Neurobiology of emotions in animal relationships: Facial expressions and their biological functions in mammals

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Abstract This article aims to analyze the biological and communicative function of facial expressions and their relation to emotions in mammals. Facial expressions and their causes constitute an important yet largely unexplored field of scientific research. While the clinical usefulness of these expressions for recognizing pain in many species has been demonstrated, there is evidence that animals can also emit facial movements with other connotations. Reports show that facial expressions have a biological function by predicting and promoting social interaction in species that form complex social groups, but their meaning depends on the social context. For animals, the unconscious identification of facial expressions also implies an emotional value by modifying the compensatory physiological response, as occurs in species that have close relationships with humans. This corpus of evidence suggests that facial expressions have a kind of communicative function and may transmit emotions and, therefore, participate in affiliative or adverse relations as animals develop. Hence, exploring whether this nonverbal behavior may perform such a dual function is necessary.

Keywords: animal relationship, facial expressions, animal behavior, emotion, communication

1. Introduction

The ability of animals to manifest facial expressions in specific contexts has spurred broad controversy among researchers in communications and emotions and constitutes a great challenge, especially for animal models (Dolensek et al 2020). We understand facial expressions as a nonverbal behavior (Lezama-García et al 2019), but what motivates animals to perform these acts?; does it fulfill some specific biological function? What do facial expressions transmit?

Efforts to understand the evolution of emotional communication include comparative studies of similarities between human facial expressions and those of other species (Parr and Waller 2006, 2007). When mentioning emotions, there are currently variations and contrasts among authors when defining emotion. Rolls (2014), for example, defines emotions as states that occur as a result of situations that motivate sensations of reward or punishment through instrumental reinforcers that can be either positive or negative. However, Waller and Micheletta (2013) define them as processes that facilitate appropriate responses to a broad range of environmental and internal situations. Although these two definitions differ markedly, they clarify that emotions are closely related to functional systems of physiology and behavior (Panksepp 1998; Parr and Waller 2007).

It has been argued that animals use visual, acoustic, tactile, and olfactory signals to interact with other individuals (Altenmüller et al 2013). Upon reaching a receptor, those signals trigger physiological and behavioral changes to respond adequately to the stimulus (Dawkins and Krebs 1978). These movements or expressions give the observer physical information such as identity, sex, age (Burrows 2008; Parr 2009), or even the emotional state of the issuer (Levenson et al 1990; Waller et al 2016; Bremhorst et al 2019). Moreover, they can inform other individuals of the habitat conditions in which animals develop.

The proposal that facial expressions are a form of communication is sustained by the fact that the animal that receives a visual facial signal responds by modifying its behavior or performing another expression (Goossens et al 2008), for example, fleeing from a threat or enjoying a pleasant situation that may lead to learning (Mendl et al 2010). While this argument is valid, observations suggest an
additional possibility: that coexistence with humans has led animals to “adopt” expressions to effectively draw our attention, as seen in dogs (Waller et al 2013; Kaminski et al 2019). However, it has been shown that some movements are only related to physiological responses rather than facial expressions. This has been reported in dogs, in whom the eyebrow movement responds to the positional change of the ocular globe, and the opening of the mouth during panting has a physiological thermoregulatory function (Bremhorst et al 2021). Changes in facial expression are also present due to the perception of pain in animals, which could imply an exclusively physiological function.

Other findings show that facial expressions may appear during situations that do not require conscious processing of stimuli, raising the possibility that animals may use these signals to indicate emotional states (Bremhorst et al 2020). Studies of equines (Trösch et al 2020) and cats (Finka et al 2019), for example, have shown that these animals generate facial movements that reflect their emotional state in both pleasant and potentially negative situations. Thus, this document aims to analyze scientific evidence on the biological role and communicative function of facial expressions, the neurobiology of emotion and how this relates to emotions in mammals.

2. Review Methodology

The methodology for the present article is schematized in Figure 1, where studies focusing on evaluating facial expressions, animal communication, and emotional evaluation in animals were selected. The following databases were consulted: Web of Science, Science Direct, and CAB Abstracts. The keywords used were ‘neurobiology of facial expression’ in combination with ‘domestic animals’, ‘nonhuman primates’, ‘companion animals’ and ‘wildlife’ and ‘facial expression’, ‘body language’, and ‘facial communication’ in combination with ‘animal emotion’, ‘aggression’, and ‘animal intention’. The inclusion criteria for the articles and books (n=124) were those about changes in facial expression in mammals (domestic, companion, or wildlife) in response to several social environments or stimuli, as well as those where the development of emotion or mental state was related to a change in facial expression. We excluded those studies where facial expression was described but not particularly related to an emotional state in animals.

Figure 1 Review methodology.
3. The biological role of facial expressions

In recent years, facial expressions have generated interest in the scientific community because research has shown that they can provide valuable clinical information, such as pain-related facial expressions (Cohen and Bets 2020). This has led to the elaboration of grimace scales for horses (Dalla Costa et al 2014), cats (Evangelista et al 2019; Evangelista and Steagall 2021), pigs (Viscardi et al 2017; Mota-Rojas et al 2020b), mice (Matsumiya et al 2012), ferrets (Reijgwart et al 2017), rats (Mota-Rojas et al 2020a; Dominguez-Oliva et al 2023), rabbits (Mota-Rojas et al 2020a), sheep (McLennan et al 2016; Häger et al 2017), and lambs (Guesgen et al 2016). The suggestion is that facial expressions can help us identify levels of animal welfare using a noninvasive method (Descovich et al 2017; Cohen and Bets 2020).

The practical use of facial expressions has been made possible by objective analyses through the facial action coding system (FACS), which describes movements of determined groups of facial muscles (Ekman et al 1978; Waller and Micheletta 2013; Waller et al 2020). Although the usefulness of observing and interpreting facial expressions has been demonstrated, several questions still need to be answered, such as what function(s) these expressions perform for animals. Do they transmit emotions or only function as a form of animal communication?

Today, we recognize that animals’ facial expressions provide two types of information. On the one hand, they can report physical sensations such as pain. Conversely, they can communicate states of intention and emotion or respond to an external stimulus (Camerlink et al 2018). According to Andrew (1963) and Fridlund and Russell (2006), the primary function of facial expression could have evolved from physiological functions. Both authors mention that facial expressions have a protective function, such as squinting of the eyes to protect the organ when exposed to intense luminous stimuli in humans, as a result of the contraction of orbital muscles to close the eyes (Landis and Hunt 1939; Ekman et al 1985; Susskind and Anderson 2008). These responses protect against sensory damage and may elicit an emotion (Susskind and Anderson 2008).

Regarding evolutionary success, facial movements are considered an adaptive trait (Schacter et al 2011; LeDoux and Damasio 2013). Animals use signals and cues to give information and intentions to a receptor that, in most cases, will react to them (Carr and Winslow 2001; Reyes 2021). Following this theory, simple signals such as hostile facial expressions can be shown before escalation to an actual attack. On the other hand, cues are passive and unintentionally change the receiver’s behavior (Lai-dré and Johnstone 2013). This can be interpreted as the automatic physiological or emotional response that leads an organism to respond to an adverse event (Reyes 2021). Due to this characteristic, facial expression has been associated with pain-related reactions when animals are exposed to noxious stimuli (Domínguez-Oliva et al 2022). Figure 2 shows the facial expressions of a Japanese macaque when expressing aggression. These examples represent how subtle facial movements can start an interaction before a full escalation to an actual aggressive face. These movements are associated with the secretion of neurotransmitters after negative and positive states such as aggression (catecholamines) or pleasure (oxytocin), allowing the interaction and development of muscle movements and, therefore, facial action units.

Camerlink et al (2018) integrated these two ideas to analyze whether pigs can use facial expressions as intention signals. They quantified differences in the facial metrics of 38 pigs during negative emotional states (aggression), using 572 images of their faces before, during, and after aggression to measure the angle of the ears and proportions of the snout and the white of the eyes. The findings showed that the pigs’ ears were more often inclined forward during aggression but were oriented backward during the retreat. The white eye proportion was larger in the animals that incited aggression than in the others (1.05 ± 0.03 vs. 0.99 ± 0.03, P=0.04). They also detected a reduction in the proportion of the snout. According to this information, backward-oriented ears and the snout proportion could indicate an intentional state (aggression) in this species. At the same time, the white of the eyes could be considered an indicator of an emotion (Figure 3).

The information described above depicts the idea that facial movements in mammals reflect voluntary or involuntary information. From an ecological perspective, these signals indicate an escalated interaction, for example, territorial fights or female-attention aggression (Lai-dré and Johnstone 2013). The possibility of mammals having different facial expressions depending on the context was reported in a study of mice exposed to a stimulus of social proximity to (i) unknown conspecifics and (ii) a predator, where the authors proposed that facial expressions can provide information beyond painful situations (Defensor et al 2012). This study evaluated several interactions, such as the vibrissae contact test (strok ing with the bristles of a brush), social proximity test with conspecifics, resident-intruder test of aggression, cat odor, and live rat exposure. All facial changes observed included ear flattening, nose and cheek swelling, and tension in the orbital muscles that appeared half-closed eyes, which protected sensitive, vulnerable body regions when exposed to stroking, conspecifics, and aggression.

In contrast, the changes were more subtle when mice responded to exposure to cat odor, live rats, and intruder mice. This is an example that the type of facial changes and their intensity depends on the context. However, this did not allow the authors to differentiate an emotional state as a form of communication (Defensor et al 2012).

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Figure 2 Facial expressions in a Japanese macaque (Macaca fuscata) during social communication of aggressive behavior. (A) Neutral. (B) Bored expression. It is possible to identify movements such as medial tension of the upper eyebrow, lowered head, and slight tension of the lower lip. These facial units might suggest a lack of positive interaction with a conspecific. (C) Alert. In this expression, muscle movements such as raising the upper eyebrow, nostril dilation, and tension of the upper lip can be observed, giving a general tense appearance toward a conspecific. (D) Warning or intimidation. In this picture, the upper eyebrow is raised, causing tension in the medial zone of this region. The dilation of the nostrils and the depression of the lower lip expose the teeth as a sign of intimidation, trying to flight from the potential threat. (E) Aggression. Raising and tension of the upper lip cause total exposure of the teeth, together with eyebrow tension. Pupil dilatation is also observed.

Figure 3 Changes in the facial expression of pigs in two situations. (A) When exposed to a stimulus that generates a positive mental state (e.g., palatable food), olfactory, visual, and tactile stimuli reach the brain and then go to the motor cortex, where they modulate changes in facial expressions during events. In pigs, relaxation of the masseter muscles and the dorsal part of the nose is observed, as is miosis due to a predominance of parasympathetic tone and the ears oriented in a forward position. (B) When the stimulus is negative, the presence of aggression by conspecifics causes changes such as mydriasis, nose-snarling, a backward position of the ears, and mouth fully open. VNO: vomeronasal organ.
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The recognition of mammals’ facial movements during exposure to several stimuli, whether a social or a threatening situation, could explain the usefulness of facial expression to support both functions, that is, that animals (i) use facial expressions as a means of communication or (ii) to transmit emotions. Human facial expressions have been shown to reliably communicate emotions (Barrett et al 2019), although they may be difficult to interpret. For example, the lip corner or the tension of the orbital muscles can be present in both emotional and social contexts (Frith 2009; Heaven 2020). This problem is mirrored in reports on other species, such as dogs, where features related to the breed interfere in reading expressions (Heaven 2020; Bloom et al 2021; Mota-Rojas et al 2021a). Despite these challenges, studies of species characterized by complex social structures, such as nonhuman primates, have found that facial movements can be helpful but may be insufficient to regulate interaction with conspecifics in cases where animals of the same group ignore the aggression of threat facial expressions, which could result in confrontation (Hinde and Rowell 1962).

Therefore, the discussion of the biological function of facial expressions faces the diversity of interactions across species and their context. In the case of nonhuman primates, a highly sociable species (Waller et al 2016), facial expressions promote interactions such as play and grooming or during the recognition of the conflict. In the case of prey species such as rodents or ruminants, facial expressions are linked to the automatic generation of an emotional state, which prepares the animal for an adverse event in cases such as perceiving a predator. Based on observations, facial expressions could constitute a way in which animals identify emotions in others and, therefore, could play a role in phenomena such as emotional contagion (Palagi et al 2015). Facial expressions may have a function in both communication and emotional communication.

4. The communicative function of facial expressions

Animals use conspicuous signals, such as emitting vocalizations, releasing pheromones, and modifying body language, to transmit information to conspecifics or other species (Smith 1977; Dawkins and Krebs 1978). Among these signals, facial expressions are considered primitive, nonverbal language facilitating individual interaction (Fridlund and Russell 2006). Indeed, authors such as Fridlund (1994) sustain that these expressions must be understood as social-communicative signals that trigger a functional consequence (Prkachin and Soloman 2008), as elements of an evolutionary adaptation that seeks to obtain a direct benefit for the emitter (Gratieto 1865; Piderit 1867). Therefore, the conscious processing of a situation or stimulus that culminates in the development of facial language functions as a coping mechanism for specific situations and, simultaneously, a possible form of interaction with peers or other species.

In any case, identifying a facial expression and discriminating its message depends on the capacity of animals to differentiate the gestures generated by a conspecific. Wathan et al. (2016) analyzed events of this kind in 48 domestic horses (Equus caballus) of different breeds and sexes. They showed the horses photographic images with facial expressions of conspecifics in different contexts: positive attention/agonistic, relaxed/agonistic, and positive attention/relaxed. The results showed that the horses approached the images with facial expressions associated with positive attention more often than those that presented agonistic gestures (n=11, K=11, P=0.001). The horses also observed positive expressions for more time than agonistic expressions (Mdn= 8.91 s vs. 2.98 s, z= -2.74, P= 0.006, r= 0.48). This could demonstrate that mammals emit facial movements to communicate information and elicit a response from the perceiver. In a second study, the authors determined that equines can successfully discriminate the facial expressions of conspecifics—a phenomenon previously observed in domestic canines (Racca et al 2012; Mota-Rojas et al 2021a)—and that observing positive images generated physiological responses as a lower heart rate (HR) compared to the readings recorded during agonistic stimuli (Mdn= -1 vs. Mdn= 1, Z= -1.94, P= 0.052, r = 0.26). This same response was observed in another study of 28 horses of different breeds and ages (4-23 years) (Smith et al 2016). Those animals responded to photographs of positive (happy) and negative (angry) human facial expressions. Compared to positive images, when exposed to the negative images, the horses manifested both a higher HR (Mdn= 19.4, CI + 6.50; Mdn= 32.1, CI + 4.01, respectively, P=0.028) and a left-gaze bias (Smith et al 2016), associated with activity in the right cerebral hemisphere for the processing of negative emotional stimuli (De Boyer Des Roches et al 2008). The complementation of these studies perhaps allows us to maintain that facial movements produced by a mammal help to obtain information, respond to the obtained cue, and possibly motivate specific social interactions.

In the domestic cat, Humphrey et al. (2020) observed that slow blinking is a form of positive state communication between animals and humans. Their study used 24 cats and their owners to evaluate the formers’ slow-blinking behavior and responses to interaction with the researcher. The results showed that in response to human blinking, the cats showed an increase in the frequency of half-blinks and eye-narrowing compared to a control group (M= 4.22 +/- 3.93 vs. 1.89 +/- 2.52, P= 0.04, and 3.39 +/- 2.45 vs. 2.17 +/- 2.26, P= 0.04, respectively). The half-blink and eye narrowing constituted interspecific communication (Humphrey et al 2020). These studies conclude that movements of certain groups of facial muscles perform a communicative function with humans (Humphrey et al 2020). These findings
reinforce that facial expressions are communicative in conspecifics and between species (Racca et al 2012; Smith et al 2016). However, as we have learned from work with dogs, interpretations can reflect individual preferences and the values different observers assign to the observed phenomena (Waller et al 2013).

In the case of dogs, Kaminski et al (2017) evaluated 24 dogs of different breeds in an age range of 1-12 years to determine the influence of human presence and attention on the frequency of the presentation of facial expressions such as raising the inner brow (AU101) and showing the tongue (AD19). When the humans oriented their attention toward the dogs, the animals responded with a greater frequency of those movements than when the humans did not pay them attention (P<0.0001). An opposite effect was reported where the presence of food did not alter the facial movements in dogs (P> 0.05). Hence, human-animal interaction and the diverse mechanisms that animals use to coexist in interspecific groups may influence facial expressions, perhaps as a form of social group regulation (Mota-Rojas et al 2021a).

Reports on primates suggest they often recur to facial signaling to transmit information on motivations, intentions, and emotions in specific contexts (Parr et al 2002). A study by Waller et al (2016) on three crested macaques (Macaca nigra) (one male, two females) used videos of unfamiliar conspecifics with three different facial expressions: bared teeth, open mouth threat, and screaming to predict social outcomes. In the first case, teeth-baring was considered an expression analogous to the human “smile” and was associated with the primates' prediction of friendly outcomes, while contrary to what can be expected, screams and threat faces did not result in conflict interactions.

Nonhuman primates are a species in which the social value attributed to facial expressions is fundamental in avoiding conflict and promoting affiliative interactions (Scheider et al 2016). For example, the threatening yawn of a monkey may generate a submissive posture in a conspecific (Brothers 1990) (Figure 4).

**Figure 4** Facial motor control and facial expression in rhesus monkeys. When animals perceive positive or negative stimuli, the relevant information is integrated and processed by several structures: the thalamus, amygdala, and limbic system. These regions have projections to the facial motor center, located in M1, and are responsible for innervating the facial muscles and generating movements of the eyes, lips, jaw, and tongue. M1, PMCvl, and M4 are responsible for controlling the movement of the lower half of the face, while M3 and SMA modulate the movement of the muscles in the upper half through the facial nerve, which innervates all mimetic muscles. (A) Neutral face; (B) bared-teeth expression seen when animals are frightened or threatened; (C) in nonhuman primates, yawning has three possible meanings: a relaxed attitude around conspecifics, anxiety, and exposure to threatening situations. AMY: amygdala; M1: primary motor cortex; M3: anterior face area of the midcingulate cortex; M4: caudal face area of the midcingulate cortex; PMCvl: premotor cortex ventrolateral division; SMA: supplementary motor area.

Other studies have shown that the social environment of great apes highly influences the facial repertoire. In a comparative study between captive and wild orangutans (Pongo abelii and Pongo pygmaeus), Frölich et
al. (2021) reported that zoo-housed animals have a larger communicative repertoire comprised of 41 gestures and facial cues. Captive-only signals included lip flip, headstand, roll on ack, etc., while similar patterns of beg mouth, play, and pout face, among others, were observed in both groups. It is suggested that this results from behavioral plasticity, where captive orangutans require constant communication with human caregivers. Likewise, in red-capped mangabeys (Cercocebus torquatus), the intensity of facial displays, including mouth, eyebrows, and ears movements, was regarded as a communication method since it changed according to the social context. The playful open mouth was particularly associated with intentional communication (Aychet et al. 2021).

Therefore, it is evident that facial expressions promote social relations by interpreting the movements and predicting the type of interaction to expect.

Additionally, the role of primate facial expression as a communicative cue is not solely relevant for conspecifics. Studies by Graham and Hobaiter (2023) have found that 57.3% of 53647 humans could understand great ape gestures (chimpanzees and bonobos) as a retained evolutionary system where humans can interpret nonhuman primates' facial communication. Nonetheless, although there might be a similarity between species, great apes lack distinct morphological features related to the gaze-signaling hypothesis (e.g., exposed white sclera to enhance eye outline and iris visibility), elements that facilitate human communication (Kano et al. 2021).

The promotion of social interactions has also been studied by others, as shown by Clark et al. (2020), who refuted this idea by evaluating the facial characteristics of crested macaques (M. nigra) during affiliative, copulatory, playful, and submissive interactions. Their results indicated that the most frequent expressions during play were jaw-stretching (AU27) and ear-flattening (EAU3), in contrast to copulation, where the only movement observed was jaw-wobbling (AU184). These differences in the presentation of one expression or another reveal the importance of the social context in which animals are placed to express and promote positive or negative social interactions through facial movements. Although the context is an important point to consider in evaluating the facial expression, this could help to differentiate the origin of the grimace and not the information that allows facial movements to be transmitted.

When a facial expression has the purpose of communication, it can take place during the development of relationships between conspecifics. The above was observed in studies of laboratory rats (Rattus norvegicus), whose facial expressions, such as orbital tightening, ear retraction, and the position of the whiskers, have been associated with the affective component of positive and negative events and identified as a way to communicate those states to conspecifics (Ebbeisen and Froemke 2021). Ear-wiggling, for example, is characteristic of receptive females in the estrus stage and an element of the sexual behavioral repertory of this species (Yakubu and Akanji 2011). In addition to the sensory function of whiskers in rodents, a protracted position of the whiskers during interaction with conspecifics can signal aggression (Brecht and Freiwald 2012), accompanied by greater whisking amplitude (Wolfe et al. 2011). The examples mentioned above are compatible with the central concept of communication, which elicits a response from a preceptor, either positive or negative, but they may also be predicted.

It is essential to mention that while similar facial movements can be seen in many species, their biological and communicative functions differ. Baring the teeth, for example, is a common signal in primates and canines, and retracting the upper lip (AU118) represents a threat signal among conspecifics of wolves (Siniscalchi et al. 2018). However, facial movement in primates facilitates affiliative interactions among conspecifics (Altenmüller et al. 2013).

In summary, the facial expressions of animals are a means of social interaction and offer a way to predict the consequences of those relations. In both cases, the movements of the mimetic muscles, or facial expressions, result from integrating the recognition of stimuli of diverse kinds with the accompanying coordinated motor response.

5. Neurobiology of emotions and their relation to facial expressions

The expression of emotions in animals has been a topic of interest in scientific research since Darwin announced his thesis (Darwin 1872) that animals can express emotions through their behavior, similar to humans. This idea has been reaffirmed by Machado and Oliveira da Silva (2020), who argue that animals can emit facial movements, especially of the ears and eyes, associated with particular emotional states. However, it has yet to be determined whether facial expressions can function as a means of emotional communication (Fridlund and Russell 2006). Several questions must be addressed: do animals transmit emotional states through facial expressions? What exactly are emotions, how are they produced, and what biological function do they perform? To respond to these questions, we must begin by defining an emotion.

In this vision, an emotion generates changes in behavioral responses and physiological and cognitive alterations (Adolphs 2017) designed to confront external or internal environmental changes, whether adverse or favorable. Based on this evidence, it is possible to establish that emotions have a regulatory function for individuals. However, when referring to the possibility of transmitting effective emotional communication, some authors mention that this can provide information about the internal state or about events in its environment that can serve as valuable information for the recipient, as seen in the presence of food or predators (Seyfarth et al. 2010; Snowdon 2021). These signals can inform others about the internal state of the animal. This approach dedicates that an emotion's biological function is not far from Darwin's original proposal (Darwin 1872). He affirmed that emotion could prepare an
organism to respond to environmental stimuli while communicating critical information and possibly contributing to the emergence or maintenance of the emotional state. In summary, animals recur to emotional states to deal with environmental and social exigencies. In this way, we can understand why emotions are considered patterns of behavioral, hormonal, and autonomous responses designed to promote individual survival (Dolencek et al. 2020).

Diverse authors argue that emotions result from cerebral states that reflect the dynamic integration of corporal signals and cognitive processes (Damasio and Carvalho 2013; Anderson and Adolphs 2014; Spunt et al. 2017). However, Dolencek et al. (2020) sustain that they should be understood as distributed cerebral states that entail complex brain networks. The regions they mention include the prefrontal and orbitofrontal cortices, insula, anterior cingulate, nucleus accumbens, ventral pallidum, amygdala, periaqueductal gray matter, and hypothalamus (Salzman and Fusi 2010; Berridge and Kringelbach 2015; Calhoon and Tye 2015; Dolencek et al. 2020; Kennedy et al. 2020). The process through which all these regions trigger emotions is a line of research demonstrating that the limbic system plays a transcendental role as a regulator because some of its structures function as an integrating center that receives the information and transforms it into physiological, behavioral, and even cognitive responses. The amygdala is one specific region of the limbic system that plays an essential role (Phelps and LeDoux 2005).

The structures that have demonstrated a significant association with the perception of emotions include the amygdala, which coordinates the emotional responses of animals. Paré and Collins (2000) evaluated four adult cats by implanting a series of microelectrodes in the lateral amygdaloid nucleus and a catheter in the femoral artery. The animals received a series of sound tones interrupted by 5 seconds of silence, followed by electrical discharges to their paws. During the silence and while receiving the harmful stimulus, the cats’ blood pressure increased significantly from the basal level (basal= 117.0.26 mm Hg; silence= 139 1.96 mm Hg; harmful stimulus= 164 3.07 mm Hg, P< 0.05). Additionally, there was greater activation of neurons in the lateral amygdaloid nucleus and a 40% increase in activity in the cortex and perirhinal cortex (1.61 0.475 vs. 2.33 0.512; P<0.05). From a neuroanatomical perspective, the amygdala acquires this capacity through its lateral and/or basolateral areas and the central nucleus, which play transcendental roles as elements of emotional neuronal circuits. We have mentioned that the amygdala’s lateral and/or basolateral areas are the regions where processed information from the thalamus, hippocampus, limbic system, and cortex – or specific areas of it, such as the primary sensory and perirhinal cortices, converge (Fendt and Fanselow 1999).

These findings confirm the importance of the behavioral response at the level of the amygdala as the behavioral expression that allows animals to confront adverse contexts. For example, perception is of visual origin upon sensing an aversive stimulus, and the image generated is transported to the lateral/basolateral amygdala complex through a complex network that commences when the retina receives the nervous stimulus. That signal is transmitted to the dorsolateral geniculate nucleus and crosses the perirhinal cortex, so the information arrives directly in the amygdala. Stimuli of auditory origin, in contrast, are transmitted from the cochlea to distinct subregions of the thalamus and auditory cortex, finally reaching the perirhinal cortex to inform the amygdala directly (Fendt and Fanselow 1999; Walker et al 2002; Phelps and LeDoux 2005).

Once the brain centers process the information, the facial expression occurs by transmitting nerve impulses through the branches of the facial nerve (VII), which triggers contractions of the mimetic muscles and the movements that characterize the various facial expressions. This increased activity of the mimetic muscles produces expressions such as frowns thanks to ample connections between the facial muscles and surface structures such as the skin and fascia, among others (Wathan et al. 2015).

The importance of the amygdala and its role in recognizing facial expressions has fostered research based on experimental models. Studies have shown that lesions in the rostral region of the lateral nucleus of the amygdala produce an inhibitory effect on the activation of the fight-or-flight response (Ursin 1965). A study by Hadj-Bouziane et al. (2012) evaluated the functional MRI activity of the amygdala and the inferior temporal cortex in six healthy macaque monkeys and others with an excitotoxic lesion in the amygdala. The animals were shown images of the faces of conspecifics with distinct emotional valences (neutral, aggressive, fearful, appeasing). The results showed that the lesioned animals suffered modulatory alterations in the inferior temporal cortex that inhibited them from presenting expressions of threats or threatening behaviors, such as lip smacking. The absence of the fear response in the temporal cortex accompanied that. That work indicated that lesions at the level of the amygdala could alter the neuronal processing of emotions in the cortex (Baxter and Croxson 2012). Moreover, it supports the hypothesis that the amygdala drives the neuronal codification of emotional identity (Jhang et al 2018).

5.1. Facial expressions and their relation to emotions

The neurobiological process of emotions leads animals to develop macro- and microcorporal reactions to detect emotional states. Authors such as Levenson et al. (1990), de Waal (2011), and Zych and Gogolla (2021) argue that facial expressions evolved together with the capacity to decode expressions and infer emotional states perceived in other animals. Significantly, this capacity has been identified in primates, canines, felines, and ungulates (Schenkel 1947; Leyhausen 1957; Schilder et al 1984). Thus, it can be suggested that animals use facial expressions to denote emotional states, which can lead to a positive or negative
interaction. The above suggests that these expressions have a bivalent function. Dolensek et al. (2020) and Girard and Bellone (2020) sustain that these nonverbal behaviors reflect some properties of emotions, such as valence (positive/negative), scalability (graduating the nature of emotional intensity), and flexibility (capacity to regulate emotions).

The possibility that facial expressions may be indicators of emotions has been analyzed by numerous authors (Waller et al 2016; Bremhorst et al 2019; Finka et al 2019; Dolensek et al 2020; Trösch et al 2020). Nawroth et al (2018) evaluated 34 goats previously habituated to the presence of humans upon showing them two images of unfamiliar people with different emotional values (positive/happy or negative/angry). They found that the goats interacted 0.5 seconds more with positive than negative faces (Wald = 3.73, d.f. = 1, p = 0.0533). They concluded that animals could discriminate facial expressions in valence and prefer positive valences. In this way, it can be understood that mammals generate movements of the face to reveal and communicate an emotional state felt by an individual.

A study of 9 dogs—Labradors and Poodles—that were shown photographs of smiling faces, unfamiliar people and familiar people, and expressionless faces found that the animals chose to interact more often with the photos of smiling faces (P< 0.05) (Nagasawa et al 2011). However, no significant difference was found among the choice of smiling, unfamiliar, and familiar rostrums/faces (P> 0.05). The results indicate that animals can learn to differentiate inexpressive faces from faces that emit some form of facial movement (Nagasawa et al 2011). Based on this ability to differentiate the purpose of the facial changes of congeners, it could be assumed that facial expressions allow animals to communicate some information and incite an emotional reaction when communicating this state.

Studies of equines have reported similar results by observing that some physiological parameters increase, for example, heart rate and the number of times they repeated the vigilance posture when shown a photo that presented angry human faces accompanied by a vocalization with the same connotation (Trösch et al 2020; Lundblad et al 2021). That evidence sustains the argument that animals recognize expressions related to emotional states and generates a new discussion as to whether animals use facial expressions to communicate or if we are dealing with an indicator of their emotions. Studies of dogs have shown that facial expressions are an important means of communication, and their interpretation can be beneficial since we assume that many of the behavioral problems this species present have an emotional basis, for example, aggression caused by frustration (Amsel 1958; McPeake et al 1999). Upon entering a delimited zone, Bremhorst et al (2019) studied 29 Labrador Retrievers trained to receive high-quality food (pieces of roast chicken). The test consisted of a methacrylate box with an opaque panel containing the reward. The reward was considered positive when the animal could reach it, while in the negative, it remained inaccessible. Those experimenters evaluated facial movements using the DogFACS tool. They found that blinking and movements of the adductor of the ears were common in positive conditions while opening the lips, jaw-dropping, and nose-licking were associated with negative situations. Their findings support the theory that animals emit facial expressions based on their emotional states. A later study with dogs by the same authors successfully replicated these results by observing that the dogs made movements of the adductor of the ears during positive emotional states while blinking, ear flattening, opening the lips, jaw-dropping, and nose licking were manifested when negative emotions were present. However, they also observed that ear-flattening and “ears down” behaviors had high sensitivity but low specificity (sensitivity= 0.89, specificity= 0.56), while the movement of the adductor showed high specificity but low sensitivity (sensitivity= 0.50, specificity= 0.90). They concluded that facial movements could not classify emotional states correctly and consistently (Bremhorst et al 2021). This does not indicate that facial expressions are not good indicators of emotions. However, they should be considered in combination with other facial or body language that should be investigated in future studies.

Work with horses has found similar facial movements where facial expressions were used as an emotional indicator. For example, Lundblad et al (2021) evaluated the heart rate and facial movement frequency of 28 horses of different breeds during 6 hours of transport in a trailer that measured 3 m x 4 m. The animals were divided into two groups, one subjected to previous short-term social isolation (30 min) and the other control. The authors found that both groups—with or without social isolation—had increased heart rates during transport (basal= 35 beats per minute; posttransport= 88 beats per minute, P= 0.008). The facial movements they were able to identify in both groups were an increase in the visible portion of the white of the eyes (P< 0.001), nostril dilatation (P<0.001), raising of the upper eyelid (P<0.001), and increased ear movements and blinking (P< 0.001). Most facial characteristics identified correspond well with previous findings on the behaviors of stressed horses.

Additionally, in horses, Lansade et al (2020) subjected the animals to two types of handling: gentle cleaning and standard grooming. They evaluated facial expressions and several physiological indicators: cortisol and oxytocin levels and the frequency and variability of the heart rate. Observations showed that oxytocin, cortisol concentrations, and heart rate did not differ before and after the grooming session. However, oxytocin levels were significantly lower in the case of gentle cleaning than in standard grooming (gentele= 14 pg/mL, vs. standard= 19 pg/mL, P<0.05). Regarding facial expressions, the authors identified the most common movements during the standard handling of the animals as an increase in the visible portion of the white of the eyes, wide-open eyes,
contracted lips, and asymmetrical ears (Mann–Whitney U: 177, P<0.0001). In contrast, during gentle cleaning, they saw more frequent movements of the central area of the neck, half-closed eyes, lip(s) extended forward with twitches, upper lip extension, and immobile ears pointing backward (Lansade et al 2018). This observation shows that facial language changes correspond to different interactions where animals respond with distinct expressions.

Studies of humans have demonstrated that viewing a threatening facial expression triggers a fear-based response in the observer. This reaction increases the physiological parameters of excitement with higher amygdala activity. This effect can occur even if the observer is unaware of the identified expression. The above explains, broadly speaking, the event called emotional contagion, in which people unconsciously tend to imitate an observed behavior (Öhman and Soares 1998; Pessoa 2005; Frith 2009). Emotional contagion has been reported in several animal species, including mice, which present pain-related behavior despite having no tissue lesion and seeing conspecifics manifesting pain (Pérez-Manrique and Gomila 2022). Likewise, observations of dogs that express a negative emotional state have found that their heart rate and behavior can be altered when they are shown a video of their owner experiencing a stressful event (Katayama et al 2019).

A study by Palagi et al (2015) evaluated 49 dogs to determine whether facial mimicry is imitated under conditions of intraspecific dyadic play and observed that movements such as jaw-dropping and play bow (typical signs of play in dogs) were adopted quickly and intensely compared to jumping and biting movements (P<0.025). They further found that familiarity affected mimicry; this form of emotional contagion occurred more frequently and rapidly the tighter the social bond among the animals tested. This finding demonstrates a close relation between facial expressions and the communication of emotions. However, some authors argue that it only mirrors a process of adaptation of animals to coexistence with humans that, over time, could have influenced the development of emotional contagion (Kaminski et al 2017; Katayama et al 2019). Moreover, as stated by Kret et al (2020), establishing a connection between facial expressions and an emotional response is challenging even in species closer to humans (great apes). Humans can suggest to a certain extent that a facial movement is related to an emotion. Still, other psychophysiological methods must be incorporated to understand its valence fully. For example, in several species, such as capuchin monkeys (Cebus apella), titi monkeys (Callithrix chopae), bonobos (Pan paniscus), and chimpanzees (Pan troglodytes), vocalization resembles humans’ syntax because the sounds and sequence of alarms differ according to the stimulus, a similar reaction when assessing facial expression (Leroux and Townsend 2020).

Although the evidence shows that the sender can manipulate facial expressions in mammals based on the manipulation/management model, this suggests that species such as dogs can interpret it as a reward. In other words, they may control the recipient’s behavior to change the response. This evidence suggests that facial expressions are produced based on emotional states and that this phenomenon has evolved in animals. Moreover, facial expressions function in animals to predict the type of interaction that may develop with conspecifics. We can deduce, then, that facial expressions perform a bivalent biological function: for communication purposes and as emotional expressions (automatic) and that inclining the balance toward one of those functions would constitute a straightforward way of understanding a much more complex reality in animals.

6. Future directions

Animals generate facial expressions following the context in which they find themselves. For this reason, these expressions have acquired clinical usefulness, such as the ability of handlers to recognize acute pain in species such as mice, rats (Langford et al 2010; Matsumiya et al 2012), rabbits, horses (Dalla Costa et al 2016), and cats (Evangelista et al 2019). This has led to the development of grimace scales for pain recognition using facial action units associated with pain. For example, in horses, ear asymmetry, orbital tension, contracted facial muscles, and nares dilation are pain-related facial features (Gleerup et al 2015; Hernández-Avalos et al 2021). However, using these expressions exclusively to detect pain limits the biological function we propose in this document. Therefore, it is necessary to design studies to determine whether these expressions can perform a predictive function related to the type of interaction that animals expect upon recognizing a specific expression and assigning it an emotional value (Camerlink et al 2018). Another urgent aspect is resolving the issue of whether the function is similar in most species or is limited to those that form complex social networks.

The idea that facial expressions help predict the expected type of social interaction could improve the relationship between domestic animals and humans. Some studies have suggested that reading facial expressions, in addition to an animal’s behavior and body language, may help handlers or owners interpret or estimate the positive or negative emotional states generated through human interaction (Mullard et al 2017; Andersen et al 2021). Those mentioned above may also aid in evaluating animal health and welfare levels before certain handling forms (Descovich 2017; Mota-Rojas et al 2020b).

Finally, evaluating facial movements in real time, or with the aid of remote technology, is an approach that may help identify animals in groups that are suffering some health problem (Mahmoud et al 2018; Camerlink et al 2018; Andersen et al 2021). In addition, the technology could aid in predicting the kinds of agonistic interactions that lead to fights among animals since events of that nature can result in severe, productive losses, injuries, or even death. It is certainly interesting to think that it may be possible to predict such behaviors based on specific facial movements that reflect the emotion of fear (Hansen et al 2021).
7. Final considerations

Facial expressions are a form of nonverbal, visual body language that animals have developed over millennia of evolution to adapt to the diverse environmental and social situations they confront. Therefore, it is valid to argue that facial expressions perform a communicative function among animals that does not always require conscious processing of the situation. Upon detecting a specific facial signal, an animal could predict the expected response type—negative or positive—and deal with the situation more favorably.

Animals may also recognize and award an emotional value to these expressions when they consciously process a situation that triggers facial movements to express a particular emotional state. An emotional response could help the animal confront a social or environmental context more advantageously. Finally, while it is feasible to think that facial expressions can express emotions, inclining the balance toward one specific function over others would constitute a simple response that does not reflect the complexity with which animals confront diverse contexts. Based on the evidence reviewed herein, facial expressions perform a dual biological function to indicate emotional states and as a way of communication.

Ethical considerations

Not applicable.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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