

Review Article

A Redefinition of Facial Communication in Non-Human Animals

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Abstract

In humans, social communication is mostly conveyed by facial expressions, which are widely shared among Mammals. Based on current knowledge, we explore the concept of facial communication from an evolutionary point of view and examine how far it might not only be performed by Mammals, but more broadly by Amniotes. As we investigate facial communication in various species, we find out that facial expressions are restrained to Mammals. However, even if non-mammals lack of cutaneous facial muscles responsible of facial expressions, they display facial signals bearing a communicative value. Thus, facial communication is not clustered to Mammals. Moreover, some facial displays are shared by almost every Amniotes, as the eye-blink which has been suggested to be related to social factors aside its physiological role. Yet, to understand the terminology of this research field, definitions should be unified. Thus, based on current data on Amniotes' facial communication, we proposed extended definitions of facial movements, behaviours and expressions: movements are visible displacements of body segments or tissues. They are motor action that do not need cognitive and emotional implication, while behaviours require the interpretation of environmental or internal stimuli, as the presence of an audience or emotional experiences. Behaviours are movements that can be involved in social communication. So facial behaviours are not cluster to Mammals but might be also expressed by other Amniote's species. Whereas facial expressions are facial behaviours generated by the contraction of cutaneous facial muscles, innervated by the cranial nerve VII, and thus only expressed by Mammals.

ABBREVIATIONS

AU: Action Unit; AD: Action descriptor; FACS: Facial action coding system; CN: Cranial nerve

INTRODUCTION

The face supports multiple functions as hearing, vision, breathing, feeding and social communication. In Mammals for example, facial expressions may display emotions and intentions of an individual [1,2] with a variable accuracy depending on the species. Several definitions of facial expressions have been proposed, sharing similarities but lacking precisions. According to Ekman [3], facial expressions are universal signals reflecting individuals' emotional states. Ying-Li Tian added that these signals can be used in social communication [4], and Harley associated facial expressions to underlying muscles [5]. Waller and colleagues [6] suggested that facial "expressions" should not be used and instead proposed facial "behaviours". They defined it as "observable facial movements associated with the typical behavioral repertoire of a species that potentially

have communicative meaning to conspecifics." As for facial expressions, the term "behaviour" has a massive amount of definition, which varies between almost every author [7-9]. Yet, Levitis and colleagues [10] proposed a definition based on the reviewing and polling of behavioural scientists: they defined it as "the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes." As the term "expression" or "behaviour" may drive emotional or communicative content, the neutral term "movement" will be used in this article to evaluate the various aspects of facial communication.

Studies of facial expressions started at the end of the 19th century [11,12] but a new impetus has been given during the 70's with Ekman's proposal of the Facial Action Coding System (FACS), allowing a unified analysis of human facial expressions based on their facial musculature [13]. Studies on animals were not abundant until the beginning of the 21st century, when research on animals' facial communication gained interest. FACS started

to be adapted for animals, first in Primates as chimpanzees [14], hylobatids [15], orangutans [16] and macaques [17], then in domestic animals with dogs [18], horses [19] and cats [20]. At the same time, studies focused on animal welfare created pain scales in many species: in mice [21], rats [22], rabbits [23], horses [24], sheeps [25,26], pigs [27], goats [28], ferrets [29], seals [30], cattles [31] and cats [32]. This increase of studies about facial communication in the last decade requires the unification of the terms used in this field.

This review focus on facial movements involved in the production of communicative signals in Amniotes in general, and not only mammals in a wider evolutionary perspective, as excluding other species than mammals may lead to underestimate the importance of facial movements in social communication and to miss information about their evolution. How far facial movements could be used as indicators of communicative abilities in non-human species is not so clear, except for the anthropoids. As many Amniotes species express behaviours related to emotions [33], they might express communicative and emotional content by facial movements too, as it is assumed to be for facial expressions in humans [5]. This evolutionary approach requires to clarify the definition of facial expression and behaviour based on the Amniotes' clade. It will be discussed by looking at anatomical, neurobiological, evolutionary and socio-ethological features of facial movements across Amniotes' species.

Facial movements in Mammals

Neuroanatomical features of facial movements: In addition to masticatory muscles and with few exceptions, Mammals' head possess cutaneous muscles –also called facial muscles- originating from bones or fibrous structures, they are the only group of muscles inserting into the skin [34]. Their contractions create lines, folds and wrinkles [35]. They have specific characteristics compared to skeletal muscles of the limbs and the trunk [36–38]. They are striated with a larger percentage of slow type fibers but possess Ruffini-like corpuscles for proprioceptive functions [36,39] instead of muscle spindles and Golgi's tendon organs [36–38,40].

However, non-cutaneous muscles as masticator muscles also contribute to some facial movements described in FACS, as Jaw drop (Action Unit (AU) 26 [14,18,20]), through the action of the digastric and masseter muscles.

Moreover, specific muscles have been newly developed along with domestication as the *levator anguli oculi medialis* in dogs, not found in wolves [41–43]. This muscle raises the inner eyebrow (AU101). Interestingly, dogs expressing more AU101 are adopted faster [18], suggesting a selective advantage because of an infant-like display.

The embryogenic origin of the head and the neck tissues are common portions of the embryonic foregut. There are five pairs of pharyngeal arches in all Amniotes [44,45]. From the first arch will develop the jaws and the masticatory muscles along with the trigeminal nerve (cranial nerve V (CNV)) whose V3 branch innervates them. Facial cutaneous muscles of Mammals are a subgroup of hyoid muscles, and they arise from the second pharyngeal arch in gestation together with the facial nerve (CNVII) [46,47].

Facial cutaneous muscles are innervated by the CNVII [34], except the *levator palpebrae superioris* which is innervated by the CN III [48] (the oculomotor nerve). This nerve is derived from the basal plate of the embryonic midbrain. The *retractor bulbi*, a non-cutaneous muscle implied in eye movements, is innervated by the CN VI [49]. Muscles implied in head movements are non-cutaneous and present a similar pattern in most mammals [50]. They are innervated mostly by CN XI and cervical spinal nerve [50].

In humans, 24 facial muscles contribute to facial expressions [51,52]. Remarkably, there are few variations of this amount between species (Table 1). Rodents, such as rats (*Rattus norvegicus*), have up to 24 facial muscles, whereas 23 are described in *Macaca mulatta*, 21 in *Lepilemur ruficaudatus*, 22 in *Tupaia*, 22 in *Pan troglodytes*, 24 in *Gorilla gorilla*, 21 in *Pongo pygmaeus*, 23 in *Hylobates* [53]. Yet, some species possess less muscles, as dogs and horses which, besides ears muscles, have both 16 muscles [34] and 18 in cats [20]. Similar number of muscles is coherent with distribution of neuroanatomical traits that appear to have been highly conserved through phylogenetic history [54] with few variabilities within clades [55]. Meanwhile, some muscles may be conserved, absent or vestigial in some taxa as a result of their specific evolutionary process [56]. However, the number of facial muscles is not the only factor of facial movement's complexity. Their combined actions with small anatomical, physiological or biochemistry variations may produce a larger variety of facial movements between taxa [57–59].

Brainstem nuclei may have evolved with ecological adaptations and reflect specializations of peripheral structures [60–65]. A strong relationship has been found between the size of neural and muscular structures and their use frequency [66]. For example, among the Apes, the larger species have a larger facial nucleus and display more expressive faces than the smaller one [67,68]. Primates with larger facial nuclei tend to have higher differentiation of facial muscles which may reflect a greater use of vision in social communication [69]. Several anthropoids have direct cortico-motoneuronal innervation to facial nerve. This allows higher accuracy in voluntary motor command of facial muscles [70–78], while in non-anthropoid Mammals axonal projections are polysynaptic via synaptic connections in the parvocellular reticular formation [79,80].

It should be noted that the facial nerve's enlargement may be observed in species which do not rely substantially on visual communication for social interactions, like the nocturnal prosimians *Tarsius* and *Otolemur* [69,81]. In *Tarsius syrichta*, the great volume of the facial nerve is probably related to the *orbicularis oculi* and *depressor palpebrae inferioris* whose fibers' structure is specialized to protect the exceptionally large eyeball [69,82].

Cetaceans are different from the other Mammals, even if they are phylogenetically *Artiodactyla* [83], they live in an aquatic environment [84]. One of their environmental adaptation is a "low" facial mobility due to modifications or disappearances of facial muscles [85]. The muscles mobilizing the eyelids are the only ones keeping a similar role with the terrestrial Mammals [85]. Cetaceans have also a massive *retractor bulbi* muscle [86],

Table 1: Comparison of facial muscles in various Mammals with their respective facial movements (the list is not exhaustive).

Muscles	Species and references	Associated Action Unit and Action Descriptor
<i>Frontalis</i>	Chimpanzee [229]	Nd
	Hylobatid [15]	Nd
	Macaque [17]	Nd
	Orangutan [230]	Nd
	Cat [20]	Nd
	Dog [18]	Nd
	Horse [19]	Nd
	Suidae [231]	Nd
	Camel [232]	Nd
<i>Procerus</i>	Chimpanzee [229]	Nd
	Hylobatid [15]	41 (Glabella lowerer)
	Macaque [17]	41
	Orangutan [230]	4 (Brow Lowerer)
<i>Mentalis</i>	Chimpanzee [229]	17 (Chin Raiser)
	Hylobatid [15]	17
	Macaque [17]	17
	Orangutan [230]	17
	Cat [20]	Nd
	Dog [18]	17, 16+17
	Horses [19]	17
	Suidae [231]	Nd
	Camel [232]	Nd
<i>Risorius</i>	Chimpanzee [229]	Nd
Mouth		
<i>Orbicularis oris</i>	Chimpanzee [229]	22 (Lip funeler), 24 (Lip pressor), 25 (Lips part), 28 (Lip suck)
	Hylobatid [15]	18 (Lip pucker), 22, 25, 28
	Macaque [17]	8 (Lip toward each other), 18, 25
	Orangutan [230]	18, 22, 24, 25, 28
	Cat [20]	118(Lip pucker), 25
	Dog [18]	118, 25,
	Horses [19]	118, 122 (Upper lip curler), 24, 25
	Rabbit [233]	Nd
	Mice [234]	Nd
	Rat [51]	Nd
	Ferret [29]	Nd
	Pig [235]	Nd
	Sheep [236]	Nd
	Camel [232]	Nd
	Dolphin [85]	Nd
<i>Levator labii superioris</i>	Chimpanzee [229]	10 (Upper lip raiser) 25 (Lips part)
	Hylobatid [15]	10, 25
	Macaque [17]	10, 25
	Orangutan [230]	10, 25
	Cat [20]	125 (Lips part)
	Dog [18]	110 (Upper lip raiser), 125
	Horse [19]	125
	Rabbit [233]	Nd
	Mice [234]	Nd
	Rat [51]	Nd
	Pig [235]	Nd
	Sheep [236]	Nd
	Camel [232]	Nd
	Dolphin [85]	Nd
<i>Levator nasolabialis</i>	Cat [20]	25, 109+110 (nose wrinkle+upper lip raiser)
	Dog [18]	10, 25, 109+110
	Horse [19]	10, 113 (Cheek puffer), 25, 109+110
	Rabbit [237]	Nd
	Mice [238]	Nd
	Rat [51]	Nd
	Ferret [29]	Nd
	Pig [235]	Nd
	Sheep [239]	Nd
	Camel [232]	Nd
	Seal [240]	Nd
	Dolphin [85]	Nd

<i>Caninus</i>	Chimpanzee [229] Cat [20] Dog [18] Rat [51] Sheep [239] Camel [232]	13 25, 109+110 10, 25, 109+110 Nd Nd Nd
<i>Depressor labii inferioris</i>	Chimpanzee [229] Hylobatid [15] Macaque [17] Orangutan [230] Cat [20] Horse [19] Rabbit [241] Suidae [231]	16 (Lower lip depressor), 25 16, 25 16, 25 16, 25 16 16, 17 (chin raiser), 25 Nd Nd
<i>Depressor labii superioris</i>	Suidae [231] Sheep [239] Camel [239]	Nd Nd Nd
<i>Depressor anguli oris</i>	Chimpanzee [229] Hylobatid [15] Macaque [17] Orangutan [230] Rabbit [237] Mice [242] Sheep [236]	15 (Lip corner depressor) Nd Nd Nd Nd Nd Nd Chimpanzee [229]
<i>Levator anguli oris</i>	Chimpanzee [229] Gibbon [15] Macaque [17] Orangutan [230]	Nd Nd Nd Nd
<i>Buccinator</i>	Chimpanzee [229] Hylobatid [15] macaque [17] Orangutan [230] Cat [20] Dog [18] Rabbit [243] Mice [244] Rat [51] Pig [235] Sheep [245] Camel [232]	Nd Nd Nd Nd 118 116 (Lower lip depressor), 118 Nd Nd Nd Nd Nd Nd
<i>Zygomaticus</i>	Chimpanzee [229] Hylobatid [15] Macaque [17] Orangutan [230] Cat [20] Dog [18] Horse [19] Rabbit [237] Rat [51] Mice [234] Ferret [29] Sheep [236] Camel [232] Seal [30]	12 (Lip corner puller) 12 12 12 12 12 12, 25 (Lips part) Nd Nd Nd Nd Nd Nd Nd
<i>Incisivii labii</i>	Hylobatid [15] Macaque [17] Orangutan [230] Horse [19] Camel [232]	18 18 18 18 Nd
Eyes		

<i>Orbicularis oculi</i>	Chimpanzee [229] Hylobatid [15] Macaque [17] Orangutan [230] Cat [20] Dog [18] Horse [19] Rabbit [246] Mice [242] Rat [51] Ferret [29] Suidae [231] Sheep [236] Camel [232] Dolphin [85] Seal [240]	6 (Cheek raiser), 43 (Eye closure), 45 (Blink) 5 (Upper Lid raiser), 6, 7 (Lid Tightener), 43, 45 6, 8 (Lips toward), 43, 45 6, 43, 45 143 (Eye closure), 145 (Blink), 47 (Half-blink) 143, 145 145 Nd Nd Nd Nd Nd Nd Nd Nd Nd
Nose		
<i>Levator labii superioris alaquae nasi</i>	Chimpanzee [229] Gibbon [15] Macaque [17] Orangutan [230] Cat [20] Dog [18] Horse [19] Ferret [29] Sheep [236] Seal [30]	9 (Nose wrinkle) 9 9 9 109+110 109+110 10, 113 (Sharp lip puller), AUH 13 (Nostril lift) Nose wrinkle Nostril lift Nostril lift
Whiskers		
Muscles described in cat: <i>Lateralis nasi, orbicularis oris, caninus</i>	Cat [20] Ferret [29] Seal [30] Rat [22] Mouse [21]	200 (whisker retractor), 201 (whisker protractor), 202 (whisker raiser) Nd Nd Nd Nd
Ears		
Muscles described in macaque <i>Auricularis anterior</i> (EAU101), <i>superior</i> (EAU102) and <i>posterior</i> (EAU103)	Macaque [17] Cat [20] Dog [18] Horse [19]	EAD/EAU 101 (ears forward), 102 (ears adductor), 103 (ears flattener) EAD 101, 102, 103, 104 (ears rotator), 105 (ears downward), 106 (ears backward), 107 (ears constrictor) EAD 101, 102, 103, 104, 105 EAD 101, 102, 103, 104
Head		Action descriptor
	Chimpanzee [229] Cat [20] Dog [18] Horse [19] Macaque [17] Hylobatid [15]	51 (head turn left), 52 (head turn right), 53 (head up), 54 (head down), 55 (head tilt left), AD 56 (head tilt right), 57 (head forward), 58 (head back) 51, 52, 53, 54, 55, 56, 57, 58 51, 52, 53, 54, 55, 56 55, 56 Nd Nd
Non cutaneous muscle		
<i>Platysma</i>	Chimpanzee [229] Hylobatid [15] Macaque [17] Orangutan [230] Cat [20] Dog [18] Horse [19] Rabbit [247] Rat [51] Ferret [29] Mice [234] Sheep [236] Pig [248] Seal [240]	Nd 21 (Neck tightener) Nd Nd Nd 12, 25 (Lips part), 116 (Lower lip depressor) Nd Nd Nd Nd Nd Nd Nd Nd

<i>Masseter</i>	Chimpanzee [229]	Nd
	Hylobatid [15]	Nd
	Macaque [17]	Nd
	Orangutan [230]	Nd
	Cat [20]	26, 27
	Dog [18]	26, (Jaw drop), 27 (Mouth stretch)
	Horse [19]	26, 27
	Rabbit [243]	Nd
	Rat [249]	Nd
	Mice [238]	Nd
	Ferret [29]	Nd
	Sheep [239]	Nd
	Pig [248]	Nd
	Camel [232]	Nd
<i>Pterygoid</i>	Chimpanzee [229]	Nd
	Hylobatid [15]	Nd
	Macaque [17]	Nd
	Orangutan [230]	Nd
	Cat [20]	26, 27
	Dog [18]	Nd
	Horse [19]	Nd
	Ferret [250]	Nd
	Pig [248]	Nd
	Rat [251]	Nd
	Rabbit [252]	Nd
	Mice [253]	Nd
	Sheep [236]	Nd
	Camel [254] [255]	Nd
Various non-cutaneous muscles	Chimpanzee [256]	26, 27
	Hylobatid [256]	26, 27
	Macaque [256]	26, 27
	Orangutan [256]	26, 27

Abbreviations: Nd = presence of the muscle in this species but no associated action is described in the literature; AU= Action Units, facial movements generated by specific muscle groups [257]; AD = Action Descriptors, facial movements without a clear identified muscular basis [257]; EAU= Ears Action Unit; EAD = Ears Action Descriptor.

present in Reptilians, Birds and almost all Mammals [86,87]. In these last species, its function is to move the nictitating membrane, the so-called “third eyelid” [88] but Cetaceans do not have one [89]. However, their well-developed *retractor bulbi*, used to retract the eye into the orbit [84], may help to close hardly mobile and particularly thick eyelids filled with a high amount of fat. Some Cetaceans have developed a specific moveable structure on their nose, the melon [91,92], which seems to be a communicative tool (orientation, reception and emission of sound) in beluga [90]. Moreover, some species perform some facial movements, as belugas can alter the shape of their mouth, without a clear communicative value identified, whereas dolphins express the “jaw clapping” which seems to be an antagonist signal [90,93].

Ecological influence on facial movements: The body size seems correlated to facial mobility in anthropoid monkeys [68], as a small body size may constrain the evolution of facial movements. However, this strict linear relation might be too restrictive as gorillas and chimpanzees present a similar number of AUs in their respective FACS but have different body size [94].

Moreover, body size is correlated to visual acuity, as eye axial length depends of the body size [95–97]. Eye size determines the distance between the lens and retina, which implies the retinal image size [98] and consequently its precision [99]. A good visual acuity allows the use of accurate visual cues to communicate [100], whereas species with poor visual acuity might develop other

communicative pathways, such as echolocation for Chiropterans [101]. Thus, visual acuity might influence the diversity of facial expressions. Yet, this hypothesis is not supported by findings on other species than Primates, as species with poor visual acuity such as rats (0.95 c/deg [102]) or cows (1.6 c/deg [103]) perform a diversity of facial movements. On the other hand, some Cetaceans have a good visual acuity (~25 c/deg in dolphin [104]) but lack facial mobility. Yet, to date, no study directly addresses this question.

Obstruction of the visual field (by trees for example) does not seem to influence the production of facial movements either, as arboreal Primates do not produce fewer facial movements than terrestrial ones [94,105]. A similar idea would be that nocturnal animals display fewer facial movements than diurnal ones, and indeed, nocturnal animals perform less eye blinks [105,106]. Nevertheless, cats are mainly nocturnal animals, and they have the greatest amount of AU described in animal FACS, including ears and whiskers movements [107],[108]. However, it is not clear how far these movements disclose communicative, cognitive, or ecological values, such as visual perception, sound localisation and tactile perception of surrounding.

Facial movements help to handle conflict or to regulate social bond [109–113]. For example, Apes live in big groups [113,114] and express complex facial displays in social interactions [15,16,113,115]. Various facial movements are displayed regarding either aggressive, submissive or affiliative

situations, as the “silent bared teeth” in Primates [14], [116,117]. Moreover, Dobson [94] demonstrated that “social group is a good predictor of facial mobility”. The difference between gorillas and chimpanzees could be clarified regarding their sociality, as chimpanzees live in big groups whereas gorillas live in small or dyadic groups [118]. Mating systems might also influence social interactions complexity [119] and brain size, more specifically the size of the cerebral areas involved in face processing [1,2,120]. Gibbons and siamangs are monogamous species and have fewer facial cutaneous muscles than their close relatives, chimpanzees [121,122]. The GibbonFACS describes fewer action units [15]. It has been suggested that monogamy induces less opportunities for social interactions and that the extension of facial movements in bigger groups could result of a necessity to increase combination of displays or to enhance understanding of signals, thus group cohesion [94].

In opposition, some solitary animals present various facial movements. Orangutans perform a wide repertoire of facial movements, almost as important as social Primates [16]. Sun bears display various types of open-mouth expressions during social play, even if they rarely take part into interactions with congeners [123]. The authors suggested that their facial expressions might not have evolved in adaptation to “complex social environment”.

Behavioral evolution: Facial movements allow individuals to share their internal states with congeners [124–127]. In this matter, facial movements are a useful tool in social interactions and even slight changes can display different intensities for the same state [116,128]. Thus, facial movements are accurate visual cues to measure emotions. The negative valence has been more studied, and many mouth movements can express negative emotions [58,58,125,129–133]. But tiny variations can change the meaning, as open mouth with exposed teeth is a sign of fear in Primates [58,129,134], but during positive contexts, the same movement without teeth exposure occurred. Some movements are also associated with positive emotions: dogs’ ears get closer during positive situations [131], horses’ ears are pulled back during a pleasant event [127] or chimpanzees’ head movements are displayed during affiliative interactions [135]. Yet, the most investigated state is pain thanks to several pain scales which allow scientists to monitor animals’ welfare. The main share changes observed in many species, that might indicate a common origin, are nose wrinkling, orbital tightening, ears flattening, open mouth, reduction of distance between ears and whiskers retraction [21–27,29,32,128,136–138].

It is important to keep in mind that AUs do not bear a signification per se but composed faces are meaningful, even if some movements are more expressed during specific situations such as stress or relaxation.

Facial movements might have evolved from physiological role to communicative tools, e.g. ears flattening might have firstly belong to a startle reflex developing later a communicative value [139]. The nose wrinkle and upper lid raiser, performed during fear, were displayed originally to protect sensitive regions (mouth, nose, eyes) from biting. Darwin suggested that disgust face helped to protect from toxic substance [140], and later evolved as a communicative tool. Moreover, some scientists

proposed that the actual anger face might be a vestigial version of aggressive biting behaviours, without proof supporting this theory [141]. Nowadays, in Primates, open-mouth without exposed teeth is observed in pleasant contexts [58,129,134], and bears also performed it during play situation [123]. Primates relaxed open-mouth -supposed to be the premise of the human smile- is a non-aggressive play signal, as the silent bared-teeth which is assimilated to smiling and laughing in humans [142,143]. This supposes that these displays are dissociated from their original function. This hypothesis is supported by the research of Davila-Ross [144], as chimpanzees open-mouth face is produced during social play and can be associated with laugh vocalizations. Yet, Canids’ horizontal and vertical lip retraction have opposite signification, respectively a submissive greeting and dominant threat [145]. Thus, facial movements’ signification varied among species, even if they share similar evolutionary patterns in Primates.

Primates can perform facial movements as soon as they are born, with smile, anger and innate movements for bitter tastes [1,146][147,148]. Facial movements seem to be shaped by mimicry of parent facial displays [149]. Exposition to facial movements of conspecifics help to develop both recognition and production of facial movements [1].

The importance of facial movements in social context can be illustrated by the “audience effect”, defined as changes in individuals’ behaviour observed by another [150], for example an increase of facial expressions in humans [151–153]. A similar phenomenon has been described in various species, such as gibbons [154], orangutans [155] and dogs when humans face them [156]. In horses, results are less clear, as an observer presence effect has been described for global behaviour [157–159] but not for facial movements -in a pain context [138]. But in another context, horses expressed differently facial expressions while an experimenter is present [160].

Facial movements in non-mammal animals

Anatomical features of facial movements: Non-mammal animals lack cutaneous facial muscles, and their rigid facial mask prevents the production of facial movements [161]. Yet, Birds possess *orbicularis oculi* muscles similar to the Mammals’ one, as the *depressor palpebrae ventralis* whose relaxation allows Birds to close their eyes [162]. Reptiles move their eyelids thanks to the *depressor palpebrae inferioris* [163]. Indeed, Birds’ and Reptiles’ upper eyelid is thick, less mobile than the lower one. Moreover, Reptiles possess the *retractor bulbi*, absent in Birds, which acts as in Mammals [164], [162].

Reptiles possess jaw muscles similar to Mammals’ ones, as the *levator anguli oris* or *pterygoid* muscles [165–168] [169]. Within the 8 muscles implied in beak movements in Birds [169], three are shared with Reptiles [165,169,170]. These muscles are used in various situation: agonistic behaviours or sexual parades [171,172]. Reptiles neck muscles are similar to Mammals’ one [173–175], whereas Birds’ neck muscles are mainly different [176]. They allow to move the head and take part into various choreography [172,177,178]. Lacking external ears, Sauropsida lack ears muscles, as they lack nose muscles. To date, no study references the number of facial muscles in neither Birds nor

Reptiles.

Even if many reptiles as turtles, snakes and crocodiles use mainly olfactive and tactile communication, some of them, especially lizards, disclose a large repertoire of visual communicative tools [179], as body movements [180]. Where Birds present feathers crown or colour spots [181], some lizards possess a dewlap for *Anolis* (extensible flap of skin under the throat) or a frill (an erectile throat fan around the neck) as facial ornaments [177,180], [177]. The dewlap and the frill are supported by the hyoid apparatus [177,182] and dewlap movements are generated by the ceratohyoid muscle [182].

The hyoid apparatus, including the ceratohyoid muscle mobilizing the dewlap, is a derivative of the 2nd pharyngeal arch, [182], like Mammals' facial muscles. Non-mammals similar to or shared muscles with Mammals are innervated by CN V like the *orbicularis oculi* in Birds [162,183] or the *levator anguli oris* in lizards [184], instead of the CN VII in Mammals [34], except for the *depressor mandibulae* in Reptiles [185]. Some muscles are innervated by the CN VI as the *retractor bulbi* in Reptiles and Mammals, absent in Birds [49,162,164]. In non-mammals, the CN VII role is to innervate glands [162], the choroid [186] and some of its fibers "mixed" with the CN V [162].

As in Mammals where the size of facial nucleus varies with facial movements repertoire, in songbirds high vocal center and *robustus archistriatalis nucleus* size are correlated with song repertoire [187] [188]. Yet, the direction of the correlation is unknown, and either it could be the number of songs which determines the size of the nuclei, or the size of the nuclei which determines the number of songs learned. More generally, brain size in Birds has been linked to sociality [189] and body weight [190]. In lizards, frequency of use and size of dewlap are correlated. The size of the muscle fibers and the motoneurons innervating the cerato-hyoideus muscle are correlated to the size of the dewlap [191].

Ecological influence on facial movements: Birds' brains, as Mammals' ones, are bigger than Reptiles' and Amphibians' brains. This difference is particularly noticeable in songbirds and Primates, and they are groups which communicate the most through long distances thanks to visual and vocal pathways [190].

Birds' eyes are proportionally bigger than Mammals' ones compared to their body size [192]. Moreover, Birds -and especially raptors- have among the best visual acuity in animal reign, reaching 140c/deg in eagles [193], or 73 c/deg in falcon [194]. Indeed, Birds rely mainly on visual information in order to scan their environment [192], contrary to Reptiles [179].

Various ecological factors are related to visual acuity as hunt distance in Birds [195] and predators' detection [196]. Blackwell and colleagues [196] did not manage to establish a correlation between visual acuity and behavioural responses, but they suggested that visual characteristics might influence behavioural responses and risk evaluation.

Reptiles have a low visual acuity, around 1.2 c/deg for *Anolis* [197]. Regarding to other Reptiles, some species can reach up to 6.8 c/deg or 4.9 c/deg [198]. Another study points that Atlantic green turtle is myopic out of water [199], contrary to Cetaceans which have a better view in air than in water. To date, no study

mentioned a possible correlation between visual acuity, body size and facial movements in Birds or Reptiles.

As Mammals, Birds eye-blink rates varied upon nocturnal and diurnal species. Indeed, diurnal species blink more than nocturnal ones [106], even if blinking might not be related to environmental properties as temperature and wind speed [200].

Both diurnal and nocturnal bird species modify their foraging behaviours at night, as diurnal Birds can be active at night too [201]. Because of the lower visibility, they perform shorter movements [202]. To our knowledge, no study mentioned behavioural differences between nocturnal and diurnal birds or reptiles. It might be because Birds and Reptiles, as *Anolis*, are mainly diurnal [203], [204], even if some species can be nocturnal [205–207].

In Birds and Reptiles, some facial or head movements have communicative values that might influence group cohesion. For example, the beak is involved in both agonistic behaviours (peaking opponent) and affiliate ones (allopreening for example) and so, is a key feature of Bird's communication [171,208,209]. The ruffling of Birds' feathers is associated with aggression, on the other hand the slicking of feather is an avoidance behaviour [161,210]. In lizards, the headbob of the *Anolis* or the dewlap movements are used to communicate with congeners and maintain or reject interactions [177,178].

Each movement can convey a specific or several significations, as food-soliciting or stressful events with head bobbing in parrots [211]. On the opposite, lizards' dewlap and frill provide information about individuals' gender and is used in competition for resources, sexual partners and preservation of territories, especially between males [178–180,212]. These movements among others are performed by head features, and thus might be considered as facial movements.

Mating style seems to be linked to communication complexity [119], but as Birds are mainly monogamous and reptiles polygamous [213], it would be difficult to investigate a potential effect on their facial movements. However, in Birds, extrapair copulation are observed and can even lead to a "divorce" [214,215]. Moreover, a positive correlation has been found between brain size and pair bond strength, and the authors suggested it might be the result of higher cooperation and negotiation [189]. These interactions could be based on specific head movements, but no study investigated yet their potential role on the stability of pair cohesion.

However, sociality alone cannot explain signal complexity. A study found a correlation between social factors and signal complexity only in lizards, with sexual size dimorphism correlated to ornaments, color and headbobs [216]. In Birds, ecological factors and allometry seem to be good explanatory factors to signal complexity. Ecology can influence sociality: because of luminosity, obstructions and interferences by acoustic or visual backgrounds which can mask signals, animals adopt strategies to enhance communication signals. Some lizards for example, which switched from terrestrial to arboreal lifestyle, developed more elaborate territorial displays [216].

Behavioral evolution: In Birds, some behaviour might have evolved from thermoregulation to communicative signal.

Feathers erections have an agonistic value, but they also can indicate health status to conspecifics [210], as Birds appears bigger, they also seem more threatening. In lizards, no study investigated in our knowledge significance evolution of their head movements.

Birds behaviours are influenced by the social context. The most relevant example might be crows and jays caching behaviours. These species pay attention to both auditory and visual presence of competitors. Jays adapt their caching location in order to cache their food at a greater distance of their conspecifics [217]. However, the recovery of food items is not influenced by the presence of conspecifics.

Moreover, various Birds modify their vigilance behaviours when they are in groups. Birds alone “regroup” their eye-blinks during feeding times, in order to better monitor their environment. Also, blink duration seems to be shorter when Birds are alone [218] and bigger the group is, longer is the time spent blinking.

DISCUSSION

Facial expressions are currently cluster to Mammals, based on the exclusive presence of cutaneous muscles in this class. They reveal internal states such as emotions, which can serve as public information and social communicative tools [1,2]. Yet emotions are also suggested to be expressed by non-mammals, as reptiles and birds. Stress-related tachycardia may have emerged in the class of Amniotes, as frogs and fishes do not disclose such phenomena during human-manipulation [219–221]. Moreover, sensory pleasure -a cognitive experience- is suggested to have already emerged with reptiles (Iguana iguana) [222]. It is however unclear if non-Amniotes have emotions as fear. As emotions are also expressed by non-mammals’ Amniotes, we explore the concept of facial communication from an evolutionary point of view based on current knowledge and examine how far it might not only be performed by Mammals, but more broadly by Amniotes.

Both Mammals and non-mammals’ Amniotes express meaningful facial communicative movements, as the headbob in parrots and lizards, the erection of facial feathers in jays and parrots or the dewlap in Anolis lizards [161], [180], [181], [211]. Social factors seem to influence the development of complex facial signals, as it has been demonstrated in Mammals with the group size, but also in lizards with sexual competition for example [216]. Facial movements are also used to enhance group cohesion, which is well described in Mammals [94]. Various other factors as mating systems [121,122] or the social context, such as the “audience effect” [154,155], seem to influence facial communication both in Mammals and non-mammals, even though the first phenomenon has only been studied in Primates. So, social factors’ influence on facial movements is not clustered to Mammals. However, it appears that sociality cannot explain alone complex communication signals [216].

Facial expressions might have been shaped by ecological factors too. For example, visual acuity is correlated with facial expressions complexity in Primates [95–97,100]. Some lizards, using facial ornaments, display an improved visual communication due to their evolution to an arboreal lifestyle [216]. But as there

is few information on this topic, these examples cannot be generalized. For example, even species with poor visual acuity performed facial expressions [102,103]. Nonetheless, facial expressions are considered as one of the most accurate visual communicative tools and should necessitate a sufficiently large visual acuity. Thus, more studies should investigate the relation between visual acuity and the diversity of facial movements.

Despite the paramount communicative function of facial movements that seems quite similar among Amniotes, their use relies on more practical basis, the facial muscles. It is well known that Mammals are the only clade to possess cutaneous facial muscles. Yet, cetaceans’ facial mask is almost entirely rigid [85]. So, an entire infraorder seems to lack facial expressions and characterizing facial communication to mammals seems unjustified. Furthermore, birds share the *orbicularis oculi* with mammals, implied in eye-blink [162]. Blinking is described as a facial expression in all FACS (AU45), but even if reptiles and birds do eye-blink too [108], [167], it is not mentioned up to now as a facial expression. Moreover, it bears other roles than physiological function and may have a communicative value at least in birds, as its frequency varied according to the audience [218]. Thus, it would be inconsistent to consider it differently in non-mammal species, at least in birds.

Some muscles involved in facial communication in non-mammals Amniotes have a common embryologic origin with the cutaneous muscles of the mammalians, as the ceratohyoid muscle in Anolis dewlap [182]. Considering the common origin with mammals’ cutaneous muscles and its use for visual communication, we suggest that dewlap might be considered as an equivalent of facial expression in non-Mammals. The fact that Mammals do not possess such ornament should not be an argument to exclude the dewlap movement of facial expressions category. It should be noted that each movement is not automatically shared by all species. For example, several facial expressions involving whiskers are only described in catFACS [107], even if other animals for which a FACS exists -as Primates- do not possess them. So, the exclusivity of a facial feature in one species should not be an argument to reject it as a valuable facial communication.

In the same way, to reject a facial communicative movement because they are produced by non-cutaneous muscles does not seem justified. Indeed, several masticator muscles -non-cutaneous- like the masseter are involved in facial action units described in FACS (AU26 Jaw drop) [15]–[21], which can lead to the “open-mouth” expression, well described in Primates’ social communication [58,129,134]. To select which species can perform facial communication based on the muscular innervation is not a justified argument too. Indeed, mammals’ cutaneous muscles are innervated by the CN VII [34] and the non-mammals’ muscles are innervated by other cranial nerve, such as the CN V [162,182,183]. But, as it has been developed earlier, muscles innervated by other nerves (as the masticatory ones) can bear a communicative value, and so in non-mammals’ Amniotes species too. Thus, facial communication should not be clustered to species with specific muscles or muscles’ innervation.

Another feature of a communicative role of facial muscles in Amniotes could be revealed by some neuroanatomical

characteristics such as brain nuclei. Their size increases with the diversity of facial movements in Primates [67,68]. Similarly, in lizards, the number of motoneurons controlling the dewlap movements increases with the frequency of its use [191]. In birds, no such phenomenon has been described related to facial movements [189], yet, birds' relative brain size is correlated with their level of sociality, as mammals' one. These correlations between neuroanatomical structures, sociality and facial movements might suggest that facial movements have an important communicative value not only in Mammals but in Amniotes too. However, more studies on non-mammal species are needed to conclude about it.

Furthermore, it should be noted that despite anatomical differences, mutual comprehension of facial communicative and emotional displays exists in interspecies interactions. For example, primates as well as domesticated species as dogs and horses can discriminate humans' emotions of joy or anger from facial movements [223–226]. This interspecies understanding provides a strong argument for an integrative evolutionary approach of the topic of facial behavior. Some studies are suggesting they also used other signals, as odors [227,228], so emotional recognition might be multimodal. The respective contribution of these items is not well understood and should also be further investigated. The ability to recognize humans' emotions might be an important tool in human-animal relationship, including animal assisted therapies.

CONCLUSION

From this review, we propose that facial communication is not clustered to Mammals and to facial expressions. Evidence comes from the presence of movements with communicative value in non-Mammals, which do not express *stricto sensu* facial expressions as they have a rigid facial mask. We propose the following definitions: movements are visible displacements of body segments or tissues. They are motor actions that do not need cognitive and emotional implication, while behaviours require the interpretation of environmental or internal stimuli, as the presence of an audience or emotional experiences. Behaviours are movements that can be involved in social communication. So facial behaviours are not clustered to Mammals but might be largely expressed among Amniote's species. Whereas facial expressions are facial behaviours generated by the contraction of cutaneous facial muscles, innervated by the CN VII, and thus only expressed by Mammals.

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DISCLOSURE

The authors disclaim that they have no financial interest or any conflict of interest for this review.

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