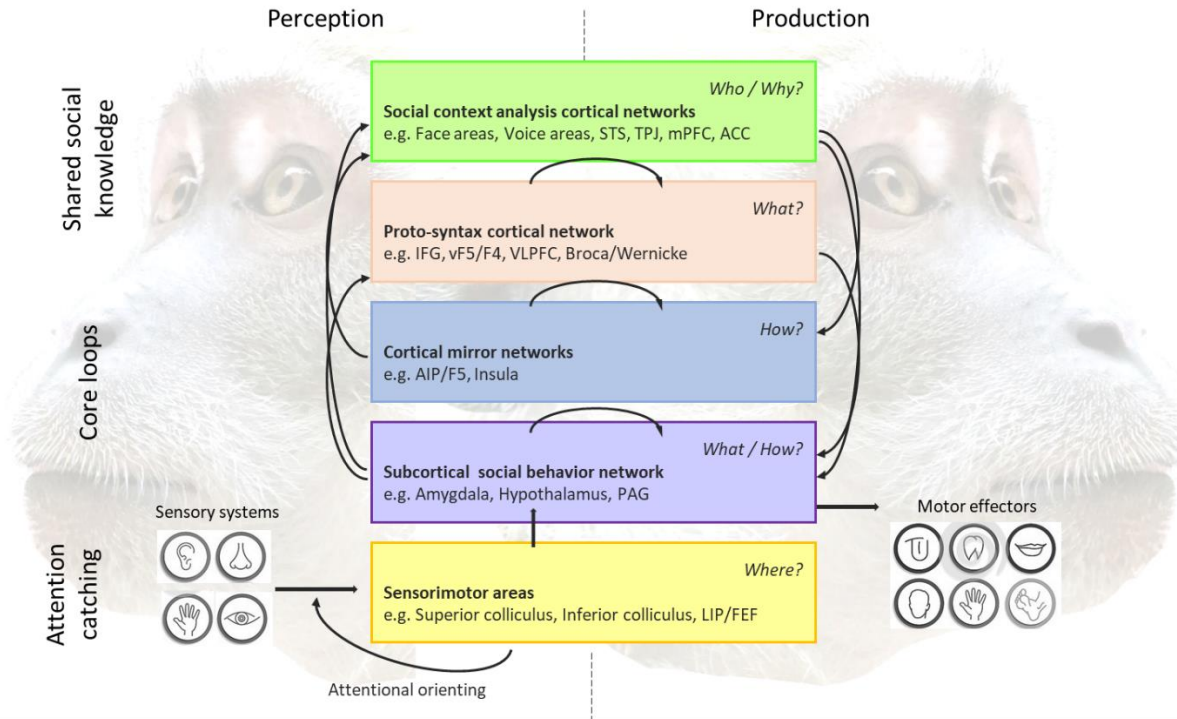


Fig. 2. — Schematic representation of the cognitive processes involved in primates’ perceiving and producing communicative signals, and their associated neural substrate. The cognitive processes depicted include: “Where the signal comes from”, by sensorimotor areas, “What is being signaled”, by the subcortical social behavior network and the proto-syntactic cortical network, “Who is signaling” and “Why”, by social context analysis cortical networks, and “How the signal is transmitted”, by cortical mirror networks. The figure highlights that the perception and production parts of these different cognitive processes are largely integrated, with the exception of early sensorimotor areas, which are primarily involved in detecting signals and orienting attention. The arrows show streams of signal processing and depict how these different processes interact with and modulate each other.

INTEGRATIVE NEURAL MECHANISMS FOR COMMUNICATION

Integration through brain nodes

The framework we have outlined — with separate perception and production of communication signals — only gets us so far. Some brain nodes, such as the amygdala, the insula, or part of the social behavior network appear to be engaged in both the perception “and” production of communicative signals, enabling rapid responses to urgent signals (Lundqvist & Dimberg 1995). Existence of such nodes having overlapping functions, illustrates Darwin’s suggestion of a direct link between the production of facial or body expressions, and the emotions felt in response to a perceived signal (Darwin 1872).

Integration through mirroring systems

Mirror neurons are neurons known to be involved in guidance of motor action that are also sensitive to the observed actions of others (di Pellegrino et al. 1992). Initially found within parietal and frontal regions of macaque monkeys, neuronal signatures of mirroring are widespread within the cortex (Rizzolatti & Sinigaglia 2008). Mirror neurons play a role in communication of attentional states, as they are active in gaze following (Shepherd et al. 2009). They might also be active for motivating imitative, cooperative and competitive behavior and in representing communicative goals and predicting signaling (Rizzolatti & Craighero 2004; Cook et al. 2014) (Fig. 2). Further mirror activity may mediate recursive cognitive contagion between individuals, that results in coordinating their movements (Palagi et al. 2020).

Integration through brain-to-brain coupling

During social interactions, humans spontaneously adopt the behavioral states of others, aligning their words and phrases and body postures, synchronizing movements, and reflexively mimicking expressions and gaze directions with parallel changes in emotion and attention (Lakin & Chartrand 2003). This synchronization is paralleled by a synchronization of “brain states” in successfully communicating human individuals (Hasson et al. 2012; Jiang et al. 2012; Yun et al. 2012; Stolk et al. 2013; Dikker et al. 2014; Dumas & Fairhurst 2021). Such contagion of behavioral states and brain activity is not restricted to humans (Sliwa 2021) and face-to-face interaction in macaques showed lipsmacking contagion mediated by activity in premotor areas (Shepherd & Freiwald 2018); yawning in chimpanzees, macaques and humans (Palagi et al. 2020); reciprocated contact calls in marmosets (Takahashi et al. 2013) possibly mediated by between brains synchronization of activity of the ACC, mPFC, and STS (Gilbert et al. 2021).

CONCLUSIONS AND FUTURE AREAS OF RESEARCH

Primates present a rich range of communication strategies in different modalities that evolved as signaling, perceiving and signaling back behaviors. The brain areas for perceiving and producing communicative signals can be described separately, but form integrated loops through overlapping nodes, mirroring systems and inter-brain synchronizations, which coordinate perception and action in the signaler and receiver brains. Moreover, multiple sensory modalities share neural pathways for signaling, and also neural pathways for receiving: a redundancy that might ensure proper communication transfer. Several points would benefit from additional research: (1) most neural mechanisms subtending primate communication strategies have been studied in only few species including macaque monkeys, humans, squirrel monkeys, and marmosets, and (2) the neural mechanisms of some communication strategies are only starting to be investigated, such as those concerning tactile and chemosensory communication. (3) The third point concerns the complementary roles of phylogeny and ontogeny: While signaling behaviors have been passed through generations and are present at birth in primates, these behaviors subsequently go through a process of modifications mediated by interaction with peers (Takahashi et al. 2015, 2017). An intriguing possibility is that a process of ritualization of these ontogenetic modifications enabled primates to produce fine communicative abilities, eventually creating different cultures in some species. More studies are needed to understand the neural mechanisms underlying social motivation and learning of signal production and perception in the developing primate brain.

ACKNOWLEDGEMENTS

The authors wish to thank Elisa Demuru and Cristina Giacoma for the opportunity to contribute to the special issue; Stephen V. Shepherd for initiating and working with us on two previous reviews, which set the stage for this article.

FUNDING

This work was supported by Agence Nationale de la Recherche (ANR-21-CE37-0016-02, ANR-19-CE37-0002-01, and ANR-10-IAIHU-06 to J. Sliwa) and the International Brain Research Organization (Return Home Fellowship to J. Sliwa).

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

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