

Review

Face perception: computational insights
from phylogenyMarlene Behrmann^{1,*} and Galia Avidan²

Studies of face perception in primates elucidate the psychological and neural mechanisms that support this critical and complex ability. Recent progress in characterizing face perception across species, for example in insects and reptiles, has highlighted the ubiquity over phylogeny of this key ability for social interactions and survival. Here, we review the competence in face perception across species and the types of computation that support this behavior. We conclude that the computational complexity of face perception evinced by a species is not related to phylogenetic status and is, instead, largely a product of environmental context and social and adaptive pressures. Integrating findings across evolutionary data permits the derivation of computational principles that shed further light on primate face perception.

Face recognition and the evolutionary trajectory

Face perception is essential for a range of behaviors, including **conspecific** (see [Glossary](#)) and individual identification, mate recognition, parental attachment, and in- and out-group membership, and for establishing and maintaining social dominance. While face perception in primates has been well studied, a recent surge in the study of other species has uncovered remarkable feats of face perception by invertebrates, such as paper wasps, and has delineated the neural correlates of face perception in mammals, such as dogs. Compelling arguments have been made encouraging the study of behavior and brain circuitry across species [1,2]; since primate brains are the product of evolution, the neurophysiological and anatomical change over evolutionary history or **phylogeny** is constrained, leading to cross-phyla continuity across cortical architecture and behavior [3]. This **convergent evolution** indicates the emergence of common mechanisms that solve a similar functional task in widely different systems. Despite the visual dissimilarity of faces across species ([Figure 1](#)), as reflected in the featural differences (such as a beak versus a nose or laterally versus frontally positioned eyes), all faces appear to share the roughly triangular shape with common first-order relations and two eyes above a nose, which is above a mouth [4].

To date, cognitive science has not regularly exploited evolutionary data, but a comparative phylogenetic analysis might offer a litmus test of the fundamental physiological and computational principles of face perception. Furthermore, comparative investigations have the potential to reveal which aspects of face perception are universal and which are **clade** specific [5]. The study of face perception may serve as a model domain for exploring these principles, and the results may have phylogenetic implications for other cognitive and perceptual skills.

A common misconception is that, over evolution, newer brain structures (**neocortex**) capable of increasingly complex behavior are simply superimposed upon existing structures [6]. Here, we evaluate whether face perception falls along such a linear continuum from the least to the most sophisticated behavior, with computational complexity corresponding to the position of the species on the phylogenetic scale. At one end of the continuum the computation might entail simply

Highlights

Face perception is ubiquitous across phylogeny, with a crucial role in social interactions and survival.

Across many species, there is evidence of preferential orientation to face-like configurations, configural processing, and the face inversion effect, as well as conspecific discrimination, face individuation, and familiarity effects.

The complexity of the face computations of a species is not correlated with their rank on the phylogenetic scale.

Environmental constraints and adaptive pressure can account for most, albeit not all, of the cross-species effects.

Future directions, including genetic and computational models, promise to elucidate the underlying mechanism of face perception across phylogeny.

¹Department of Psychology and Neuroscience Institute, Carnegie Mellon University, Pittsburgh, PA, USA

²Department of Psychology, Ben Gurion University of the Negev, Beer Sheva, Israel

*Correspondence: behrmann@cmu.edu (M. Behrmann).

detecting a coarse, face-like configuration and, at the opposite end, might involve individuating face identity and familiarity. We conclude that there is no correlation between computational complexity and phylogenetic status, and propose instead that the data support an account in which differing environmental pressures drive **adaptations** to support face perception [6].

We focus specifically on the perception of facial identity and not on face-related functions, such as eye gaze and attraction [7] or emotional expression [8] (also see [9]). We also only briefly review human **subcortical** structures (Box 1), many of which are implicated in these non-identity functions [10], and which may have a greater role when the cortex is underdeveloped (Box 2). While we emphasize recent studies, some older papers warrant inclusion. Last, given the vast literature on primate face perception, we treat this topic cursorily. However, we do refer the reader to existing reviews [7,11–14] and to the ongoing debate regarding the relevance of nonhuman primate data for understanding human face recognition ([15–19]).

Similarities and differences in computational processes of face recognition

While face processing is ubiquitous across phylogeny, different mechanisms might be used to accomplish this task [15]. Commonalities in computational processes, representations, and neural structures across species may be especially informative with regard to convergent evolution. Evidence for convergence across systems that are phylogenetically distant from each other attests to the significance of these mechanisms in accomplishing this critical functional task [20,21], and is suggestive of an independently evolved mechanism that is largely invariant of **niche specialization** and adaptation [5,7]. Figure 2 summarizes these different processes on the y-axis, from less to more demanding computations, with the associated cross-species evidence plotted on the x-axis. We include in each cell those species in which there is positive or even partial positive evidence for a specific ability. Importantly, the absence of evidence (an empty cell) is not tantamount to evidence of absence and may merely reflect the difficulty of studying these processes in nonverbal species [22]. We also include human infants in this figure, given the relevance of their face perception skills as a potential link across phylo- and ontogenesis [23]. Last, because faces can be represented at the: (i) category (i.e., face versus nonface); (ii) conspecific (i.e., own-species face versus other species face); and (iii) individual (i.e., own-species face 1 versus own-species face 2, independent of familiarity) level, we consider all three levels of specificity.

Face-like configurations and simple discrimination

The simplest computation, that of orienting preferentially to a face, is based on ‘first-order’ relations (e.g., two eyes above the nose, which is above the mouth; a basic spatial layout that is common across all faces; Figure 1). This orienting is ubiquitous across species and perhaps present during the third trimester of human pregnancy as measured by a fetus turning its head to face-like configurations of lights projected through the uterine wall [24]. Monkeys also show face detection, and the middle-lateral face patch, one of the nodes in the face-processing neural hierarchy, has a causal role in face detection based on the contrast relationships between face parts [25].

Dogs, especially pets versus kennel dogs, differentiate faces from nonfaces [26–28], and this preference is assumed to be the basis of attachment in species reared with parental care, such as chicks [23]. It is surprising then that this orienting preference is also evident in land tortoises, which are solitary, have no parental care, and do not live in social groups. Tortoises placed at the starting point in a test apparatus preferably oriented to a schematic facial versus nonfacial configuration [29] (Figure 3A), as is also true for human infants [23]. Lower-order vertebrates, such as cichlid fish, orient to the face versus the body of the fish [30] (Figure 3B), and archerfish,

Glossary

Adaptation: through natural selection, the process by which a species comes to be better suited to its ecological habitat.

Clade: group of organisms believed to have evolved from a common ancestor (sharing a branch on a cladogram).

Configural processing: ‘first-order’ configural relations (i.e., two eyes, nose, mouth with the eyes symmetrically above the nose, which are above the mouth) are important for face classification, whereas ‘second-order relations’ refer to the features and their metric distances or relations.

Conspecific: belonging to the same species; in this context, recognition of faces of animals from the same species, for example, human faces for humans and macaque faces for macaques.

Convergent evolution: evolutionary process whereby distantly related organisms independently evolve similar or analogous structures or functions to adapt to similar necessities or pressures, for example, face recognition.

Neocortex: the six layers of the cerebral cortex involved in higher-order brain functions and the most recently evolved part of the brain.

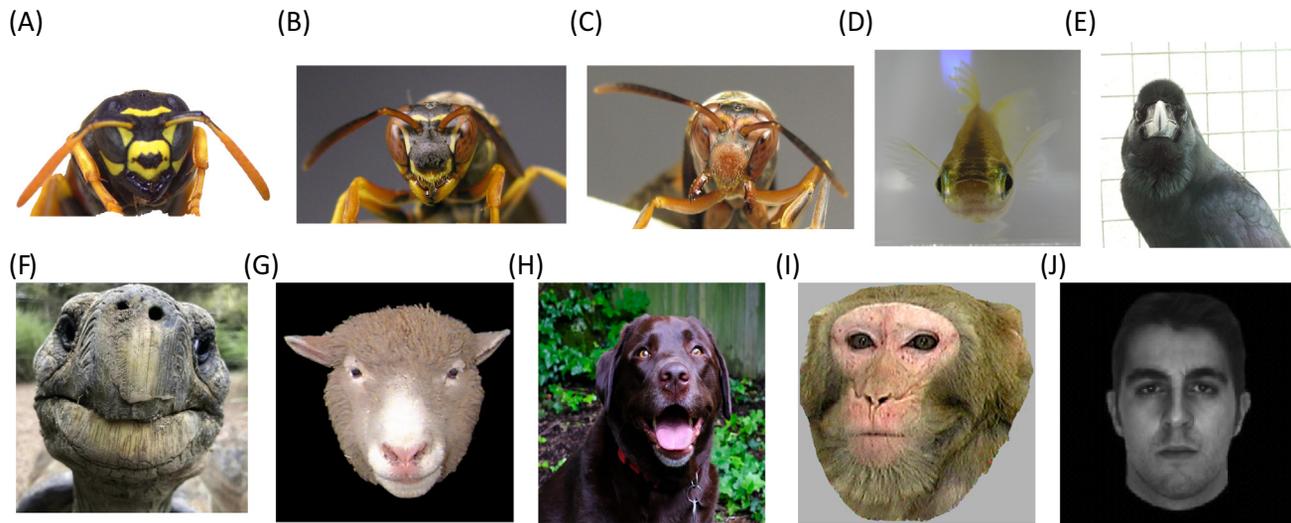
Niche specialization: process by which evolution (via natural selection) adapts a species to a particular characteristic of its ecological habitat.

Ontogeny (ontogenesis): developmental history of an organism that occurs within its own lifespan.

Phylogeny (phylogenesis): evolutionary history of a species with reference to lines of descent and relationships between groups of organisms.

Subcortical: group of deep neural structures that lie beneath the cortex.

Taxa (or taxon, singular): groups of organisms of any rank that are classified as a unit (i.e., phylum, family, species).



Trends In Cognitive Sciences

Figure 1. Diversity in the appearance of the face within species (A–C) and across species (D–J). (A) *Polistes dominula* (paper wasp) face [20]. (B) *Polistes fuscatus* (paper wasp) face [32]. (C) *Polistes metricus* (paper wasp) face [32]. (D) Medaka fish. (E) Crow face [100]. (F) Tortoise face. (G) Sheep face [62]. (H) Labrador retriever face. (I) Macaque monkey face [151]. (J) Human face [152]. Reproduced, with permission, from <https://mcm-www.jwu.ac.jp/~fukamachi/english.html> (D).

with training, discriminate between faces [31]. Last, some, but not all, subspecies of paper wasps differentiate between faces and nonfaces [32] (Figure 3C).

Orienting to a face is observed across phyla and is not necessarily associated with the social milieu of the species. Sensitivity to the face configuration might reflect a canonical visual computation resulting from, for example, a bias to the upper visual field, which is tuned to distant, extrapersonal space and is useful for perception [33] (but see [23,34] arguing that the top-heavy bias is more complex than just an upper field preference). This upper field bias, with the midpoint of the face serving as the rough centroid for fixation, may have a more fundamental role, such as monitoring predators overhead, and might have been co-opted to serve face perception. This top-heavy preference is associated with the superior colliculus [35] and might link face orientation in species that have no cortex with that of human infants, in whom cortex is still underdeveloped [23,36] (Box 2).

Inversion

Human adults and infants recognize faces disproportionately better when the faces are shown upright versus inverted [23,37]. Inversion is often explained as a consequence of the observer's limited experience with inverted compared with upright faces [38]. Perhaps surprisingly, then, given their prehensile tail, the findings regarding an inversion effect in nonhuman primates are inconsistent [7,15], and results differ across subspecies (e.g., chimpanzee versus rhesus macaque), stimulus type, and paradigm. A meta-analysis of the inversion effect revealed a small but not statistically significant cost for inverted versus upright faces (relative to nonfaces) that held independent of family of species [39]. One possible explanation is that the variability of the findings among nonhuman primate species may be a consequence of the differing amount of exposure to inverted versus upright faces during development.

Dogs demonstrate an inversion effect [40], as do both cichlid and medaka fish [41,42] (Figure 3B) but carrion crows do not [43]. As evident, the sensitivity to orientation does not obey a linear

Box 1. Assaying face perception in the human subcortical pathway

Evidence of a contribution from subcortical structures to face perception in humans would be consistent with conservation over **ontogeny** [93]. Hypothetically, once the human cortical face system is bootstrapped over development, subcortical contributions may become redundant and, hence, pruned. Assessing face recognition in human subcortex is challenging because the structures are small, located deep, and have a low signal-to-noise ratio [118]. Nevertheless, robust selectivity to face images [119,120], even independent of emotional expression, has been observed in neuroimaging data [10].

This subcortical contribution to face perception has also been confirmed in studies using a Wheatstone stereoscope [121], which enables eye-specific stimulus presentation [122,123]. Visual input is propagated in an eye-specific fashion from the retina to layer IV of striate cortex [124,125] (Figure 1A). Therefore, one can present multiple images sequentially to the same (monocular) or different (interocular) eyes (Figure 1C) for same/different judgments. Given that the percept is the same for the observer (Figure 1C, middle column), the observer is unaware of which eye receives the input [126,127]. Improved performance to two repetitions of a face to one eye versus presentation of one image to each eye is sufficient to infer a subcortical versus cortical face perception network (although V1 may be involved to some extent).

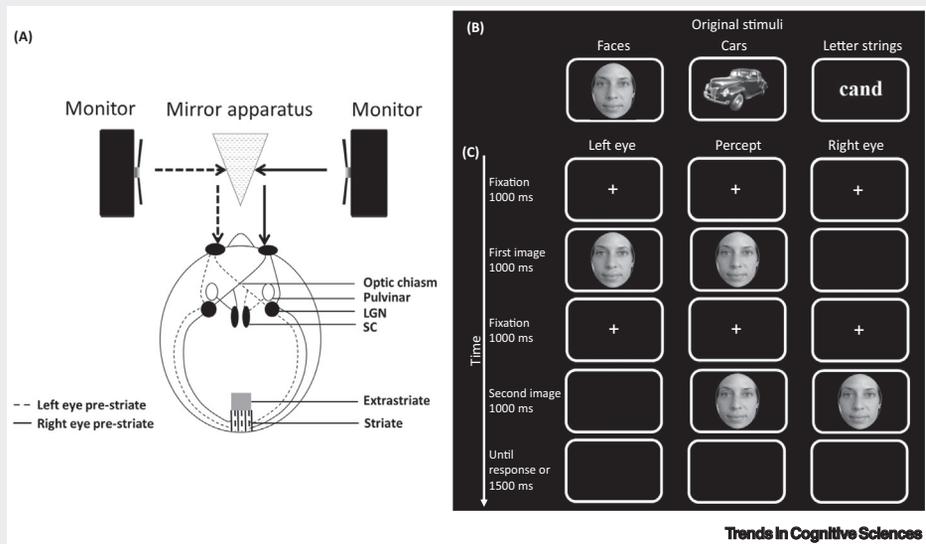


Figure 1. The setup and paradigm used for examining subcortical contributions to face processing. (A) Visual pathway, experimental set-up, and an example of a single trial and stimuli. Superior monocular over interocular (B,C) discrimination was observed when faces, but not when cars or letter-strings, were repeated to a single eye [(B) on right] [122], consistent with mediation by an evolutionarily older system. Moreover, the monocular benefit was present only for low- but not high-frequency versions of the face images, reflecting the propagation of coarse magnocellular information through the subcortical pathways [128–130]. Last, there was a monocular advantage for top-heavy face-like configurations (two blobs for eyes and a lower blob for mouth) but not for nonface-like configurations (three diagonal blobs), as used in infant experiments, providing additional evidence of the sensitivity of subcortical computations for faces [23,131]. Furthermore, there was no monocular advantage for inverted faces [122] or for faces in the composite face effect paradigm [132], a gold-standard marker of holistic processing. The absence of these more complex computations in human subcortex is seemingly at odds with the inversion and conspecific effects in fish and paper wasps (see main text) but, in animals without cortex, the lower order system may suffice for these computations, homologous to the learning that takes place cortically in humans. Abbreviations: LGN, lateral geniculate nucleus; SC, superior colliculus.

trajectory across the evolutionary scale and is also likely an outcome of experience with upright and inverted faces.

Configural processing

The ability to perceive not only the facial features, but also the distance and relational properties between the features (i.e., the ‘second-order relations’ [4]) constitutes **configural processing**. Here, we set aside the debate about the exact nature of configural or ‘holistic’ processing [44]

Box 2. Face perception in infancy

If 'ontogeny recapitulates phylogeny' [133,134] as often claimed, the study of developmental pathways can provide important insights into the mechanisms of evolutionary change. In human ontogeny, there is consensus that newborns show a bias to orient to face-like stimuli (or top-heaviness, see main text) [36], even with an underdeveloped cortex [23] (but see [34]). Converging evidence suggests that this ability is largely mediated by the subcortical visual pathway [23,135–137], and this is bolstered by the finding that a face preference is elicited only with stimuli shown to the temporal (which links to subcortical regions) but not nasal (which links to cortical regions) hemifield [138]. The subcortical pathway may bias visual input to the developing cortex early in life and, in so doing, bootstrap relevant cortical mechanisms [136,139]. Although some argue that cortical face circuits are already fully operational at birth [140], based on the stronger frequency-tagged responses (in EEG frequency tagging study) for upright over inverted face-like configurations, these signals may reflect the feedforward propagation of signals from subcortical computations (it may also be that proto-organization is in place and the feedforward signals tune these existing biases [141–143]). That infants also show an inversion effect [144], even in the absence of refined cortex (as in medaka fish), is consistent with findings of a preference for upright faces, and a potential functional contribution of homologous brain structures over phylogeny.

Just as there are nonlinearities over phylogeny, there are also nonlinearities over ontogeny. For example, although there is a strong right-hemisphere EEG response to faces in 4–6-month-olds, this is no longer observed in 5-year-olds [145,146] or even in school-aged children [147] (but see [140,148] for a more continuous trajectory across development; see also nonlinear functions in [149]).

The contribution of subcortical structures to face perception suggests that there is both conservation across phylogeny and ontogeny and that, rather than being relieved of their duties following the bootstrapping of cortical representations [23,150], subcortical structures continue to contribute actively to face processing across the lifespan of the observer.

and consider any form of integrative processing to be germane for configural computation. Human infants engage in configural processing [45] but whether nonhuman primates do so remains controversial. In some studies, monkeys appear to be less sensitive to relational processing than either chimpanzees or humans (for examples, see [15,46], respectively). Interestingly,

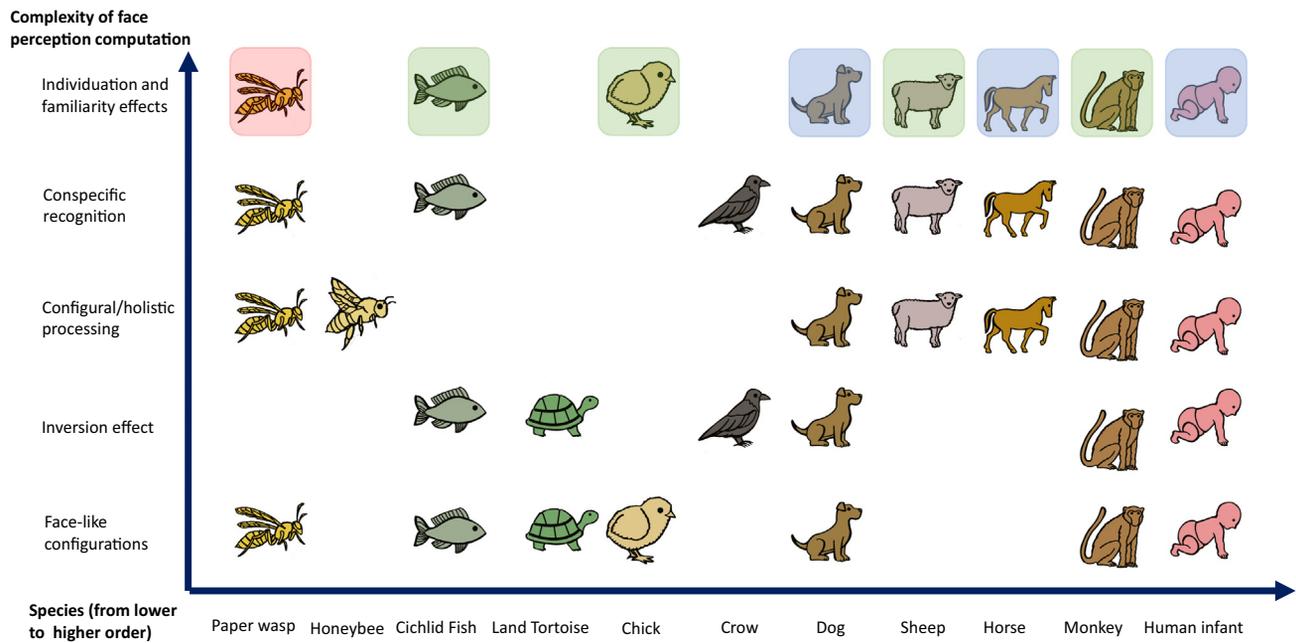


Figure 2. The complexity of computations for face perception (y-axis) across different species (x-axis). Note that an empty cell does not indicate the absence of the computation in the particular species, but may simply reflect the fact that there is no available evidence. In the upper row, 'Individuation and familiarity effects', the red frame denotes species that only discriminate conspecifics, the blue frame denotes species that only discriminate between human faces, and the green frame denotes species that discriminate both conspecifics and human faces.

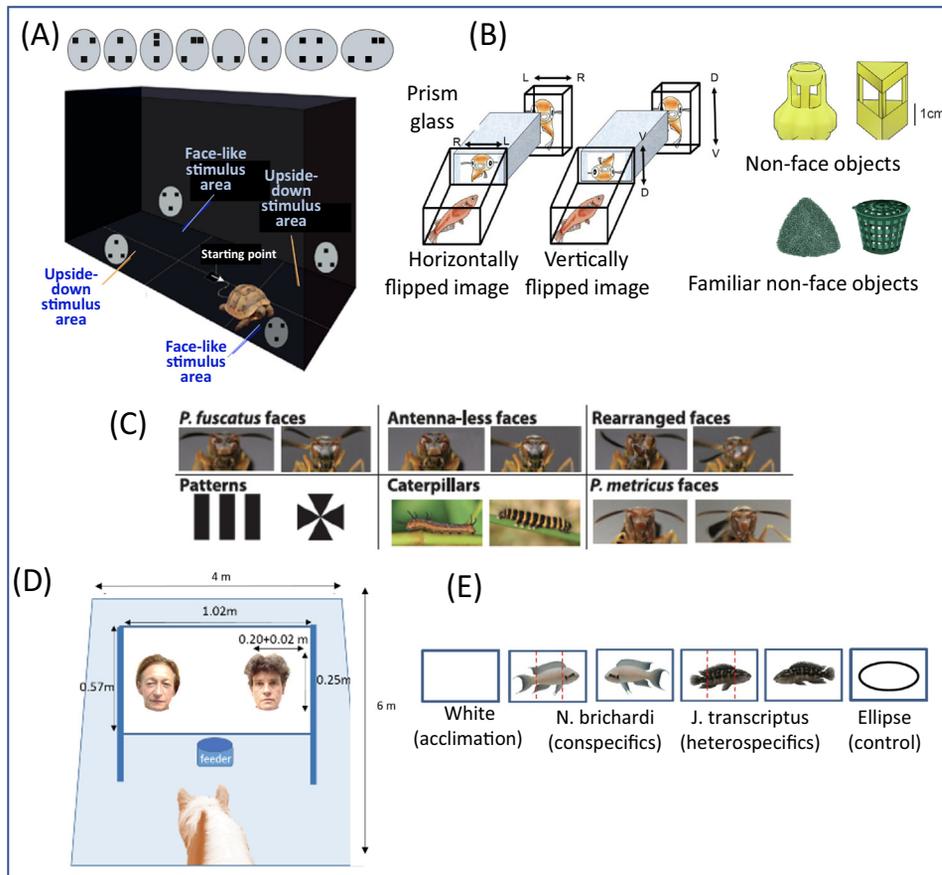


Figure 3. Examples of behaviors achieved by different species. (A) Different stimuli (top row) and testing apparatus (bottom) used in a study of land tortoises [29]. Face-like configurations are indicated by a blue line and inverted faces by an orange line. The first area entered after the subject was placed at the starting point was taken as the index of preference. (B) Left: the experimental set-up for medaka fish [41] used prisms, with horizontal and vertically rotated images of the fish, along with examples of unfamiliar and familiar (from hatching) nonface objects. (C) Images used for training wasps. Wasps were trained to discriminate between pairs of images. Pairs are shown in the same row. Top row left to right: *Polistes fuscatus* faces, antenna-less faces, rearranged faces; Bottom row left to right: patterns, caterpillars, *Polistes metricus* faces [32]. (D) Experimental set-up to evaluate the preference of horses for discriminating novel versus recurring faces [52]. The horse is facing toward the screen on which two faces are shown and the feeder is placed below the screen. (E) Tanganyikan cichlid fish focus on the face of conspecific fish better than on the face of heterospecific fish (red lines indicate locations where measurements were taken) [65].

however, monkeys do show decreased tuning to individual features within upside-down faces [47] and also show the ‘Thatcher illusion’, in which changes in the orientation of features (e.g., the eyes) are perceived only when faces are upright, and not when faces are upside down [48].

Surprisingly, some lower-order species adopt holistic processing [49]. Trained on targets and distractor faces comprising inner face features and an outer contour, both of which could be recombined across images, both honeybees and wasps recognized the target face using only the inner features. However, they were even more accurate when the inner and outer portions of the face were correctly combined (‘part-whole task’) and less accurate when the inner features of the target were combined with the outer features of the distractor (‘composite face effect’) [20]. Some species of paper wasps, such as *Polistes fuscatus* (*P. fuscatus*) differentiate among wasp

face images more rapidly and accurately than nonface or manipulated (scrambled features or antenna-less) faces [32] (see Figure 3C).

Many studies have explored the configural processing of human faces by nonhuman species. Such studies do not directly inform an evolutionary perspective, but do reveal the extent of the perceptual competence of a species in perceiving homogeneous, complex visual patterns. Both expert (previously trained for such experiments) and naïve dogs can discriminate faces based on configural information (faces intact, inverted, blurred, scrambled, or in gray scale [40]). However, only expert dogs can discriminate their owner's face when part-based information was visible (only eyes, nose, or mouth), with the eyes being an especially salient feature ([50] also see [51]). Horses also perceive faces holistically and recognize images of faces across viewpoint, in real-life, whether as a monochrome image, or even with changed hairstyle or eyes covered [52] (also see [53,54]) (Figure 3D). Sheep also process faces holistically and, with little training, identify faces presented from varying perspectives [55]. It remains a possibility that these animals are largely relying on one or more features of the face, for example, focusing on the mouth or the nose, which remain largely stable over image manipulation, rather than exploiting configural information per se, but this should still be fully determined.

The evidence for holistic processing in species that lack cortex is provocative. Moreover, the potential neural substrate enabling this ability, the mushroom body and antennal lobe, is differentiable in wasps that do or do not show pattern recognition [56,57]. Burke and Sulikowski [58] note that there is currently insufficient evidence to determine when, over evolution, holistic processing arose and what specific selection pressures led to the emergence of such a mechanism.

Conspecific recognition

A more challenging perceptual computation, that of recognizing conspecifics (faces from the same species as the observer), is easily accomplished by humans, including infants, and by non-human primates that appear to use a similar representational space to that of humans [18,59]. Monkeys [59] and chimps [60] differentiate conspecifics and, in marmosets, the functional correlates of face perception are organized similarly to those of humans [19]. Dogs [28] can categorize different breeds and can generalize to novel instances of dogs [61]. Horses [52], sheep [62], carrion crows [63], and rainbow trout [64] also recognize conspecifics, and Tanganyikan cichlid fish discriminate between conspecifics using facial, and not body, patterns (Figure 3E) [30]. These findings are also consistent with the meta-species trend of attention to the eye region [65], another instance perhaps of the top-heavy bias (and subcortical computation).

P. fuscatus paper wasps, but not a close relative, *Polistes metricus*, can recognize conspecifics even though the two species do not differ in other types of visual learning [32] (Figure 3C), and *P. fuscatus*, but not *Polistes dominula*, use facial patterns to identify conspecifics using a holistic processing approach [20]. These family or subspecies-specific competencies are thought to result from adaptation to the environmental and social context; while *P. fuscatus* have acute vision, live in well-lit nests populated by groups of cooperating queens, *P. metricus* nest alone and there is no pressure to compete among queens (for possible candidate genes for individual recognition, see [66]).

Individuation of faces and familiarity effects

Here, we consider individuation as well as familiarity effects in face perception. Whereas individuation does not require that the observer have a mnemonic representation, recognizing a familiar face requires not only precise encoding of the input, but also the (re)activation of an existing representation.

Nonhuman primates, including capuchins [67], discriminate familiar from unfamiliar conspecific individuals although they do not show sensitivity to the frequency of exposure: notwithstanding the more frequent interactions with in-group than out-group individuals, they have equal recognition of both groups of capuchins. However, familiarity recognition appears not to depend on the sociability of a species because orangutans, a less gregarious primate family, also demonstrate better discrimination of familiar faces. Sheep can recognize 50 other sheep even after a 2-year absence [68], and young chicks show effects of familiarity with greater pecking in the presence of an unfamiliar versus familiar chick [69], even across changes in face, age, and gender [70]. Last, group-living cichlid fish recognize individual and familiar fish faces [71], and *P. fuscatus* wasps show signatures of individuation [20] and familiarity, as reflected by fewer aggressive interactions with known versus unknown wasps [72].

Many studies examining the differentiation between individual instances of human faces explore the ability to represent identity across substantially different inputs of the same face. Independent of viewpoint, facial expression, and other major transformations, humans recognize large numbers of faces [73], especially familiar faces [14,74]. Human infants individuate faces [75] and 6-year-olds recognize familiar faces across highly varying images [76]. Several nonhuman species have also been tested on their discrimination skill, albeit for human faces, and monkeys show neural activation in response to individual human faces [13]. Horses can discriminate between unrelated humans, fraternal twins, and identical twins [77], and can identify a photograph of their keeper even if not viewed for 6 months [78]. Sheep can select a learned human face shown from novel viewpoints (even from 2D images) and with different hairstyles [55]. Chicks can recognize familiar over unfamiliar faces [70] and archerfish also discriminate human faces [31]. Unsurprisingly, dogs can recognize specific human faces even under suboptimal conditions, such as uneven illumination [79].

Neurobiological bases of cross-species face recognition

Convergence across the phylogenetic scale may also be relevant when considering whether neural mechanisms underlying face perception might be universal. There is a well-established overlap in neural circuitry [13,68,80,81] and temporal dynamics [82] of face processing between humans and nonhuman primates [18].

In dogs, electroencephalography signals to faces reveal a peak waveform component at 100–150 ms post onset, similar to that recorded from humans [83]. In addition, fMRI studies with dogs reveal greater face than object activation in several brain regions, including the bilateral temporal cortex, as is also true for humans [84,85]. Unlike in humans, however, this is less robust because the face selectivity is only evident when a uniform field is used as the baseline but not when scrambled faces are used [86]. Both human and dog observers evince neural activation to conspecifics, but this signal is, again, more selective in humans than in dogs [87].

Sheep also evince a neural face signature, with 7% of neurons recorded responding preferentially to faces in face-responsive cortex [88], although this percentage is low compared with that of macaques at 97% in face patches, ML and MF [13]. No selective neural firing to images of conspecifics is evident in the avian pallium of pigeons [89], perhaps reflecting the predisposition of these birds to attend to local rather than global configural properties of the input [90]. In young domestic chicks, neural activity, mapped using the immediate early gene product c-Fos, revealed significantly higher activation in the hippocampus of the right hemisphere and the septum of the left hemisphere [69] in response to unfamiliar over familiar cage mates. Together, these findings uncover neural signatures of face perception across multiple species.

Insights from phylogeny: synthesis

The ingenious development of newer methods and analytic procedures have permitted a fine-grained description of face perception and the underlying psychological and neural correlates across the evolutionary scale. To explore principles that govern the behavior and brain function of different species, we have reviewed evidence of well-established computations engaged in face perception, for example, face detection, effects of face inversion, holistic processing, conspecific identification, and individuation and familiarity effects, and their neural bases.

Convergent evolution and face recognition

The first conclusion drawn from this review is that the sophistication of face perception competence does not correlate with the ranking of the species on the evolutionary scale. For example, dogs evince sensitivity to face orientation (“inversion effect”) but nonhuman primates do not do so reliably. Similarly, young chicks and paper wasps are precocious in their recognition of conspecifics and, whereas horses and sheep process faces holistically, as is true for paper wasps, nonhuman primates may not [15]. The second conclusion is that there is convergence in computational abilities across species, leading to the provocative suggestion that there are universally adaptive mechanisms that facilitate face recognition. For example, both convergence toward holistic face processing in distant **taxa** (primates and wasps), as well as divergence of this ability among closely related taxa with different recognition behaviors (e.g., *P. dominula* versus *P. fuscatus*), are indicative of possible general computations. What might such adaptive strategies entail? We have suggested that a simple computation of ‘top heaviness’ may be one, but there are other possibilities. For example, the geometry of shape (e.g., a triangular face layout) above another shape (body) may also suffice. However, these simple computations of coarse geometry are insufficient for explaining the array of perceptual processes including the differentiation among individuals within a species.

That the theoretical continuum of computations from simpler (face detection) to more complex (familiarity and individual discrimination) is violated across- and even within-species, even just within humans [91], challenges assumptions about the hierarchical complexity and ordering of face perception across phylogeny. The factors most likely to trump the linear sequence across phylogenesis are the social and environmental pressures of the species and the extent of experience with faces in their niche [3,6], consistent with the ‘ecological intelligence’ and ‘social intelligence’ approaches [56]. Characteristics such as imprinting, hunting, social dominance, and domesticity appear primary in sculpting the nature of behavior. This is well exemplified by young chicks approaching objects that are similar to natural social partners and showing filial imprinting on the objects [92] and by conspecific recognition only by those wasps that nest with a colony of queens [56].

However, lest we overplay the role of nurture, nature always appears to offer a reprise: subspecies of paper wasps show mutations in genes associated with learning and visual processing [93]. In addition, in humans, fMRI activation patterns of face selectivity are more similar in mono- than dizygotic twins [94], as are fiber tracts in the face network [95]. That solitary land tortoises orient to face-like configurations also challenges an account entirely reliant on nurture: such a computation is expensive and not obviously adaptive for the lifestyle of the tortoises. This orientation preference in the tortoises may be a happy accident of evolution in which homologous brain structures instantiate a top-heaviness or upper visual field bias [33], which is present in primates [35], solitary tortoises [29], and rodents [96]. One might then ask whether this upper field bias is a fundamental feature of phylogeny, perhaps an inherited proto-organization that permits further bootstrapping [97]. However, what explains the ubiquitous presence of this bias across species? One possibility is that the ability to monitor predators hovering above in the upper visual field has been co-opted in the service of face perception.

As is standard fare on the nature–nurture seesaw, both nature and nurture likely interact and reciprocally constrain the evolution of face perception. This is well illustrated by the finding that there is high morphological variability in facial features compared with other body features but only in *P. fuscatus* wasps that have face perception skills and not in non-colony wasps [98]. Moreover, there are alterations in the eye facet of *P. fuscatus* wasps that permit the high resolution of small images, such as facial details [99]. There is also variability among crows, the flocking of which reveals variability in bill shape and eye shape that may promote individual identity differentiation [100] and this is also true for facial features and fin morphology in bottlenose dolphins [101]. On some accounts, faces have evolved to signal individual identity, and regions surrounding single nucleotide polymorphisms that are face associated show heightened diversity [98], possibly reflecting a genetic basis for varied phenotypes that even pre-dates humans. Whether this diversity of facial characteristics is of functional relevance remains speculative: do crows or dolphins really use the feature differences to discriminate across conspecifics? If so, this phenotypic diversity might have evolved to better support individual (and mate) identification. A pathway for this complex process is one of dynamic interactivity between physiological changes and social factors: social interactions result in changes in hormone titers, which affect behavior and, in turn, have widespread physiological consequences [102]. These changes then alter social behavior, and the interactivity continues.

We have restricted our review rather narrowly to studies of face recognition, but human face perception is strongly influenced by environmental and contextual factors [103]. The faces that co-occur in particular scenes permit predictions for subsequent occasions (e.g., identifying Paul McCartney's face will result in the likely activation of John Lennon's facial representation) and the influence of top-down constraints on the perception of face identity. Consistently, blood oxygen level-dependent (BOLD) responses in the fusiform face area are modulated depending on the contexts in which faces are expected [104]. Moreover, in humans, face perception and the processing of familiarity can influence social behaviors, such as prejudice, stereotyping, and in-group bias [105]. Future investigations might target these more complex interactions between face processing and other cognitive and social processes and explore their presence in other species.

Future directions for elucidating computational principles govern face recognition

Face processing offers an interesting test case for exploring convergent evolution across a diversity of species the faces of which differ (Figure 1). Of course, definitive conclusions must be tempered given the lack of evidence, obvious gaps, and even inconsistencies in the literature. With a large enough sample of species examined and more formal analyses, different patterns within- and between-species might yield insights beyond those gleaned from the well-established studies of primates [13].

A further direction that might illuminate patterns of convergence and divergence of face perception across species involves simulations using artificial neural networks. For example, neurobiologically inspired deep convolutional neural networks (dCNNs) of ventral visual cortex, which achieve high levels of face recognition [14, 106], have elucidated general biological principles of face representations [107–109]. Applying such models to simulate the smaller, less sophisticated brains of lower-order species and identifying the overlap of computational principles in such networks, such as the inversion effect, promises new insights into phylogenetic mechanisms of face perception. Indeed, even single neurons can be modeled as a DNN, offering proof of computations that might emerge from simple biological systems [110]. Inversion effects and holistic processing may be implementable by a relatively simple mechanism that has large, overlapping receptive fields and specific patterns of connectivity [111], and this architecture may yield computations that cut

across visual systems from honeybees and wasps to primates. This spatial integration account is consistent with recent findings that population receptive fields and visual field coverage are reduced and shifted downward for inverted relative to upright faces [112], and are altered in individuals with impaired face recognition ('prosopagnosia') [111].

Of note, the hypothetical role of receptive field properties is not mutually exclusive with the top-heavy bias associated with the superior colliculus. Together, these might account for the bias toward face-like configurations and the preferential discrimination between faces and nonface stimuli and, combined with experience with conspecific faces, might result in a complex face perception system. More sophisticated aspects of face processing, such as identity discrimination, might require additional computations implemented in primate cortex or even in structures such as the mushroom body and antennal lobe in wasps [53,93]. Thus, while the layers of dCNN models of human face recognition simulate cortical regions along the hierarchical ventral visual pathway [107,113], in other animals, the architecture (composition of layers, hierarchy, and network depth) may be simpler [110], but the same computational principles may apply nevertheless.

A related (and also underexploited) approach involves the adoption of genetic algorithm models that simulate biological evolution and are often used to search for the optimal solution efficiently via a natural selection process. Genetic algorithm models achieve high accuracy in face recognition [114,115] but have been primarily used for improving image analysis and applications such as biometrics. The specific analysis of the output of such models, together with a review of the properties and representations discovered by successive generations of these models, could reveal key aspects of the computational mechanism. With well-reasoned assumptions about selective pressure and an evaluation of algorithmic features preserved over increasingly complex iterations, the model might uncover necessary and perhaps sufficient properties of the face recognition system across evolution.

Last, despite differences in architecture, learning parameters, and objective functions, computational models can evince 'direct fit' by optimizing over millions of examples, akin to the overparameterization of the brain [116]. Assuming the training examples are numerous and curated to reflect the 'face diet' of a particular species, simple interpolation in a model can efficiently result in generalization to new exemplars. Such models are offering increasingly interpretable accounts of human performance and even of the underlying neural constraints that result in the accuracy and rapidity of primate face recognition [106,109,117].

Concluding remarks

Based on this brief foray into face recognition across phylogeny, we conclude that there is no linear scale on which simpler competencies in lower order species, such as invertebrates, manifest at one end and more complex computations in higher order species, such as nonprimate mammals (e.g., dogs and sheep), emerge at the other end. There is also no clear ordering of animals along the continuum, and many species, including wasps, chicks, and fish, violate a linear evolutionary prediction. Instead, there appear to be both convergences toward similar computations in distant taxa and divergence among closely related taxa. We have reviewed the evidence of neural, computational, and genetic properties that might support this complex phylogenetic scenario. Much remains to be learned to both replicate existing findings and determine more definitively the particular capabilities of different species in the domain of face perception (see [Outstanding questions](#)). Although we are ultimately left with uncertainty, several promising future empirical directions exist. Additionally, simple computational models with informed biological constraints and extensive training and experience may advance our

Outstanding questions

Is face recognition necessarily learned from experience and from the statistical properties of the input in all or only in a subset of species?

Do animals experience critical or sensitive periods and perceptual narrowing during the early development of face perception?

Relatedly, do animals show preferential recognition of their own age or sex, as is true of humans?

Do any species other than humans (and sheep) show a hemispheric superiority for faces?

Are the remarkable face perception abilities documented in, for example, horse and sheep face perception, directly related to the utility or functional/adaptive nature of this ability?

Are dCNNs used as computational models of face processing in the ventral visual pathway of humans and nonhuman primates able to capture the face recognition characteristics of animals with a more simplified face network?

How can we reconcile the relatively high prevalence (~2–3%) of congenital face recognition deficits (congenital prosopagnosia) reported in humans with the notion that proficient face recognition skills are associated with evolutionary pressures for reproduction and survival?

Relatedly, to what extent do other animals also exhibit congenital deficits in face processing?

Are there genes, preserved across evolution, that are associated with face recognition abilities?

Do any animals show the markers of expertise in face recognition, as evident by their invariant recognition of hundreds of faces and rapid acquisition of identity for new faces?

Is face recognition in animals better with more naturalistic visual input, such as dynamic, rather than static, images?

understanding of the principles that underly face perception. These principles could apply to visual cognition, more generally, and to its origins and evolution across phylogeny.

Which animal model, if any, should be used to study face processing in humans?

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None declared by authors.

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