# Why are embodied social signals concentrated towards the rostral region? — The rostrum concentration hypothesis

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The authors have no competing interests to declare.

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## Abstract

Although frequently embodied, the relationship of animal social communication with body layout has rarely been investigated from a unified cognitive perspective. Across animal taxa, socially relevant signals, ranging from facial expressions and gaze to colouration and morphology, are strikingly concentrated towards the anterior region of the body. Here, we propose the Rostrum Concentration Hypothesis (RCH), a conceptual framework positing that social signals preferentially evolve and converge along the rostral body axis across bilaterian animals. We argue that this pattern does not reflect shared anatomical homology, but rather emerged from convergent interactions among body layouts, sensory organ concentrations, attentional biases and socio-ecological demands. Drawing on evidence from various taxa spanning from primates to insects, we suggest that the rostral concentration of social signals reflects the coevolution of signal production and receiver cognitive mechanisms. By reframing ‘facial’ communication as a broader organizational principle of the body layout, the RCH reduces the risk of anthropomorphic interpretation and bridges research across behavioural ecology, cognitive science, sensory ecology and evolutionary biology.

## Introduction

Embodied communication through social signalling is a universal form of social interaction among individual animals that exhibits remarkable diversity, ranging from instantaneous, such as emotional expressions, to those that evolve over thousands of generations, such as colouration to convey reproductive status or social hierarchy within a group. Moreover, the body parts used for such communication are thought to be unique to taxonomic groups, as importance varies based on species-specific socio-ecological factors, such as group size, population density and ecological niche. Among the body parts that convey social signalling in the animal kingdom, human faces are remarkably unique and encapsulate vast quantities of information and various social cues related to sex (Dunbar & Barrett, 2007), identity (McKone et al., 2007), emotional states (Schmidt & Cohn, 2001) and attentive states (Kobayashi & Kohshima, 1997; Tomasello et al., 2007).

Humans, particularly, manifest emotions via complex facial expressions, which are socially communicative movements governed by specialised neural systems acting on facial muscles (Cattaneo & Pavesi, 2014; Rinn, 1984) that can, in turn, influence the behaviour of others. For instance, humans possess dedicated neural mechanisms involving multiple cortical regions specialised for conveyance of facial expressions and to enable perception of the emotional states of others from facial cues (Adolphs, 2002; Kanwisher & Yovel, 2006; Hadders-Algra, 2022). Although the human face is composed of highly complex features, including configuration of the eyes, eyebrows, mouth, cheek muscles and nose, as well as various specialised dynamic movements that facilitate remarkably rapid detection and recognition of faces (Zhang et al., 2023).

Charles Darwin initially recognised the significance of comparing the facial expressions of animals and humans, along with associated cognitive abilities (Darwin, 1872; Ekman, 2006). In his seminal work, ‘*The Expression of the Emotions in Man and Animals*’, Darwin proposed that the emotional expressions of modern humans have evolved from those of our animal ancestors rather than products of societal influences, suggesting comparability (Darwin, 1872), a proposition that has sparked considerable controversy (Boakes, 1984). While the degree of comparability of the facial expressions of humans and animals remains a contentious subject, recent research has provided evidence that the intricate facial muscle movements of non-human primates have similar functions as the facial expressions of humans (Leopold & Rhodes, 2010; Parr et al., 2008; Vick et al., 2007). Moreover, even under a more restrictive definition of facial expressions, as social or emotional signals characterised by immediate changes conveyed through facial cues, laboratory mice (Langford et al., 2010) and macaws (Bertin et al., 2023) can also exhibit discernible facial expressions.

These observations collectively raise the possibility that the potentially unique communication patterns of the human face may instead reflect a broader, cross-taxa principle to preferentially organise social information along the rostral body axis. Similar to facial expressions, many vertebrates, including primates, birds and fishes, have the ability to recognise individuals based on idiosyncratic morphological variations of the face. Interestingly, such facial-based individual recognition is not limited to vertebrates, as paper wasps have likewise been reported to discriminate familiar from unfamiliar individuals based on facial colouration (Tibbetts, 2002). These converging lines of behavioural evidence indicate that the face plays a vital role in the transmission of social signals across diverse taxonomic groups. Given the 550 million years of evolutionary divergence between protostomes and deuterostomes, these forms of social signalling are unlikely to be attributed to traits inherited from a common ancestor. Indeed, the mechanisms responsible for face recognition differ substantially between these two groups. Whereas vertebrates process faces hierarchically through distributed neural networks, insects often rely upon more localised and circumscribed neural regions (Freiwald et al., 2016; Jernigan et al., 2024). Accordingly, we propose two central questions: (1) why are social signals expressed through anatomical parts identified as the ‘face’ and (2) why such convergence emerges as a general evolutionary tendency across distantly related taxa.

However, many previous works have relied on the human-centric and anatomically defined categories of ‘face’ and ‘facial expression’, which impose considerable limitations to clarify the universal relationship between social signals and body structure in animals. Such frameworks inherently embody a somewhat circular structure, as social signals are simultaneously defined in terms of function and anatomically constrained proximate mechanisms. Hence, there is no consensus on whether a specific physiological substrate of the facial musculature is required for a social signal to qualify as a ‘facial expression’, or whether signal emission from the head is sufficient to serve as a social function, such as emotional expression. Therefore, this review article aims not to resolve this definitional ambiguity, but rather to establish a framework to examine the general tendencies of social signals emitted from the rostral body axis, without concentration on any particular taxonomic group.

Here, we propose the RCH, a new conceptual framework that integrates prior findings of the evolution of social signals (Figure 1). This hypothesis postulates that, across bilaterally symmetrical animals, social signals tend to be universally concentrated towards the rostral (anterior) part of the body, thereby providing a perspective that reinterprets the evolution of ‘facial-like’ structures as a manifestation of the general organizational principle of body layout. In accordance with cross-disciplinary evidence from ethology, comparative psychology, evolutionary biology, neuroscience and anatomy, the plausibility of the RCH was examined and an integrative framework was established to further clarify embodied non-verbal social communication cues.

## 1. Core ideas of the RCH

The RCH posits that social signals tend to be concentrated towards the rostral direction. While most commonly conveyed by the facial expressions of humans and non-human primates, this pattern is not restricted to these taxa. Moreover, in many cases, such signals are produced through mechanisms entirely distinct from the facial musculature characteristics of mammals. The RCH can be condensed into the following three presumptions.

1. Social signals tend to be expressed from anatomically rostral body regions across a wide range of taxa.
2. The underlying neural mechanisms and the specific anatomical structures involved are not necessarily the face or facial musculature, but rather shaped by species-specific sensory and motor systems, as well as socio-ecological factors.
3. The concentration of social signals is not accidental, but instead guided by the constraints imposed by body layout. Specifically, the concentration of sensory organs and associated neural systems, and behavioural demands, such that social encounters are typically initiated from the anterior direction.

The first presumption simply reiterates the central claim of the RCH, whereas the second presumption states that the rostral concentration of social signals, observed across a wide range of taxa, is not homologous, but rather can arise convergently through unique mechanisms. These claims were deliberately not formulated in terms of the specific locus of the ‘face’, but rather in coordinate terms; namely, along the rostral direction. This framing is intended to circumvent bias towards the human face and diminish the risk of anthropomorphic and anthropocentric interpretations. The third presumption argues that the concentration of social signals cannot be dismissed as a trivial coincidence, but instead reflects the tendency of following the basic body layout of bilaterally symmetrical animals.

Moreover, animals with an antero-posterior body axis typically encounter conspecifics from the front, suggesting that the rostral concentration of social signals is a natural and efficient consequence of these constraints.

In the following section, currently available evidence of the evolution of social signals is discussed to substantiate the plausibility of the RCH.

## 2. Towards an RCH framework for the concentration of social signals

In this review, we present evidence of the general tendency that social signals concentrate at the anterior end of the body, a concept we refer to as the RCH. Here, the term ‘rostrum’ is not used to denote a specific anatomical structure, such as the mammalian face or the avian beak, but rather as an inclusive concept broadly referring to the frontmost region of the body in order to avoid anthropocentric conceptualisations as well as frameworks overly biased towards the anatomical characteristics of any particular taxonomic group. Likewise, the social signals expressed at the rostrum are not restricted by an actual mechanism of production, temporal scale or degree of conscious control. In other words, the RCH refrains from assuming anatomical homology and does not posit homology to the mechanisms underlying the expression of facial signals. Consequently, the RCH enables a focus on why social signals tend to emerge from any particular body region while avoiding the risk of anthropomorphic interpretation.

How universal, then, is the concentration of social signals towards the rostral region across the animal kingdom? A non-negligible body of evidence across taxonomic groups supports the RCH (see Section 4). These findings are derived from largely unrelated taxa and are often expressed via different mechanisms. Hence, it is more reasonable to regard such mechanisms not as inherited ancestral traits, but instead as convergently evolved in response to behavioural advantages.

Nevertheless, a framework is lacking that can clearly explain why social signals tend to be concentrated towards the rostral region, even though this is not necessarily the case among all species. This lack of a conceptual basis has rendered a broad generalisation premature. In particular, we still lack (1) comparative evaluations of whether the relative importance of social signals is greater in the rostral region than other body parts, and (2) experimental results demonstrating whether signals expressed in this region reliably modify receiver behaviours. Rather than precluding synthesis, this lack of systematic evidence highlights the need for an explicit framework to guide future comparative and experimental studies.

In the literature, such investigations have progressed most extensively in studies of facial expressions, facial individual recognition and perspective-taking of primates, including humans (Huber & Lonardo, 2023; Leopold & Rhodes, 2010; Pérez-Manrique & Gomila, 2018). While a detailed review is left to the existing literature, the face functions of primates, as a specialised body region for the transmission of social signals, and correspondingly, cognitive and neural mechanisms, such as holistic processing for facial recognition (Tanaka & Farah, 2003), have evolved preferentially (Lee & Sung, 2023; McGraw & Hill, 2000) to efficiently process social information derived from the face. Moreover, a substantial body of behavioural evidence supports the existence of face-based social signalling by non-primate mammals. For example, sheep, cattle and domestic dogs are reportedly capable of individual recognition based on facial cues (Leopold & Rhodes, 2010). In addition, many mammals, such as elephants, sheep, dolphins and mice, exhibit discernible facial expressions (Langford et al., 2010; Leopold & Rhodes, 2010), including some that have been suggested to share striking similarities with those of primates (Kendrick, 1994; Leopold et al., 2006).

Although animal studies other than mammals remain extremely limited, several lines of evidence suggest that the morphology or colouration at or near the rostral region may be associated with social information. For example, the bill length and colouration of sparrows and American goldfinches have been correlated with social and condition status (Lee & Sung, 2023; McGraw & Hill, 2000). Additionally, facial stimulation of pigeons has been reported to elicit social behaviours of conspecifics (Shimizu, 1998). Likewise, the colour patterns of the rostral region of reptiles and fishes are known to reflect dominance rank or aggressive motivation (Balzarini et al., 2017; Lappin & Husak, 2005; Muske & Fernald, 1987). In many anurans, the vocal sac has been suggested to function in the production of acoustic signals involved in species recognition, mate choice, male spacing and territory defence, as well as visual signals (Starnberger et al., 2014). In addition, among invertebrates, the facial colouration patterns of paper wasps have been associated with reproductive success (Tibbetts et al., 2015), whereas horn-like structures arising on the head of fruit flies function as indicators of individual fighting ability (Dodson, 1997). Similarly, the facial colouration of jumping spiders functions as a signal of health or foraging ability (Taylor et al., 2011). In the context of comparing the importance of body regions as sources of social signals, almost all prior studies have demonstrated only correlations between particular social states and morphological or chromatic traits near the rostral region. However, whether these traits actually function as social signals that influence receiver behaviours remains largely unresolved.

In contrast to largely correlational evidence, individual recognition signals concentrated in the rostral region have been rigorously tested in fishes (Hotta et al., 2017; Kohda et al., 2015; Satoh et al., 2016; Sogawa et al., 2023; Wang & Takeuchi, 2017) and paper wasps (Sheehan & Tibbetts, 2011; Tibbetts, 2002, 2004). These studies employed stimulus models and the rostral (facial) and body regions of familiar and unfamiliar individuals were experimentally recombined to examine the behavioural responses of conspecific receivers. This approach demonstrated (1) the relative importance of individual-specific information emitted by the rostral region and (2) that such information can directly alter receiver behaviours. Consistent with this pattern, previous controlled behavioural studies have shown that damselfishes rely on facial cues (i.e. ultraviolet-reflective patterns concentrated in the 'facial' region) to discriminate conspecifics from closely related heterospecifics (Siebeck et al., 2010). Structures referred to as the 'face' or 'head' of insects and vertebrates are not homologous from developmental or anatomical perspectives. Accordingly, facial recognition of vertebrates, including mammals and social wasps, is a superficially similar phenomena, but does not represent traits inherited from a common ancestor. Moreover, the body parts that produce signals along the rostral direction are diverse, including the eyes, facial muscles, chromatophores and vocal sacs. Thus, even when producing superficially similar signals, these structures are evidently not homologous organs, but rather better understood as convergent forms of social cognition that evolved independently under shared evolutionary constraints and advantages associated with cephalisation (see Section 3). To address why social signals tend to cluster in the rostral region, the concentration of sensory organs should first be considered as a pre-adaptive condition that may have facilitated the evolution of rostrally concentrated social signalling.

## 3. Rostral concentration of sensory organs

The sensory organs of bilateral animals show a broad propensity to concentrate at the rostral end of the body. This trend is known as the progressive process of cephalisation, which is associated with the emergence of specialised feeding structures near the mouth (Hombría et al., 2021). Clusters of Hox genes, which play key roles in segmental organization, were already present more than 550 million years ago and evolved alongside the major modern animal body plans established during the Cambrian period (Zhang & Nei, 1996). Indeed, non-bilaterian lineages, such as sponges, ctenophores and placozoans, reportedly lack Hox genes (Biscotti et al., 2014). The Hox cluster can consist of up to 15 genes, including Hox1–5, which contribute to head specification and were likely already present in the last common ancestor of chordates, lophotrochozoans and ecdysozoans (Hombría et al., 2021).

The eyes, antennae, multiple feeding appendages, and other sensory structures are concentrated at the rostral end of arthropods, cephalopods and vertebrates, accompanied by a marked rostral concentration of the nervous system. Hence, these animals possess a well-developed brain. Reflecting an extreme degree of cephalisation, these lineages exhibit advanced sensory integration and a wide range of intelligent cognitive abilities (Ginsburg & Jablonka, 2019; Veit, 2023). In particular, vision accounts for the processing of a substantial portion of neural information, and the development of eyes at the head, including the convergently evolved camera-type eyes of vertebrates and cephalopods, is tightly coupled with elaboration of the central nervous system (Nilsson et al., 2023). Developmentally, the eyes arise as extensions of the central nervous system itself (London et al., 2013). Taken together, the evolution of vision exemplifies cephalisation as an integrated transformation of both sensory organs and the nervous system.

In bilaterians, the concentration of sensory organs at the head has clear adaptive significance. The evolution of directional locomotion has led to the differentiation of the head and tail of bilaterians and the anterior end of the body became the first to encounter environmental stimuli during movement (Brusca et al., 2016). The accumulation of sensory organs at the head represents an adaptation for the rapid detection of external inputs, likely conferring survival and predation advantages. The accompanying rostral concentration of the nervous system enabled increasingly refined sensorimotor coordination, fundamentally reshaping behavioural interactions and cognitive capacities, thereby contributing to the ecological and evolutionary transformations that culminated in the Cambrian explosion (Hsieh et al., 2022).

In sum, the rostral concentration of sensory organs is a general trend in bilaterian animals and is not restricted to either protostomes or deuterostomes. Because sensory inputs, including encounters with other individuals, are typically first registered by the rostral end, sensory information about conspecifics preferentially reaches the head. Correspondingly, when a receiver is targeted with social signals, it is reasonable to expect that the use of rostral signalling organs would support salient and faster social interactions. Therefore, the next question to be posed is whether the concentration of social signalling within the ‘head’ or ‘face’ is beneficial.

## 4. Cognitive and socio-ecological benefits

The previous section outlined the general tendency for the concentration of sensory organs towards the rostral region of animals, which may have provided, under existing developmental and functional constraints, a relatively efficient evolutionary pathway for the emergence of complex social signals. As a central assumption of the RCH, socially relevant signals tend to be preferentially expressed towards the rostral direction in a wide range of animals, particularly among bilaterians exhibiting pronounced cephalisation. This pattern is unlikely to be a matter of chance, but rather the spatial clustering of sensory inputs that arose from the basic body layout of bilaterally symmetrical animals that may have biased the evolution of signal expression towards the same region. In humans and some other mammals, for example, individual recognition relies on holistic processing of the relative configuration of multiple facial features, including the eyes, nose and mouth. Similarly, the perception of facial expressions and attentive states inferred from gaze draws not only on these primary features, especially the facial muscles (Cattaneo & Pavesi, 2014; Rinn, 1984) and eyes (Kobayashi & Kohshima, 1997; Tomasello et al., 2007), but also additional visual cues, such as changes to facial colouration patterns driven by vascular dynamics and the mouth (Jack &

Schyns, 2015; Wells et al., 2016). These components function as complementary sources of information that jointly support the interpretation of social signals. Importantly, in humans, the expression of emotions and intentions through the face does not arise from a single sensory organ or motor structure, but instead emerges from the coordinated activities of multiple sensory organs, motor effectors and peripheral physiological cues concentrated in the rostral region.

Moreover, certain ecological constraints and demands may have accelerated the concentration of social signals towards the rostral region of many animals, as it may be advantageous that the rostral axis coincides with the direction of locomotion. The mammalian face has been described as a developmental and evolutionary novelty that integrates sensory, communicative and feeding functions into the anterior head region throughout evolution (Higashiyama et al., 2021), rendering the anterior region particularly advantageous for communication. Indeed, the social interactions of many animals are typically initiated from the anterior part of the body (Hotta et al., 2019; Satoh et al., 2016; Tibbetts, 2002). This universal feature among motile animals provides a plausible evolutionary explanation for why social species tend to express social signals via the anterior or rostral region. Although the specific anatomical bases differ, analogous examples include the facial colouration patterns of social wasps and fishes, which function as individualised identity signals (Satoh et al., 2016; Tibbetts, 2002), and the bill morphology of sparrows, which has been suggested as a signal of social hierarchy (Lee & Sung, 2023). Although the upright bipedalism of humans implies that the head is not necessarily always projected forward during social interactions, such modes of encounter are pervasive among other bilaterally symmetrical animals, suggesting that the concentration of social signals in the human head reflects a characteristic inherited from quadrupedal ancestors.

Additionally, when considering the ecological benefits of signal concentration towards the rostral region, it is crucial to recognise the empirical evidence that many animals are highly sensitive to the eyes and gaze of others. Many mammals, particularly primates, exhibit a strong attentional bias towards faces. One of the most striking manifestations of this bias is the simulacra effect or the face pareidolia, which refers to the tendency for primates to perceive the ‘face’, particularly the configurations of stimuli that are, in themselves, meaningless or randomly arranged (Taubert et al., 2017; Tomonaga, 2025). Moreover, some vertebrates can detect the direction of the eyes or gaze of other individuals and utilise this information as social signals. Gaze following is defined as the ability of an individual to orient its gaze in the same direction as that of another individual, which has been reported in primates (Kano & Tomonaga, 2009; Ruiz et al., 2009; Tomasello et al., 1998), non-primates mammals (Kaminski et al., 2005; Tschudin et al., 2001), birds (Bugnyar et al., 2004; Jaime et al., 2009; Loretto et al., 2010) and reptiles (Wilkinson et al., 2010).

In contrast, fishes and some other animals tend to avoid the eyes and gaze of conspecifics and heterospecifics (Coss, 1978; Karplus et al., 1982). However, this avoidance behaviour paradoxically suggests that these species possess a high perceptual sensitivity to the eyes and gaze of other individuals. Indeed, individuals of group-living cichlid fish have been observed to fixate on the ‘face’ region of conspecific models before other body parts (Hotta et al. 2019). Additionally, the eyes of marine fish serve as key visual stimuli that can elicit social behaviours (Karenina et al., 2013). Among birds, jackdaws have white irises that help to prevent competitors from commandeering a nesting site (Davidson et al., 2014).

Regarding the evolutionary origins of gaze sensitivity widely observed across the animal kingdom, the ‘evil eye hypothesis’ argues that such sensitivity evolved as a strategy to avoid predators (Hampton, 1994). According to this hypothesis, heightened sensitivity to the gaze of others, particularly predators, is an adaptation that enables animals to judge when it was safe to move or emerge from hiding. To function as a signal, a cue must be detected by the receiver. The term ‘sensory exploitation’ is defined as the evolutionary process by which cues become communication signals under the influence of such sensory biases (Endler & Basolo, 1998). If receivers are predisposed to focus on the eye region, signallers may gain an advantage by exploiting this perceptual bias and placing social signals in close proximity to the eyes (i.e. rostral region). Moreover, these rostrally concentrated signals may be fed back through specialised perceptual and cognitive processes that become increasingly refined and accentuated.

## 5. Outlook and prediction of the RCH

The RCH can be implemented as a concrete research programme. Here, three predictions were outlined but have not yet been fully validated and remain preliminary. Accordingly, a rigorous evaluation of the RCH will require the integration of broader comparative studies, the accumulation of observational data on natural behaviours, and controlled laboratory testing of cognition. Specifically, the RCH posits three major predictions:

1. Among various body parts, the relative importance of social signals is greater in the rostral region.
2. Multiple types of social signals, especially those related to individual recognition and emotional expression, tend to converge towards the rostral direction.
3. The degree of signal concentration is correlated with socio-ecological factors, including social complexity and ecological context.

The first prediction is based on an adaptive perspective that natural selection favours morphological configurations that maximise signalling efficiency. Because sensory receptors and feeding organs are often concentrated in the rostral region, this area is structurally predisposed to express social signals. Consequently, ecological and social benefits are expected to refine and intensify signalling in this region. The face arguably plays a central role in the social communication of primates as a multicomponent signal, serving as a body region that attracts greater attention and conveys more information than other parts (Waller et al., 2024). However, relatively few empirical studies have quantitatively compared the salience or signal strength of facial versus non-facial cues.

The second prediction rests on the assumption that sharing a common signalling locus reduces the costs of communication. When a particular social signal is expressed via the rostral region, other signals are likely to converge at the same site, thereby promoting the multifunctional evolution of facial structures. The multicomponent basis of social signals expressed via the rostral region is particularly prominent among primates (Jack & Schyns, 2015; Waller et al., 2024). However, evidence suggests a multicomponent nature of the rostral region of fishes, which are among the most basal vertebrate lineages. For instance, in the group-living cichlid of the African Great Lakes, colour variation of the rostral region is used for individual recognition (Kohda et al., 2015), and aggressive motivation is likewise expressed as a rostral pattern (Balzarini et al., 2017). Furthermore, such face-based individual recognition may, as in primates, rely on holistic processing that integrates the relative configuration of facial features (Kawasaka et al., 2019). The cichlid exhibits relatively complex social systems and is generally regarded as a highly social fish (Wong & Balshine, 2011). Whether this clustering of multiple social signals in the rostral region and sophisticated cognitive processes represents a mere coincidence or reflects an association with social complexity requires comparative investigations, as anticipated in the next prediction.

The third prediction, involving the degree of rostral concentration, should correlate with socio-ecological factors, such as social complexity, population density and the diversity of other signalling modalities. For example, reduced facial hair of primates has been proposed to correlate with social systems and brain size ('social face hypothesis'), and is thought to enhance the efficiency of transmitting social signals, such as facial expressions (Albohn & Adams, 2022).

## 6. Limitations and considerations

It is important to note that the proposed RCH does not fully account for all social signals of animals. Specific ecological factors, such as camouflage colouration and predation pressure, may facilitate or constrain the rostral concentration of social signals. Moreover, it is important to carefully consider the ecological and social contexts in which such social signals function. Numerous social signals of animals are emitted from the non-rostral body end or regions other than the face. For example, the plumage colouration of many birds can function as social signals (Baker & Parker, 1979; Mason & Bowie, 2020). Additionally, the facial area of the African grey parrot does not play an important role in individual recognition, even though this species processes visual information of the whole body holistically (Prikrylová et al., 2023). Similarly, in caser of paper wasps reviewed in this paper, not only facial features but also body patterns and specific behaviours may function as social signals (Legan et al., 2023; Tibbetts, 2002). However, these facts do not warrant rejecting the RCH outright.

To date, the reasons why signals are expressed from one body region in some species but from a different region in others have received little attention, and most cases have largely been examined in isolation. The RCH argues that, as a general tendency, signals are more likely to be concentrated towards the rostral end, implying that animals that emit social signals from non-rostral regions do so for reasons that warrant explanation.

For example, socially induced changes to the colouration of the bearded dragon lizard occur primarily around the face. Because these colour changes are expressed in conjunction with head-bobbing displays, facial colouration may enhance the efficiency of signal transmission (Smith et al., 2016). In contrast, other lizard species express signals from non-rostral body regions (Cooper Jr & Burns, 1987). Therefore, evaluation of the RCH requires examining how signal expression is coordinated with behaviours and identifying the ecological or interactional conditions that confer advantages to signalling from non-rostral regions. If typical encounters are not frontal or displays are coupled with wing spreading of birds, signal salience may be shifted away from the rostral region.

Accordingly, the RCH is not invalidated by any single observation, but would become unnecessary only in the absence of heuristic value for guiding investigations of behavioural phenomena. In this sense, we argue that the scientific utility of the RCH lies in its productivity, especially the capacity to generate testable predictions and stimulate the discovery of new empirical patterns.

## 7. Conclusion

In this review, we proposed the RCH as a unifying framework to clarify the tendency of embodied social signals to be expressed towards the rostral region across bilaterian animals from an adaptationist viewpoint. Rather than treating faces, beaks or other anterior structures as taxon-specific adaptations, this framework reinterprets ‘facial-like’ signalling as an emergent consequence of shared developmental constraints, sensory biases and selective pressures acting on the anterior body axis. By shifting the focus from anatomically defined categories to a perspective based on the body layout, our approach provides a conceptual bridge between research traditions that have previously developed largely in parallel, including studies of facial expression, individual recognition, sensory ecology and social cognition.

Throughout this review, we have primarily focused on the perspective of the signaller in order to clarify why social signals are preferentially concentrated at the rostral region. However, the evolutionary dynamics underlying the concentration of rostral signals are unlikely to be fully understood without considering the cognitive system of the receiver. A growing body of evidence suggests that receivers exhibit strong attentional biases towards the rostral region and employ specialised perceptual strategies, such as holistic processing and cross-component integration, when extracting social information from this part of the body, implying that evolution of signal placement and the perceptual and cognitive mechanisms of receivers have likely been tightly coupled. From this perspective, the rostral signal concentration may reflect not only where signals are easiest or cheapest to produce but also where they are most efficiently detected, integrated and acted upon by receivers. For example, eye-tracking studies of primates have demonstrated that individuals selectively and preferentially focus on the face rather than other body regions (Sato et al., 2019). This suggests that the face aggregates rich social information and serves as a primary source for receivers to actively extract social cues.

Importantly, we do not argue that the rostral concentration of social signals is an inevitable outcome of social evolution, as such signals may also be expressed on non-rostral body regions or across the entire body, particularly under ecological or functional conditions, such as long-range advertisement, camouflage constraints, and sexual signalling. Nevertheless, under shared constraints imposed by directional locomotion, cephalisation and perceptual salience of the anterior body, rostral concentration represents a recurrent and favoured solution in the evolution of social communication.

Future research will be essential to test and refine the RCH. Comparative studies that explicitly quantify the relative importance of rostral versus non-rostral signals across taxa and socio-ecological contexts are particularly needed. In addition, anatomical and developmental investigations will be crucial to determine whether similar rostral signals across lineages reflect convergent evolution or shared evolutionary origins. Finally, integrating receiver-focused approaches, such as eye-tracking, neurophysiological measurements and behavioural analysis, will allow for the direct examination of how rostrally concentrated signals are processed and evaluated. Together, these lines of inquiry will help to clarify how body structure, perception and social signalling co-evolved to shape the remarkable diversity of communication systems observed across the animal kingdom.

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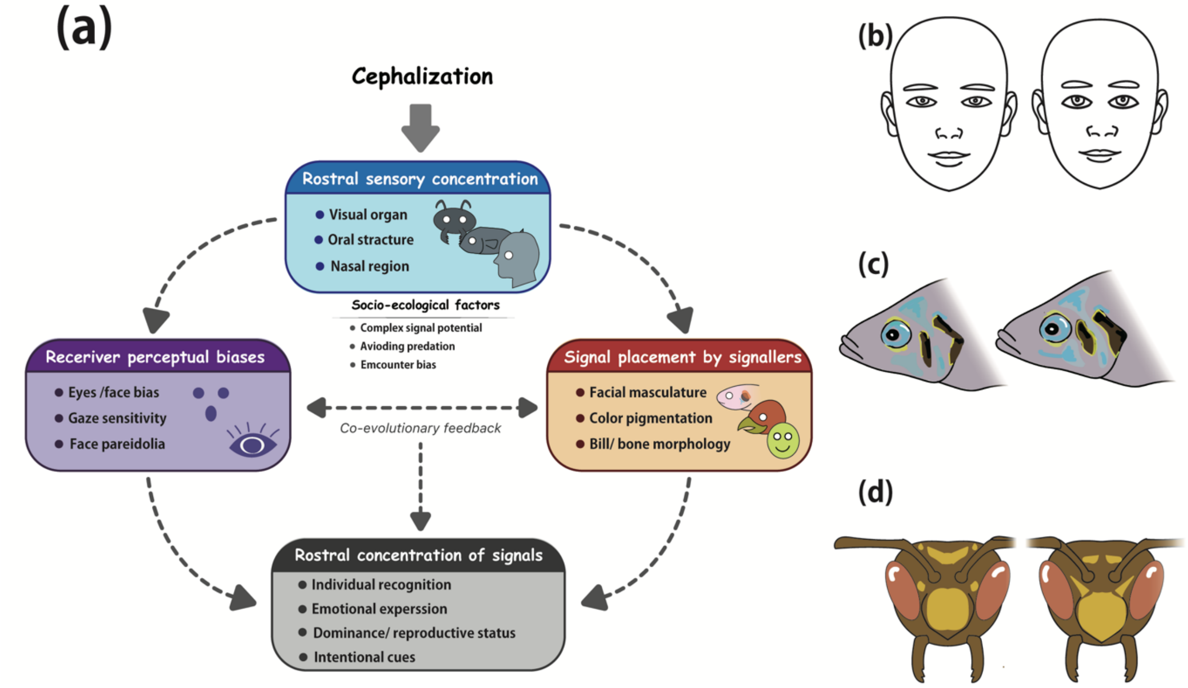

Figure 1. A conceptual diagram of the RCH. (a) The RCH posits that, across bilaterally symmetrical animals, social signals tend to be preferentially concentrated towards the rostral region of the body. (b) The human face, as a representative example of multifunctionalised social signals concentrated towards the rostral direction, simultaneously conveys a wide range of social information, including sex, individual identity, age, emotional state and attentive states. In the context of individual recognition, the existence of specialised neural and cognitive mechanisms dedicated to processing facial information has been suggested. (c) In the group-living cichlid, the rostrum region can convey signals related to both individual identity and aggression, indicating that social signals are multifunctionalised in this region. (d) Individual paper wasps can discriminate familiar from unfamiliar conspecifics based on facial colouration patterns, which also serve as predictors of reproductive success, suggesting

functions as multifunctional social signals. However, the facial structures of paper wasps are not evolutionarily homologous to the faces of vertebrates.