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A natural history of vision loss: Insight from evolution for human visual function

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ABSTRACT

Research on the origin of vision and vision loss in naturally “blind” animal species can reveal the tasks that vision fulfills and the brain’s role in visual experience. Models that incorporate evolutionary history, natural variation in visual ability, and experimental manipulations can help disentangle visual ability at a superficial level from behaviors linked to vision but not solely reliant upon it, and could assist the translation of ophthalmological research in animal models to human treatments. To unravel the similarities between blind individuals and blind species, we review concepts of "blindness" and its behavioral correlates across a range of species. We explore the ancestral emergence of vision in vertebrates, and the loss of vision in blind species with reference to an evolution-based classification scheme. We applied phylogenetic comparative methods to a mammalian tree to explore the evolution of visual acuity using ancestral state estimations. Future research into the natural history of vision loss could help elucidate the function of vision and inspire innovations in how to address vision loss in humans.

1. Introduction

1.1. A natural history approach to understanding blindness

Research about blindness reveals behavior in the absence of vision, and it also affords more general information about how visual information and other sensory information is processed in living organisms. However, even determining what it means to see, or not to see, for humans and other mammals is an obstacle which has not benefitted enough from a natural history approach (see for example Shmuelof and Krakauer, 2011), as it has in studies from crustaceans to fish (Porter and Sumner-Rooney, 2018) and, exceptionally, subterranean mammals (Emerling, 2018; Emerling and Springer, 2014). Here we attempt to understand blindness with insight from the history of organismal lineages as they change through time. Over 36 million people in the world are blind, and over 253 million have some form of moderately impaired, or low, vision (Bourne et al., 2017). The number of people visually impaired from age-related disorders, such as glaucoma and macular degeneration, is on the rise, with additional problems brought about by the onset of diabetes, which is also on the increase (Diabetes, Type 2, 2012). The exploitation of interdisciplinary research findings, in particular perspectives on vision loss taken from evolutionary biology, will ultimately enrich translational research applications and thus human visual health more broadly.

Vision has played an important role in the evolution of humans. We are primates, which could be considered the most visual mammals, and visual behaviors are thought to have been driving forces in primate brain evolution (Barton, 1998; de Sousa and Proulx, 2014), with humans and chimpanzees showing the highest visual acuity. And yet, vision is not a defining feature of our species; humans who lack vision perform human specific tasks by employing other senses. It has even been suggested that in the recent evolution of *Homo sapiens*, visual or visual spatial functions may have been relatively reduced to allow for higher cognitive abilities (Pearce et al., 2013). While individual humans cannot be defined by dependency on vision, visual stimuli are relevant to human societies. Neandertals, a species with whom humans shared a common ancestor at least 430,000 years ago (Posth et al., 2017), included partially sighted and disabled individuals (Trinkaus and Villotte, 2017; Trinkaus and Zimmerman, 1982), implying that the inclusion of members with vision loss has long been a feature of human social groups.

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1.2. Functional evolution: a task-based approach to vision and vision loss

A functional evolution, or task-based, approach may help disentangle visual *sensory ability* at a superficial level from *perceptional functions* linked to vision, but not solely reliant upon it. In human cognitive neuroscience there is a new idea that neural organization is task-based and not sensory-based (Amedi et al., 2017; Pascual-Leone and Hamilton, 2001). This task-based organization has been referred to as the metamodal hypothesis, and the mechanisms causing it are also under debate as the functional selectivity hypothesis e.g., (Collignon et al., 2013; Dormal and Collignon, 2011) and as supramodality e.g., (Pietrini et al., 2004; Ricciardi et al., 2014). Thus, one aspect of a task-based approach is to consider that the link between a behavioral task and a sensory system can potentially become disentangled. This is because the brain is organized to achieve tasks, with the role of any given sensory system being secondary to that.

Such an approach is also common in ethology and evolution and is known as functional evolution. A task-based approach considers the evolution of sensory and nervous systems by framing them in a behavioral context (Nilsson, 2013; Nilsson and Bok, 2017). Phenotypes are subject to natural selection, and that changes genotypes. As such, it is important to keep in mind that variation in *behavior* is directly subject to natural selection. When variation in behavior presents, for any reason and due to changes in any structure, it will be directly subject to natural selection, influence sensory structures, and influence genomes. This is the opposite sequence from which visually guided behaviors are produced: they are the product of the structures of sensory and motor systems, which develop as a result of gene expression. As such visually guided behaviors are both the final aspect of phenotypic production and the aspect directly subject to natural selection (Nilsson and Bok, 2017). Therefore, to understand the evolution of the visual system, it is important to consider the evolution of visually guided behaviors.

Here we extend the task-based, functional evolution approach set forth by Nilsson (Nilsson and Bok, 2017) for understanding the emergence of vision, to understanding the evolutionary loss of vision as well. Because complex visual function is dependent on such a complexity of neural and sensory structures, visual loss does not simply eliminate tasks served normally by vision from the behavioral repertoire. There is a growing appreciation that because neural organization itself is task-based, "visual" behaviors can persist even in the absence of visual structures (Amedi et al., 2017; Pascual-Leone and Hamilton, 2001). The natural history of the emergence and loss of vision reveals much about the tasks that vision commonly serves, and how the tasks can continue to be served in the absence of vision. Tapping into the behaviors and brains of blind animals gives unique insight into what both vision and vision loss are in terms of this task-based, functional evolutionary framework. The senses are a means to functional end, and vision might have arisen as the most useful sense for a number of tasks, yet there is potential for other senses to compensate when vision is unavailable.

Natural variation that results from the evolution of species is underused for determining the relationship between visual ability and the tasks it permits. Phylogenetic comparative methods use information about the evolutionary history (i.e., phylogeny) of naturally occurring traits that vary between species. The relationships between variables, such as the relationship between an anatomical structure and its behavioral function, are tested in powerful statistical models. Jourjine and Hoekstra (2021) outlined how manipulative and comparative approaches can be combined to test the association between behaviors and other biological variables. The triangulation of phylogenetic models, naturally occurring models, and experimental manipulations permits a given association to be tested multiple times. In order to obtain the data necessary to test an association in multiple ways, it is helpful to choose a "model clade", that is a group of related species which vary naturally in the variables of interest, and can also be experimentally manipulated to hone in on the mechanism. This framework can be used for translating knowledge about experimental models as well as blind animal species to humans conditions. Consider these examples of crossmodal visual cortex activation related to visual deprivation discussed by Chabot et al. (2008). Fig. 1 shows (A) an experimental manipulation involving the production of a mutant breed of anophthalmic ZRDCT/An laboratory mice (*Mus musculus*; Chabot et al., 2008), (B) an experimental manipulation involving bilateral enucleation in Syrian hamsters (*Mesocricetus auratus*; Izraeli et al., 2002), and results in (C) naturally blind mole rats (*Nannospalax ehrenbergi*; Bronchti et al., 2002). (D) A combined framework across rodents can test whether the mechanisms driving the crossmodal plasticity are analogous and arose independently due to shared environmental pressures, or are homologous and conserved from a common rodent ancestor. (E) This could be expanded to allow comparison to human conditions. (F) A phylogenetic model can be improved by including model clades, numerous taxa, distances between species, and more specific evolutionary parameters to best determine whether associations found in experimental models are likely to be conserved in humans as well.

1.3. Naturally blind animal species

Vision loss helps us understand what tasks vision fulfils because either 1) the task is lost or 2) it is taken up by a less typical sense. As an example of the former, it is often taken for granted that vision is important for identifying possible mates (Setchell, 2016). Evidence for this comes from diversity of coloration patterns. We are not aware of any species showing strong sexual dimorphism in coloration patterns that is also lacking vision. This suggests that a role of vision is to identify coloration patterns that serve as cues about potential mates. As an example of the latter, vision is important in localizing distant objects. Evidence for this comes from the biodiversity of sensory strategies. In many species, vision alone can be used for localizing distant objects. However, in species in which vision is severely limited, the more unusual system of echolocation can be used to identify distinct objects. This suggests the task – localizing distant objects – is strongly related to vision but can also arise through another complex adaptation.

Here we examine the behavioral context in which vision loss occurs, by drawing examples from blind animal species in which vision is a trait that existed in an ancestor, but is no longer exhibited, as it had been lost over the course of evolution. Blinded animals and naturally blind animal species have different conditions. In humans, for example, blindness is a condition that inflicts *individuals* who are characterized by the lack of ability (i.e., disability) in vision compared to what is typical for the species. This would be similar in other taxa that are visually dominant, such as other primates or birds of prey (Bringmann, 2019; Coimbra et al., 2014). Human blindness is always a loss of normal function, and therefore is considered to be a disability. Humans are not necessarily unique in this respect; blindness also exists throughout the animal kingdom whenever an individual of a seeing species lacks vision. For example, an individual dog might suffer blindness due to glaucoma (and in particular certain breeds, this occurs at high incidences), retinitis pigmentosa or night blindness (Bouhenni et al., 2012; Bunel et al., 2019; Kondo et al., 2015). Of course, laboratory animals may be intentionally made blind for experimental purposes (Chader, 2002; Karlen and Krubitzer, 2009; Levkovitch-Verbin, 2004; Piche et al., 2007; Seruca et al., 2010; Wiesel and Hubel, 1963). Similar to blind humans, such blind *individual* animals are also disabled, and therefore provide more direct comparisons to blind humans. In contrast, an entire taxon may lack vision because either: 1) vision never arose in the evolutionary lineage comprising all species ancestral to it, or 2) an evolutionary event led to the loss of vision at some point along its lineage. Species are typically termed “blind” in the second case, where vision is an ancestral character that has been lost in the lineage. They are called blind presumably because compared to closely related species; they are characterized by a lack of vision. So-called “blind species” are species in which the wild-type individuals lack vision, therefore *individuals* are not disabled by blindness (Goering, 2015). However, similar to the case of a blind

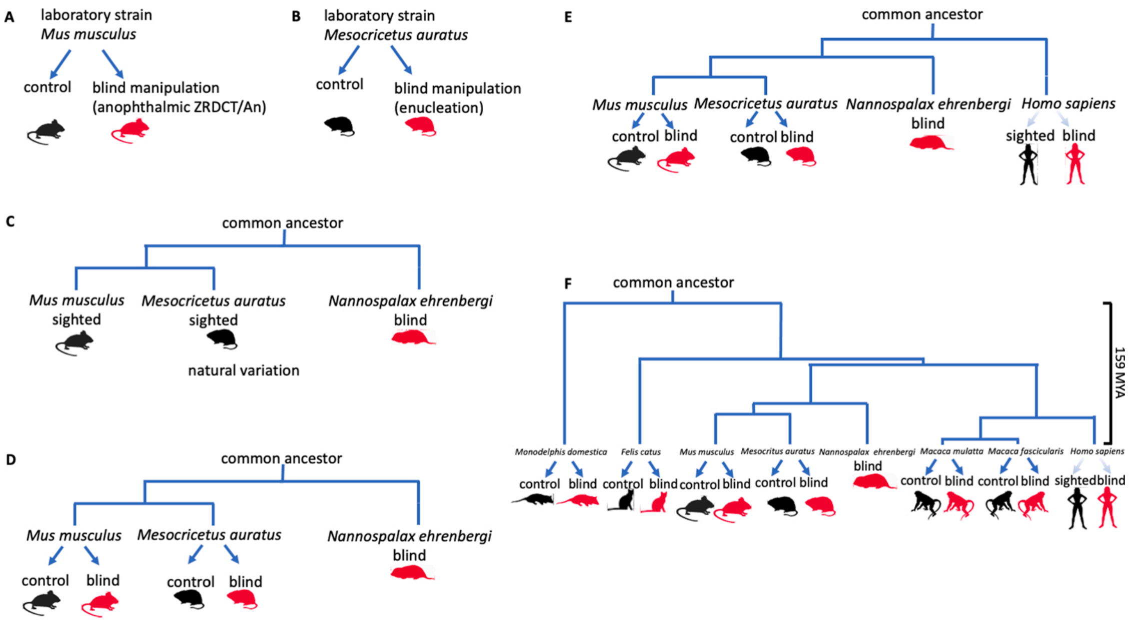

Fig. 1. A framework for translating basic science findings about vision loss from evolutionary and experimental studies to human conditions, based on Jourjine and Hoekstra (2021), with the aim to determine whether associations found in experimental models are likely to be conserved in humans as well.
(A) An experimental manipulation involving the production of a mutant breed of anophthalmic ZRDCT/An laboratory mice (*Mus musculus*; Chabot et al., 2008).
(B) An experimental manipulation involving bilateral enucleation in Syrian hamsters (*Mesocricetus auratus*; Izraeli et al., 2002).
(C) A phylogeny showing natural variation in rodent vision, including blind mole rats (*Nannospalax ehrenbergi*; Bronchti et al., 2002).
(D) A combined framework including natural variation in rodents as well as experimental studies.
(E) The combined framework, with the inclusion of human conditions.
(F) An example of how a combined framework can improved with an expanded phylogenetic model.

individual, in a blind species there has been a loss of a visual function for the species, rather than merely the lack of vision ever having had occurred.

We draw on what we know about the natural history of vision and visual loss to better understand blindness generally, to then shed light on human blindness. First, we discuss the evolutionary emergence of vision in a clade ancestral to the vertebrates, to highlight the tasks related to it from a functional evolution perspective that takes into account natural history (depicted with phylogenetic trees showing how species are related). Then, we describe the loss of vision in mammalian lineages, and how what might be considered "visual" tasks continue to be achieved. Then, we consider human and nonhuman primate vision (and the tasks it enables) in comparison to vision in other mammals. Of particular importance is the understanding of vision as a way in which eyes and brains process information to perform tasks in response to visual stimuli. We recommend describing visual function and visual loss in individual humans by drawing on terminology already in use for describing species level differences in visual function and task performance.

2. The origin of vertebrate vision and its subsequent loss

2.1. Origin of vision

Vision is an ancestral characteristic of vertebrates (Fig. 2). However, is *not* universal to all animals. More generally, sensitivity to light (photoreception) is more widespread, but is not vision per se. Of all animal species, about 1/3 have vision, 1/3 are blind, and the remaining 1/3 have photoreceptors but do not have vision (Bainbridge, 2009). Photoreceptors can be found in nearly all groups of organisms, including not just animals but also plants, fungi, and unicellular organisms. It has been suggested that a light sensitive patch may be a shared derived feature of all bilaterian animals (those with bilateral symmetry, a major phylogenetic grouping), based on the finding that *Pax6* and related genes controlling eye development occur in diverse clades, that is the different branches of a phylogenetic tree grouped by a common ancestor (Gehring and Ikeo, 1999).

Nilsson (Nilsson, 2009, 2013) developed a classification of

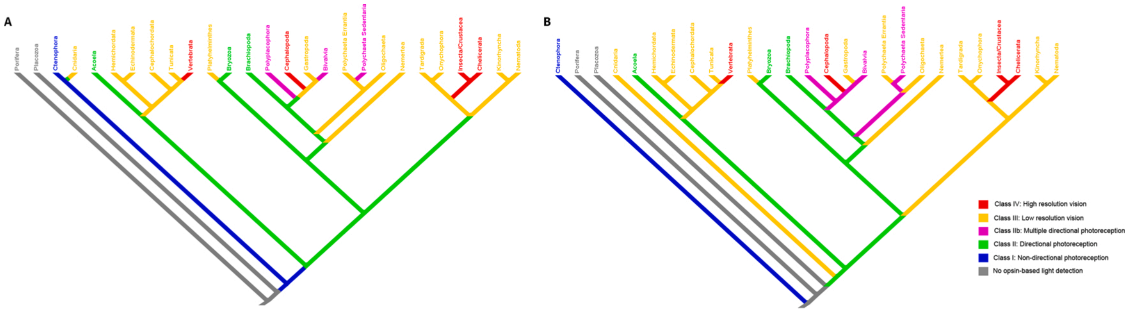

Fig. 2. Phylogenetic tree showing branches of animals where photoreception is present, after Nilsson (2013). Given uncertainly about the basal relationships, two different tree topologies are presented: 2A based on Nilsson (2013), and 2B similar to that of Moroz et al. (2014). Evolution of classes of photoreception (character states) based on Nilsson (2013).

photoreceptor-controlled behavior to better interpret the origin of vision as distinct, yet derived, from photoreception. Nilsson defined photoreceptive abilities primarily in terms of the tasks it enabled animals to perform, and secondarily described the anatomical features that provide the mechanisms for the execution of the tasks. The classification scheme suggests that photoreceptive abilities have evolved independently in parallel in several lineages of animals, following very similar sequences through up to four stages (see Fig. 2). Photoreceptor evolution is characterized by changes in 4 aspects of visual performance: (1) speed, (2) acuity, (3) [luminance] contrast sensitivity, and (4) spectral sensitivity (Nilsson, 2013). Behavioral advances build upon already existent visual abilities and structures in a predictable sequence of change: lower class photoreceptive behaviors, and their corresponding anatomical and neural structures, serve as pre-adaptations or exaptations for the evolution of new behaviors and structures (Nilsson and Bok, 2017). This is in line with several recent ideas about new behaviors can emerge in a short period of time; for example, neural reuse is the idea that new behaviors can arise by using the existing neurological structures that can provide the necessary computations rather than developing new brain areas (Anderson, 2010; Dehaene and Cohen, 2007).

Nilsson's tree of photoreceptive behaviors shows that the common ancestor of the basal animal lineages (Porifera and Placozoa) lacked opsin-based photoreception, let alone vision (but note that some of their larva are phototactic; Rivera et al., 2012). Vision emerged in a eumetazoan clade in a stepwise fashion (Nilsson, 2013), based on phylogenetic information from Philippe and colleagues (Philippe et al., 2007; Philippe et al., 2009; indicated in Fig. 2A). However, there is a lack of data available for deep metazoan phylogeny due to a lack of fossil evidence, thus it is unclear whether the first animals had photoreception, and/or whether they had neurons. We further explore the pattern of vision evolution in animals using Nilsson's classification of vision given a more recent phylogeny from Moroz and colleagues (2014) who suggest there were two independent origins of nervous systems, in ctenophores and in a clade including bilaterians and cnidarians (indicated in Fig. 2B). According to Moroz and colleagues' phylogeny, photoreception must have arisen at least twice, in ctenophores and in a clade including bilaterians and cnidarians. Yet even in this more complex tree, each clade shows a sequence from no photoreception to stages of increased photoreceptive capacity, and in both clades this is congruent with the emergence of neurons. Placozoans and Porifera are the two animal phyla that have never evolved vision, and do not even have opsin-based light detection. Placozoans and Porifera also lack neurons and muscles (Moroz et al., 2014). However, in all other animal phyla there are member species that have a light-dependent chemical reaction that is coupled to a signaling system, a function which employs opsins (a class of 7-transmembrane proteins), and there are neurons and muscles to provide flexible information processing and behavioral response.

Non-directional photoreception (Class I) is the lowest level of photoreception and is found among the ctenophores (comb jellies), which also have the essentials for sensorimotor function: neurons and muscles. Behaviors guided by this level of photoreceptive input are monitoring the ambient light intensity and functions in circadian rhythm, protection from sunlight (UV/blue radiation), depth control in water, and non-directional shadow detection (Nilsson and Bok, 2017). This type of photoreceptor response, called phototaxis, may also be seen in any organisms with light detection, however such movements do not involve neurons and muscles. For example, Euglena is a single celled eukaryote with an eye spot that can move towards or away from a light source (Wolken, 1977).

Directional photoreception (Class II) characterizes some living deuterostomes and lophotrochozoans. In this kind of light perception, a "directional photoreceptor" is shielded so that it detects light in one direction, but not in any other direction. They have the ability for phototaxis (without spatial resolution), steering toward or away from a surface (if burrowing), body positioning towards a light source, and alarm responses to directional changes in luminance. Example organisms have eyespots that function like this. These include cubozoan planula-larvae that have single cell eyespots assumed to function both as photoreceptor and effector organs, thus affording a behavioral response. Also, polychaete larvae have two-celled eyespots that contain a rhabdom-bearing receptor cell that can resolve the wavelength and polarization of light, and a pigment cell that detects photons.

Low-resolution vision (Class III) involves simultaneous readings of the luminance in different directions, is present in cnidarians and three bilaterian groups. In the natural world this behavior can be achieved with a pit or cup eye. It is limited to low spatial frequencies, and as such can detect whole objects. It also is limited to low resolution light "samples" for big regions of space which is useful for monitoring of self-motion (to control speed and direction of locomotion) and object avoidance. An example organism is the typical flatworm, whose version of a pigment-cup eye is formed by one or a few pigments cells forming a cup around a number of rhabdom-bearing photoreceptor cells.

High-resolution vision (Class IV) has evolved within three of the bilaterian clades with low resolution vision: vertebrates, cephalopods, and arthropods. It enables what are referred to as "advanced behaviors" (Nilsson and Bok, 2017) such as detecting other animals as in pursuit and escape (Proulx et al., 2014; Wang et al., 2013), engagement with other animals in communication, and object manipulation. In all three clades with Class IV photoreception, a complex eye (camera-styles in vertebrates and cephalopods; compound in arthropods) is present and enables vision across far distances.

Eyes do not typically fossilize, so the fossil evidence for vertebrate eyes comes from the mineralized skeleton of the encircling bones, which indicate that vertebrate eyes capable of movement and focus appeared before 400 million years ago (Young, 2008). The most primitive vertebrate eyes are those of the jawless fishes (agnathans), of which two groups survive today, the lampreys and the hagfish. The relationship between hagfish, lampreys and jawed vertebrates remains unresolved, making it difficult to pinpoint the origin of the vertebrate eye. The hagfish "eye" seems not to function in vision; instead, it seems more likely to act only in maintaining the circadian rhythm. As such, it is similar to the pineal complex of jawed vertebrates (gnathostomes), an organ that is absent in hagfish. However, the lamprey's camera-like eye is similar to that of jawed vertebrates, including a lens, an iris and extra-ocular muscles. Given that lampreys and jawed vertebrates diverged 500 million years ago, if the camera-like eye is a shared ancestral characteristic it must be at least that old (Lamb, 2011).

2.2. Measuring visual acuity

Visual acuity is the most readily available indicator of visual performance. In humans, normal vision corresponds to acuity of 20/20. This means a person with this level of acuity can read an eye chart located 20 feet away as well as a person with normal vision would read the same eye chart were it 20 feet away (U.S. Social Security Act, 2006; the metric equivalent is 6/6). Another measure of visual acuity is the cycles per degree (cpd) that can be resolved by the organism. A cycle is a full contrast change, generally depicted as a black stripe next to a white stripe, and the greater number of stripes that can be resolved within a degree of visual angle is a converging measure for visual acuity as such an ability corresponds to higher level abilities such as letter recognition in a standard optician's Snellen test. Importantly this measure using stripes can be more easily assessed in non-human animals by having one response for stripes and another alternative for a uniform gray surface (because stripes that appear too small to be resolved at high cycles-per-degree essentially blur together and the black and white stripes are seen in combination as gray; see Fig. 3). A level of visual acuity of 20/20 corresponds to 30 cpd of visual angle. Uncorrected, very low visual acuity compared to what is normal for humans is considered blindness.

Here we will primarily use the U.S. definition of legal blindness as someone having a best-corrected visual acuity 20/200 or worse, as this is the most commonly used threshold for recognition of a clear visual

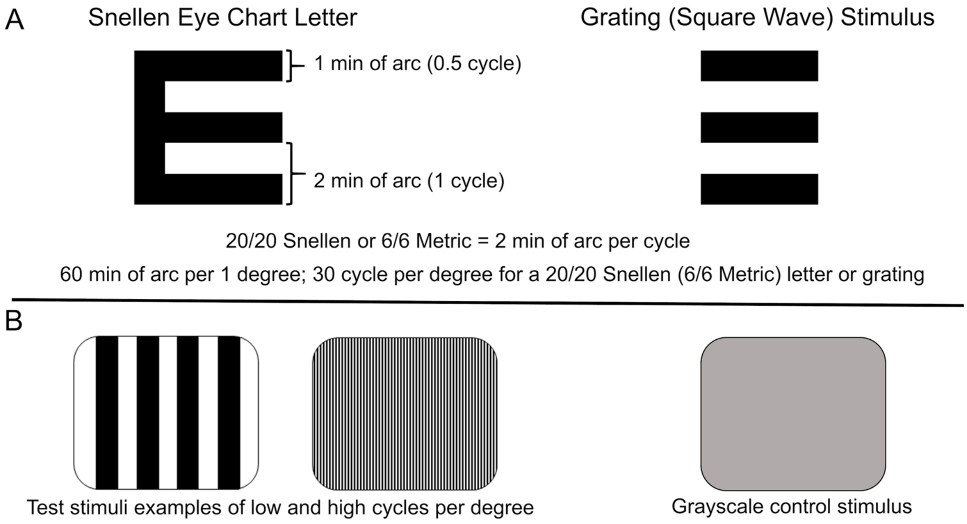

Fig. 3. Illustration of how cycles per degree are measured, and how visual acuity is assessed. (For a comparison of human visual acuity classification schemes see Supplementary Information Table 1).

A. The standard Snell Eye Chart letter E is used with humans. Each horizontal bar of the E is equal to 1 min of arc and corresponds to 0.5 cycles; the equally-size white space between the bars complete one full cycle. The size of the stimulus at 20 feet (or 6 m) is used to assess normal vision by optometrists. Letters are not necessary to assess this. A square wave grating maintains the same properties of the classic Snellen letters without superfluous information (i.e., the vertical bar in the letter E) and can be used to test acuity across different species.

B. An example of how square wave gratings can be used to test visual acuity. The individual being tested must be trained to respond differentially to gray versus stripes, starting with the largest stripes (corresponding to the lower number of cycles per degree). The cycles per degree can be increased until the stimulus can no longer be reliably distinguished from gray. For example, if you are able to see the smaller striped stimulus, stand further from the figure until you can no longer tell it apart from the gray one (to mimic lower visual acuity).

disability (this corresponds to 6/60 in metric and 3 cpd; "Meaning of blindness as defined in the law," 1983). It is worth noting, though, that the World Health Organization (WHO) provides a number of further classifications that might be useful for future consideration of comparative studies of visual acuity in its International Classification of Diseases 11 (World Health Organization, 2018). In humans, one generally distinguishes between low vision and blindness primarily using the visual acuity of the better eye using the best possible correction. In imperial measures and WHO terms, a person is classified as having low vision if they are able to see at 20 feet what a person with normal vision could see at 70 feet (i.e., low vision is an acuity at or below 20/70 vision, a limit corresponding to 8.6 cpd), and a person is classified as blind, even beyond a severe visual impairment, if they are only able to see at 20 feet what a person with normal vision could see at 400 feet (i.e., WHO blindness is an acuity at or worse than 20/400 vision, a limit corresponding to 1.5 cpd; World Health Organization, 2018). Since many forms of visual impairment affect the eye in a non-uniform manner, the ICD also states that those with a visual field of less than 10 ° visual angle should also be classified as blind, and this is more generally thought of as "tunnel vision" due to having a limited field of view. As noted, the definition of legal blindness in the United States specifies an acuity of 20/200 or worse, and also considers a field of view of 20 ° or less.

2.3. *Loss of vision in vertebrates*

A broad understanding of vision loss can be gleaned from the diversity of vertebrate species that share this feature. These species provide numerous convergent examples of vision loss and vision evolution which could be used in powerful investigations into the relationship between these features and other behavioural, cognitive, and ecological traits (Jourjine and Hoekstra, 2021).

Extreme reduction or total loss of visual function that is linked to extreme reduction or loss of the eye (hereafter, "species blindness" affecting "blind species") occurs in most vertebrate groups including cyclostomes, teleosts, amphibians, and reptiles (Rochon-DuVigneaud, 1943). Species blindness typically occurs in species that live in caves, murky water, or underground, and are represented in many taxonomic groups. Blind species show an extreme reduction in eye function, and their anatomy is indicative of Class I or II photoreception at most, rather than vision. Yet, unlike pre-sighted species, blind species exhibit an array of behaviors, including some of those defined as "advanced behaviors" even in vertebrates with high-resolution vision (Class IV). Some examples of blind vertebrates are described here.

Blind cavefish are among the best studied blind vertebrates but are exceptional since they differ from sighted surface fish populations of the same species, *Astyanax mexicanus,* at the *population* level, and the two are capable of producing fertile, eyed offspring (Ojha and Watve, 2018). Blind cavefish completely lack bilateral eyes due to the apoptosis of developing retinal cells and thus lack vision (Rétaux et al., 2016) yet retain a structurally intact pineal eye that functions in shadow detection behavior (Yoshizawa and Jeffery, 2008). Blind cavefish show dramatic differences in behavior compared to surface fish, such as a loss of shoaling, schooling and aggressive behavior, related to loss of visual detection of conspecifics. These factors seem to be related to very different strategies in the variants of this species dependent on their different environments. For cavefish, food is particularly scarce, so they more actively seek food and show increased olfactory sensitivity (and larger olfactory structures). Further assistance in energy conservation come from reduction in brain size in cavefish compared to surface fish (Moran et al., 2015). Group behavior lacks the same benefits: predation risk is low so it is not helpful to shoal or school (Yoshizawa, 2015). Females show reduced (although not eliminated) selectivity for larger males, suggesting that, in the absence of vision, less informative mechanosensory cues are relied upon (Yoshizawa, 2015).

The bilateral eyes and pineal organs of aquatic blind European cave salamanders, also known as olms (*Proteus anguinus*), are regressed, but both contain light-sensitive photopigments – as does their skin (Kos et al., 2001). *Proteus anguinus* shows several potentially compensatory specializations of other senses, including excellent directional underwater hearing and the detection of magnetic fields (Schlegel et al., 2009). Further, they can detect prey and communicate socially to attract mates by chemical signaling to a greater extent than sighted surface-dwelling amphibians (Schlegel et al., 2009).

Another group of blind amphibians are the caecilians, comprising nearly 200 species of the cryptic taxonomic order Gymnophiona that are limbless due to being fossorial or stream dwelling (Wilkinson et al., 2011). They have rudimentary eyes that are covered in skin and sometimes bone, which contain only rod opsin (Rhodopsin) - visual pigments suitable for photon detection in low-light conditions with low resolution, and lack evidence for photopic vision (Mohun et al., 2010). These animals rely heavily on olfaction and have tentacles that work as a second olfactory organ (Wilkinson et al., 2011). Much is unknown about this order, which displays quite a bit of diversity, but as a group they show interesting social behaviors. Caecilians are the only amphibians that reproduce via internal fertilization (Wake, 1992), and there is parental investment by maternal skin-feeding (Kupfer et al., 2006; Wilkinson et al., 2008).

Similarly, snakes' limbless morphology and poor vision are thought to be due to their fossorial ancestry of burrowing behavior, and more extreme fossoriality seems to have led to further losses in the "blind snakes" of the infraorder Scolecophidia such that they only retain the rod opsin visual pigment (Simoes et al., 2015). The tiny brahminy blind snake (*Indotyphlops braminus*) is completely fossorial and can be mistaken for an earthworm. Its eyes are reduced in size and lie under translucent scales. This is the only species of snake that is obligatorily parthenogenetic; that is, all individuals are females and reproduction is asexual (Nussbaum, 1980).

Exceptionally, there are no blind species of birds. No birds are dedicated to fossorial living and although cave-nesting birds can echolocate, they depend on habitats outside the caves and rely on vision over echolocation (Jordan Price et al., 2004). Birds are also the taxonomic class of animals with the highest visual acuities. A recent study estimated a minimum of 4 cpd for the nocturnal Western barn owl (*Tyto alba*) –- due to a tradeoff for relatively high visual acuity under low light (Orlowski et al., 2012); and a maximum of 138 cpd for the wedge-tailed eagle (*Aquila audax*) – the highest for any animal (Caves et al., 2018). Moreover, several eagles, vultures, and falcons have visual acuity equivalent to humans and chimpanzees, and, in fact, these are likely to be low estimates as much is yet to be understood about the structure and function of bird foveae (Bringmann, 2019; Coimbra et al., 2014).

Given the high importance of vision in birds, those cases of reduced vision in birds might be particularly useful to understanding the evolutionary pressures involved in vision loss; unfortunately, there is a dearth of data on this topic. The transition to nocturnality in birds may affect the visual system by either increasing visual sensitivity for low light (i.e., large pupillary aperture, rod-dominated retinae) or by reducing visual function in favor other senses (Martin et al., 2007). While the former is observed mainly in nocturnal flying foragers (e.g., owls, nightjars), the latter is seen in island dwellers like kiwi, kakapo, moa, and elephant birds. Therefore, reduction of vision in birds seems to be an adaptation of flightless species in habitats with abundant food sources and lacking predators, observed mainly on islands. In fact, it seems that a combination of external factors and subsequent predictable changes in daily behaviors (potentially limited to the developmental biases in given taxa) mark a pathway for visual reduction and eventual vision loss in some species without any costs on survivability and reproduction.

The flightless, nocturnal kiwi (*Apteryx*) presents a real-time example of vision reduction which can be used to understand evolutionary pressures involved in vision loss. Among avian species, kiwi have the smallest visual fields, a very narrow binocular field, the smallest eyes relative to body size, and extremely reduced visual brain areas (Martin et al., 2007). The fact that kiwi are nocturnal but nonetheless have very small eyes is an indication that the species has not undergone selection for night vision. This might present a unique case of adaptive regressive evolution, where the reliance on eyesight became obsolete and instead of adapting for the activity period, the entire visual system (including eye and brain regions) is no longer under selection and has become nearly vestigial. A recent survey of 160 free-living Okarito kiwi (*Apteryx rowi*) found that one-third of the birds had ocular lesions in one or both eyes, while some of them have been shown to be completely blind; These birds were in good physical condition, subsequently survived for at least 4 years and were successful in mating (Moore et al., 2017). This suggests that vision might not be necessary in the ecological niche of these animals and it might be used as an example of adaptive regressive evolution. Several non-mutually exclusive hypotheses have been put forth to explain the reduced vision of kiwi. The first explanation suggests that vision in kiwi is a remnant from a common ancestor (the moa) which relied on vision for avoiding predators. As kiwi virtually lack any predation pressure their survivability is not affected by their lack of vision. A second explanation points to kiwi's high energetic devotion to other sensory systems: auditory, olfactory, and tactile (they have unique tactile mechanoreceptors at the tip of their bill; Cunningham et al., 2009). Kiwi do not rely on their visual system for foraging or pray detection, while relying more on olfaction and tactile perception. Vision might be used exclusively for detecting circadian light-dark periodicity and determining suitable periods for foraging. A third explanation is also related to kiwi's ecological niche: It might be that the combination of food availability, low resource competition, lack of predation, and auditory reliance for mate recognition has created conditions allowing survivability of blind or visually impaired individuals that would not necessarily lead to adaptation per se. In that respect, the combination of ecological and social circumstances allowing that survivability can be thought of analogous to the human condition in some ways. Similarly, the recently extinct Malagasy elephant birds (Palaeognathae, Aepyornithiformes), the largest flightless birds that ever lived, were shown to have disproportionately small visual areas and quite large olfactory bulbs, inferred from digital reconstructions of endocasts from two species – *Aepyornis maximus* and *Aepyornis hildebrandti* (Torres and Clarke, 2018). To our knowledge, this is the only living example of a species undergoing this process and as such this case of a flightless, nocturnal bird losing vision provides a unique opportunity to study the evolutionary conditions and behavioral and physiological mechanisms that eliminate a reliance on visual information for survival and reproduction. This example can be compared to the reduction in vision and concomitant reliance on touch and smell in rodents (Martin and Osorio, 2010).

3. Origin and loss of vision in mammals

3.1. *Comparative vision in mammals*

Thus far we have used specific cases to illustrate how vision and vision loss relate to the tasks animals can perform. These relationships between the function of vision and "vision -substituting senses" and the tasks in animal can perform can also be tested quantitively provided sufficient comparative data. Phylogenetic comparative methods use information about species evolutionary history to test hypotheses about evolution. Here we explore how these can test hypotheses about the origin of widely available metric, visual acuity, in mammals generally and specifically in humans. Thus, we demonstrate how it is possible to consider human vision in the context of other mammals who share much of their evolutionary history. This context reveals the relationship between vision in humans and vision in mammal species used as models in translational research. We first demonstrate how phylogenetic comparative analyses can be used to examine the evolution of vision and vision loss. We then describe some of the most extreme cases of vision loss and vision evolution in mammals, including humans.

We investigated visual acuity in mammals, using estimates from behavioral tests or, when not available, calculated anatomically based on peak density of ganglion cells, obtained from published studies and compilations (Heffner and Heffner, 1992b; Heffner et al., 1999, 2008; Kirk and Kay, 2004; Veilleux and Kirk, 2014). Note that the research methods are unevenly distributed across the phylogeny, with some clades disproportionally represented by anatomical or behavioral data ($\chi^2 = 116.59$, df = 34, $p < .0001$) so future research providing both measures in all clades would be beneficial for linking structure and function (Supplementary Information File 1 and Supplementary Information Table 2). Visual acuity in these 114 species (all with some vision) ranged from 0.10 cpd in the microbats to 64.28 cpd in the chimpanzee (with humans at 64 cpd), with a mammal visual acuity median of 3.80 cpd, and a mean of 8.86 cpd (95 % CIs [6.20, 11.51]). All mammal species (except chimpanzees) have lower visual acuity than what is considered normal for humans. In this dataset, 64 (56 %) species have a level of visual acuity, that is in the range of "sighted" (including low vision) humans, and 50 (44 %) have visual acuity in the range of legally blind humans (i.e., 3 cpd or less).

To demonstrate how to investigate what ancestral mammalian vision was like, and how different clades deviate from this, we used a time-scaled mammalian tree generated by TimeTree (Kumar et al., 2017) to infer the evolutionary history of species' visual acuity to compare different groups in terms of their i) ancestral states (Fig. 4) and ii) rates of evolution (Fig. 5; see Figure legends for information about the methods used to create them). For these analyses we included a total of 120 species: 114 species for which visual acuity had been estimated, plus 6 species with subcutaneous eyes for which the visual acuity was coded as 0 cpd (see Supplementary Information File 1 for values; Fig. 4). Comparable data were only available for mammalian species, so the ancestral state reconstruction was conducted for the therian mammal clade (non-egg-laying mammals, which include placental and marsupial mammals), with the monotreme clade (egg-laying mammals) treated as an outgroup. The dataset is limited to extant taxa because similar data were not available for fossils, although such data would have improved the temporal precision of the estimate.

The ancestral state analysis (using maximum likelihood) predicted that the ancestral visual acuity of the therian clade was 4.49 cpd (Fig. 4). Several clades of placental mammals show increases in visual acuity from the predicted placental ancestral state (value: 6.23 cpd), including the primates, ungulates, and carnivores. Low visual acuity seems to be a primitive feature in marsupials (Todorov, 2020). In addition, several clades show increases in visual acuity followed by secondary reductions: major clade: rodents, bats; minor clades: cetaceans, strepsirrhines, arctoid carnivores.

When assuming that vision evolves through a process similar to Brownian motion (i.e., random evolutionary change, a common assumption in evolutionary biology), our analysis indicates that in Chiroptera (bats) and Rodentia (rodents) the rate of evolution has slowed down (Fig. 5). This implies that these lineages had adapted to environments with low requirements for visual acuity early in their evolutionary history and their vision has is not changing at the expected background level. Opposite to that, in haplorrhine primates (simians and anthropoids) the rate of Brownian motion had increased, indicating a recent (in evolutionary terms) exploration of ecological niche, which demands rapid improvement of vision (probably related to frugivory, predator detection etc.).

3.2. Vision loss in mammals

Among mammals, no species lacks eyes entirely, and all species retain vestigial visual structures with some sort of non-visual photoreceptive function. Blind species of mammals refers both to those that are microphthalmic and those who, in addition to being microphthalmic, have fused eyelids and subcutaneous eyes. Microphthalmic mammals ("eyes less than 2 mm"; Cooper et al., 1993b) include the echolocating microchiropteran bats, several species of insectivores and aquatic shrews, the bathygerid Ansell's mole rat (*Fukomys anselli*), and the blind river dolphins (*Platanista gangetica*; Cooper et al., 1995).

As demonstrated by Figs. 3 and 4, all eutherian (placental) mammal species that are considered blind belong to clades characterized by a reduction in visual acuity compared to the ancestral therian mammalian condition. For example, most rodents with some vision have low visual acuity (median 1.7 cpd) ranging from 0.4 cpd in the Transcaucasian mole vole to 6.21 cpd in the red-rumped agouti. Behavioral studies show that the visual acuity of rodent translational models is especially low: in mice it is 0.5 cpd, and in rats it is 1 cpd (Prusky et al., 2000). Several rodents show reductions in visual acuity in line with fossoriality, such as the bathyergid mole-rats, range 0.3–0.5 cpd (anatomical estimate), and mole-lemmings, range 0.4–0.9 cpd (anatomical estimate).

Other senses may serve a role in functions formerly of the visual system. Echolocation is the ability to locate objects, a task also related to vision (i.e., Class III photoreception), using auditory information; It is found among clades that host microphthalmic species such as bats, cetaceans, and shrews (Buchler, 1976). Bats and cetacean have the best high frequency hearing of any mammals, which is important for sound localization (Heffner and Heffner, 2018). Microchiropteran bats have specialized sound-emitting laryngeal sonar and central nervous system adaptations related to echolocation (Corcoran and Moss, 2017). Most

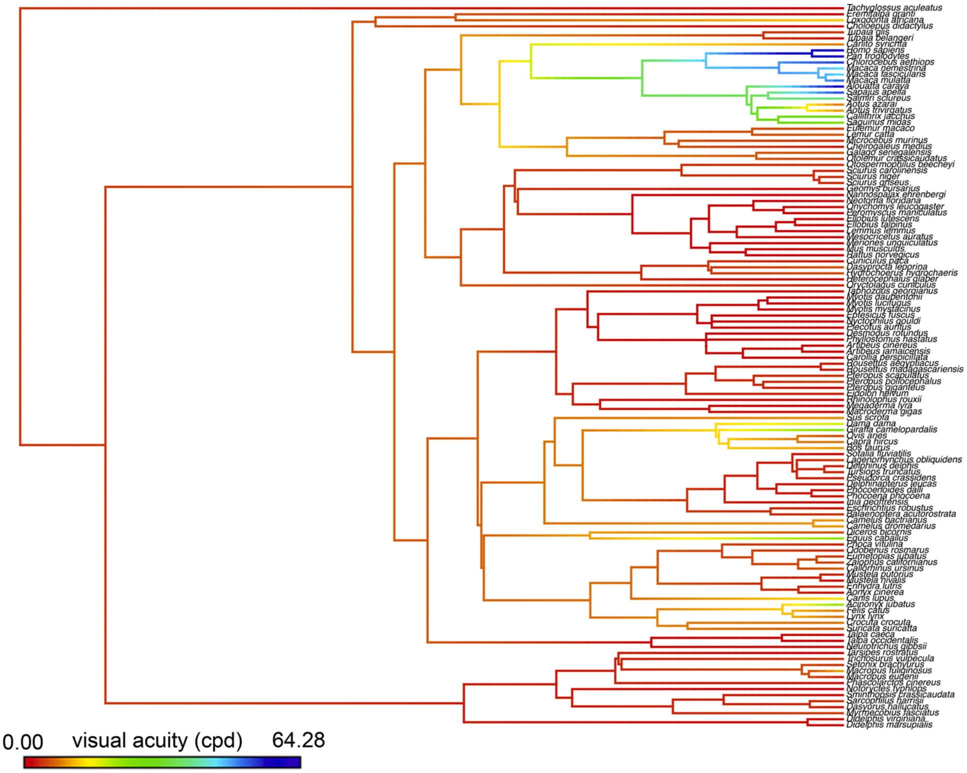

Fig. 4. Phylogenetic tree showing ancestral trait estimation of visual acuity of therian mammals. The prototherian species *Tachyglossus aculeatus* is the outgroup. Chronogram (phylogenetic tree where branch lengths represent absolute time) generated by TimeTree (Kumar et al., 2017). Ancestral character estimation using maximum likelihood in the R package phytools. This estimates the evolutionary parameters and ancestral states for Brownian evolution (random change). The reconstruction is based on visual acuity measurements for 114 mammal species plus 6 species without vision (see text for details). Note that from four different mammalian orders there are six species assumed here to have "zero" visual acuity: from Rodentia blind mole rats (*Nannospalax ehrenbergi*), from Afrosorcida golden moles (*Eremitalpa granti*), from Notoryctemorphia marsupial moles (*Notoryctes typhlops*), and from Eulipotyphla true moles and shrews (*Neurotrichus gibbsii*, *Talpa occidentalis, and Talpa caeca*). (See Supplementary Information File 1 for data and code).

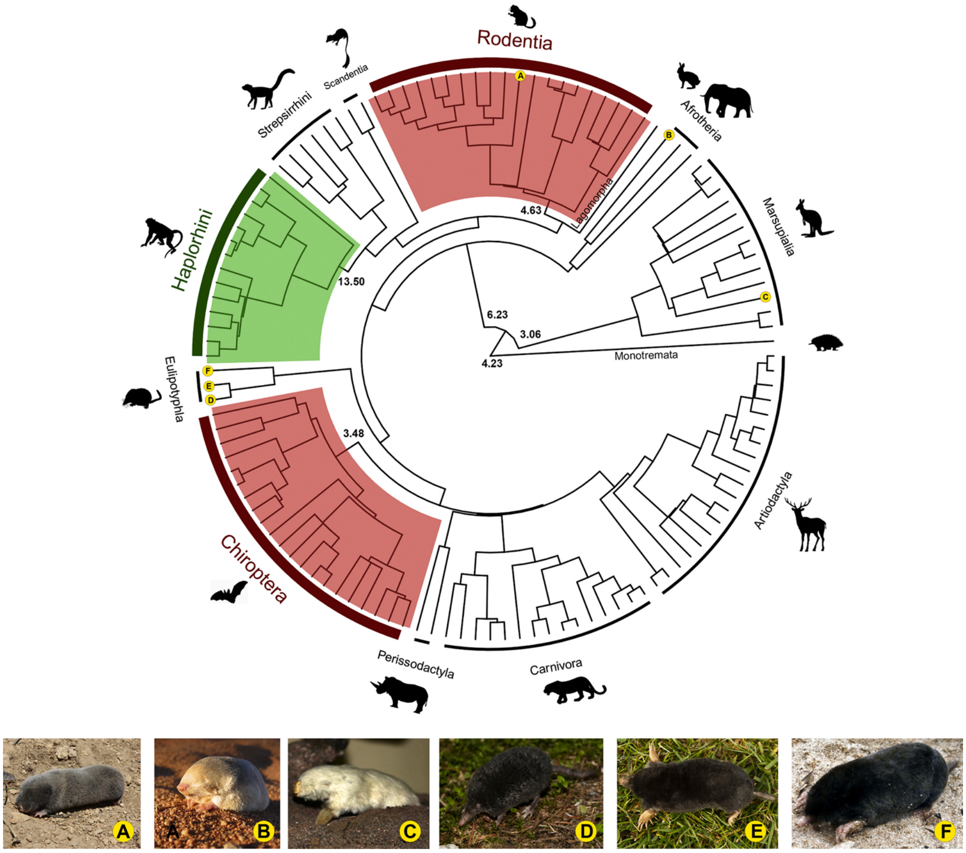

Fig. 5. Phylogenetic tree showing shifts in the rate of evolution. Green indicates increased rate of evolution, red indicates decreased rate of evolution. Data and tree are the same as in Fig. 4. Ancestral character estimation calculated from branch lengths and evolutionary rates of change in visual acuity in the R package RRphylo. Images below of naturally blind mammal species with fused eyelids, A. *Nannospalax ehrenbergi*, B. *Eremitalpa granti*, C. *Notoryctes typhlops*, D. *Neurotrichus gibbsii*, E. *Talpa occidentalis*, F. *Talpa caeca.* (See Supplementary Information File 2 for image sources).

microchiropterans use echolocation for orientation, detecting prey and localization. However they also use visual guidance in these behaviors, and when echolocation and vision provide conflicting cues, visual cues are preferred (Chase, 1983; Orbach and Fenton, 2010). Microchiropterans have massively enlarged auditory cortical areas in the brain (Metzner, 1991) but there is major gap in the knowledge of their visual systems, particularly the visual cortex. The advanced auditory abilities of both cetaceans and bats seem to also have been co-opted for social functions. In particular, the underwater acoustic environment of cetaceans has proved a good transmitter for communication for social and sexual functions (Janik, 2014). It is also interesting that both bats and cetaceans are among the few groups of mammals in which some species have demonstrated a capacity for vocal learning, the ability to imitate the vocalizations of conspecifics (Jarvis, 2019).

The blind river dolphin (*Platanista gangetica*) is a toothed whale and lives in the murky water of the Ganges river, and is comprised of two different subspecies, susu (*Platanista gangetica gangetica*) and bhulan (*Platanista gangetica minor*). The residual eye of the blind river dolphin is not image forming due to atrophy of the lens and is mostly covered by darkly pigmented skin, but it has a pinhead sized opening for light. It seems to be capable of light detection, and possibly directional photoreception only (Herald et al., 1969; Pilleri, 1979). The retina of the blind river dolphin is relatively small for an odontocete (toothed whale) but has the typical laminar structure (Dral and Beumer, 1974; Purves and Pilleri, 1973). The blind river dolphin neocortex is unusual for a odontocete: the visual cortex is restricted in size and could have been “taken over” by adjacent auditory cortex, and exceptionally the visual cortex has a lower neuron density than the auditory cortex in layers III and IV (Knopf et al., 2016). The blind river dolphin has echolocation (biosonar detection) in which it emits lower intensity sounds and higher repetition rates than oceanic odontocetes, possibly due to the high amounts of clutter and echo in the shallow river habitat (Jensen et al., 2013). The blind river dolphin also uses clicks an octave lower than in similar sized odontocetes, and have bony maxillary crests which may contribute to intra-aural distance and achieve a better low frequency sound location ability (Heffner and Heffner, 2016; Jensen et al., 2013). As is the case for other odontocetes, click vocalizations are used primarily for echolocation in wayfinding and foraging for prey (Jensen et al., 2013), and to a much lesser extent, in communication (Mizue et al., 1971). Blind river dolphins live individually or in groups of up to 10 individuals (Baki et al., 2017). Unusually for odontocetes, blind river dolphins have a form of vibrissae which may provide tactile sensation to detect prey (Drake et al., 2015).

Mammalian species with fused eyelids, in which the entire eyes are subcutaneous, are limited to four distantly related groups that have limited exposure to light because they are subterranean: spalacids (rodents), talpids (soricomorphs), chrysochlorids (afrotherians), and the genus *Notoryctes* (marsupials) (Fig. 5). In these species, it has been suggested that there are adaptive pressures for eyes to be covered and reduced in size because they pose a problem for subterranean locomotion (Begall et al., 2007). To permit a systematic comparison across a wide variety of species we classified these species as having "zero" visual *acuity*, but should be noted that spectral sensitivity (color vision) also contributes to visual *ability*. There is much yet to be determined about the possible diversity and functionality of photopigments in vision, and a capacity for "photopic vision" has been suggested for some taxa with fused eyelids (e.g., *Talpa*, (Glosmann et al., 2008).

The best studied example of a naturally blind mammal with total lack of vision (Class 1 photoreception) is the Middle Eastern blind mole rat, a spalacid mole-rat. Note that spalacid mole rats are a separate family of rodents from bathyergid mole rats, so although both present convergent features related to fossoriality such as magnetoreception, they also differ in terms of visual structures and sociality. For example, photopic vision has been documented in bathyergid mole rats which have microphthalmic but not fused eyelids (Caspar et al., 2020; Kott et al., 2010). The genus *Spalax* in fact includes several other species, collectively known as the blind mole rats. It is the Middle Eastern blind mole rat *Nannospalax ehrenbergi* (previously referred to as the *Spalax ehrenbergi* "superspecies" which has since been further subdivided into several species; Nevo, 2011) in particular which has been studied for decades by E. Nevo at the University of Haifa. Features of the visual system are reduced in size and function, but all visual structures of the brain and eye are present, and some of these serve in circadian photoperiod functions (Pevet et al., 1984). The retinae are minute (less than 1 mm) (Cooper et al., 1993b), the optic nerves are small in diameter (50–80 μm) (Nemec et al., 2007) and each comprised of only about 1000 unmyelinated axons (<1% the number axons in a rat's optic nerve) (Bronchti et al., 2002). In the newborn, retinofugal fibers enter the dorsal lateral geniculate nucleus (dLGN), however over 90 % of these fibers pruned in *Nannospalax ehrenbergi*, versus 50 % in sighted rodents. Compared to hamsters and rats, the adult LGN and Area 17 (V1) are reduced in size (Cooper et al., 1993b). On the other hand, features of the eyes which serve photoperiod functions are enlarged. The IGL of the dLGN is involved in circadian rhythms and is enlarged (Cooper et al., 1993b). *Nannospalax* eyes function in entrainment of circadian rhythms and contain a fully functional photopigment, the cone opsin LWS (David-Gray et al., 1999, 1998). There is also an enlarged a gland in the eyes used to groom fur, the Harderian gland (Cooper et al., 1993a).

The absence of vision has also been thought to enhance processing of other animal senses. Such a shift could in some cases lead to achieving tasks better than when constrained to vision. Blind mole rats show several forms of cognitive enhancement involving nonvisual senses. They seem to have a knack for spatial navigation unusual for rodents. They outperform laboratory rats and Levant moles in having both faster learning and longer memory duration for a maze (Kimchi and Terkel, 2001b). Interestingly, in spite of the aforementioned reductions in size of visual brain structures, the brain of *Nannospalax ehrenbergi* is larger than that of a laboratory rat, even though it has a body just half the size (Frahm et al., 1997). Although regions involved specifically in vision and audition, such as the superior and inferior colliculi, are larger in rats, most regions of the brain are larger in *Nannospalax ehrenbergi,* including the olfactory bulb, hippocampus, cerebellum, thalamus, neocortex, somatosensory cortex, and motor cortex (Frahm et al., 1997; Mann et al., 1997; Rehkamper et al., 1994).

There is debate over which senses "take over" in the absence of vision. Bronchti and colleagues (Bronchti et al., 2002, 1989; Heil et al., 1991) argue that audition takes over the visual pathway in subterranean mammals. Supporting this notion is experimental data from auditory take-over of visual pathways in ferrets (Pallas and Sur, 1993; Sur et al., 1990). However, unlike in experimental animals, in the blind mole rat the visual pathway provides an *additional* rather than *alternative* pathway for auditory inputs. In neonatally enucleated hamsters auditory information is conveyed along the visual pathway (Izraeli et al., 2002). In the anophthalmic mutant ZRDCT/An mouse, auditory information is conveyed along the visual pathway.

Nevo argues that only the somatosensory sense takes over visual cortex function in *Nannospalax ehrenbergi* (Nevo, 1999). The relatively large brain of *Nannospalax* has been attributed to the increased sizes of brain components with somatosensory function (Mann et al., 1997). *Nannospalax ehrenbergi* have the poorest known hearing of any mammal: they cannot locate sounds that are emitted for less than 0.5 s, and they also have the smallest auditory range, linked to having the lowest sensitivity for high-frequency sounds (Heffner and Heffner, 1992a). Also, tonotopy (the spatial arrangement of where sounds of different frequency are processed in the brain) is only one dimensional, so would not naturally take over the organization of V1 which is retinotopic and two dimensional. This might pose problems for re-mapping of sensory function given existent neural architecture (Dehaene and Cohen, 2007). However, it should be noted that the environment of fossorial mammals is best characterized as one-dimensional (Heffner and Heffner, 1992b), so even spatial behaviors might rely on a different mapping than that supported normally by vision.

Other senses also play important roles in the spatial and social behavior of *Nannospalax ehrenbergi.* They rely on species- and sex- specific olfactory cues as they are very aggressive with conspecifics (particularly males) and scent-mark territory boundaries to prevent interactions (Zuri et al., 1997). In addition, *Nannospalax ehrenbergi* use magnetoreception in spatial orientation as a primary mechanism of short and long distance orientation (Caspar et al., 2020; Kimchi and Terkel, 2001a).

It is important to note that most of the species described here are only poorly known. The environmental factors that led to vision deprivation also led to animals being difficult to uncover and observe. However, these animals provide important clues about how the mind works, and we hope to draw attention to their potential to enlighten.

3.3. *Primate vision*

Primates stand out among mammals for their unusually advanced vision, and humans are among the most visual of all primates, particularly in terms of acuity and contrast sensitivity (Ridder et al., 2019; Adams et al., 2017). Primate visual acuity ranges from 2.84 cpd in fat-tailed dwarf lemur (*Cheirogaleus medius*) to 64.28 cpd in chimpanzees (*Pan troglodytes* based on Spence (1934)); but note that due to methodological and individual variation this may not actually be higher than in humans), with a median of 17.44 cpd. Advances in visual ability are considered to be primate specializations, and early primates are thought to have been arboreal visually guided predators who used their dexterous hands in hunting (Ross and Kirk, 2007; Cartmill, 1992). Several primate lineages show increases in spectral sensitivity from a likely dichromatic ancestral state, notably the catarrhines which are all trichromatic. Also, large-bodied catarrhines have the highest visual acuity of all primates (de Sousa and Proulx, 2014), with humans and chimpanzees ranking as the mammals with the highest visual acuity. There are also several features of higher-level vision that are shared and derived (synapomorphies) in primates. Trends towards increasing binocular vision, linked to orbital convergence, are seen in convergent primate lineages, including the catarrhines. This change is related to expansions in visual brain structures in size and neuron number (Barton, 2004). In all primates examined, visual cortical regions have neuron numbers higher than the cerebral cortex average (Collins et al., 2010). In macaques, the most neuron-dense region, V1, has an average of 177 million neurons/g, which is over four times as much as the cortical average of 37 million neurons/g (Collins et al., 2010) and cerebral cortex that is predominately visual in function covers 52 % of its surface area in macaques, and 27 % in humans (Van Essen, 2004). Visual inputs play an important part in other derived aspects of primate brain structure, including subcortical structures (de Sousa et al., 2013), visual cortex cytoarchitecture (de Sousa et al., 2010b), surface organization and convolutions (de Sousa et al., 2010a), and higher-level cortical areas involved in social learning and tool use (Todorov and de Sousa, 2018). A particularly interesting feature of the primate brain are mirror neurons, involved both in hand actions and in visually perceiving the action conducted by another being, which are motor neurons in F5 of the premotor cortex that is connected also with the posterior parietal multisensory hand area AIP (Rizzolatti et al., 1996). F5 is best known as a hand motor area and AIP functions in tool use – its coordinates extend to incorporate a tool in one's own peripersonal space. Also neurons of the multisensory face area (ventral intraparietal area, VIP) with connections to F4 are active both in perceiving an object approach (visually or by touch) a specific coordinate on an own animal's own face and seeing an object approach the mirrored coordinate on the face of another (Ishida et al., 2009). Primates also show adaptations for processing visual cues for conspecific visual recognition ability, particularly about the face and anogenital regions (Kanwisher et al., 1997; Kret and Tomonaga, 2016).

The evolution of vision in primates seems to have had profound effects on the evolution of other senses. In primates (and other groups of mammals) visual ability has coevolved with auditory ability. Species with good sound localization ability also have narrow fields of best vision (foveae), and from this it has been inferred that sound localization ability exists to assist vision by guiding an animal's eyes to focus on the source of the noise (Heffner and Heffner, 1992b). Primates have good sound localization ability compared to most other mammals (Heffner, 2004). Humans have the best sound localization ability of primates, and among mammals are only outranked by cetaceans (Heffner and Heffner, 2016). On the other hand, visual ability in primates has been proposed to be inversely related to olfactory ability (Gilad et al., 2004) but this relationship is disputed (Gilad et al., 2007; Matsui et al., 2010; McGann, 2017).

No primate species could be considered blind, but there seem to have been evolutionary tradeoffs between different aspects of visual functionality. Dichromacy and nocturnality were likely ancestral conditions for primates, yet three nocturnal groups of primates, dwarf lemurs, lorises and galagos, and owl monkeys, all developed monochromacy as a result functional loss of the short wavelength opsin gene (Jacobs et al., 1993, 1996; Tan and Li, 1999). Importantly these taxa show increased eye size and demonstrate a tradeoff in spectral and contrast sensitivity, demonstrating a shift in functional priorities rather than a loss of visual functionality. Indeed, the evolution of pigments suggests that both trichromacy and dichromacy are positively selected for (Yokoyama and Takenaka, 2005).

4. Summary and future directions

There are convergent patterns and clade specific trends in the evolution of visual loss in the species described here which may give insight into vision loss, and translational research linking animal models to humans, more generally. We review them here and recommend future research directions.

1) **Vision loss has occurred in lineages where visual acuity is relatively low, and there is strong dependency on other senses.** Example blind and microphthalmic vertebrates reviewed here belong to clades where vision is low, such as snakes, cetaceans, and rodents. In the ancestral state reconstruction, the subterranean blind species with subcutaneous eyes all belong to clades with low visual acuity. Future research could estimate how likely blind species are to emerge from clades characterized by low dependency on vision and greater dependency on other senses.

2) **In the vertebrate groups with highest visual acuity, birds and primates, there is no species with a complete lack of vision.** The kiwi presents an opportunity to study vision loss and helps to reveal factors that can lead to vision loss in a bird; Such an exceptional case might highlight the extent of phylogenetic constraints on vision loss. However, more often within birds and primates, trade-offs between different visual features seem to have occurred. For example, nocturnal owls and owl monkeys have relatively reductions in highest visual acuity and color vision, and this has been linked to better acuity in low light. Future research could identify what ecological constraints prevent the emergence of blind species, in particular by comparing primates to birds.

These first two points have relevance for the animal models that are often chosen for the study of visual impairments for human visual health. For example, there are many rodent models of induced impairments (Piche et al., 2007) and many naturally occurring impairments in canine models (Bunel et al., 2019). The species in these studies generally have much poorer visual acuity than humans. Using phylogenetic targeting (MacLean et al., 2012) could be an approach to elucidate what occurs when a blind species emerges from a clade that otherwise has good visual acuity, and provide unique insights on sensory compensation arising from environmental and other constraints.

3) **Visual loss is related to the enhancement other senses, and the extent to which other senses are represented neurologically.** Vision is a particularly neurologically demanding sense. Future research could investigate whether the evolutionary loss of visual function enables the brain to improve the processing of other senses by redelegating neural structures and networks to other senses. There is extensive evidence for compensatory plasticity in blind individuals, such that the other senses have increased sensitivity due to increased use (Kupers and Ptito, 2011), though it has also been theorized that the high plasticity of the visual cortex is essential for these enhancements (Merabet and Pascual-Leone, 2010; Pascual-Leone et al., 2005).

From this perspective, the many sensory capabilities observed in non-human animals with poor vision might suggest novel approaches to assisting visually impaired humans (Porter and Sumner-Rooney, 2018). One option could be to mimic animals like bats and their use of sonar and echolocation to assist with a task like distance perception and obstacle avoidance; indeed, echolocation has inspired approaches both technological such as the EyeCane (Maidenbaum et al., 2014) and behavioral such as training humans to echolocate (Thaler and Goodale, 2016), with echolocation being found to rely on the visual cortex in humans with blindness (Thaler et al., 2011). An evolutionary approach can provide a new perspective, new data, and new inspiration for how to assist those with sensory impairments; It can also reveal potential ethical concerns if such approaches were used for sensory enhancement rather than just sensory rehabilitation (Almeida and Diogo, 2019). The human mind's potential to create experience ranges beyond the capacities of its sensory organs, and this suggests great potential for non-invasive forms of vision restoration such as sensory substitution (Proulx et al., 2015) for assistance when the current standard ophthalmological care has reached its limits. This comparative approach also provides a new approach to developing assistive technology for the visual impaired, as applications need not be human-like, and the most successful approaches might arise elsewhere in the evolutionary tree.

Understanding this might be especially useful in the development of sensory substitution devices that translate information from a format used normally by an impaired sense into a format that an intact sense can process instead. For example, such a device, "The vOICe"(OIC for "Oh I see") turns images into sounds that still contain the spatial information contained in a grayscale image by scanning an image from left-to-right and turning each column of pixels into frequencies (Meijer, 1992). Lower pixels are represented by lower frequencies, and higher pixels by high frequencies; horizontal location is relayed by stereo tuning if using two earphones or by the timing of the scan from left-to-right (Proulx et al., 2015). Other sensory substitution devices turn an image into something that can be touched, such as the BrainPort that uses electrical stimulation on the tongue (Bach-y-Rita and Kercel, 2003). Which sense is the best to substitute for impaired vision? There are general considerations in terms of the amount of information that needs to be presented (Brown et al., 2014) and the spatial resolution that can be provided (Haigh et al., 2013). Considering sensory systems from an information theoretic perspective, such as calculating information processing capacity in bits per second for the human eye (Jacobson, 1951), ear (Jacobson, 1950), and in evolutionary studies of the different classes of vision (Nilsson, 2013), reveal the interdisciplinary interest in the challenge of accounting for the high capacity of vision by the other senses or by technology. Yet this review notes that the nature of the task that requires sensory information might be more crucial than which sense is used. Therefore, the aim instead could be to determine which sense is the most appropriate substitute for impaired vision and the tasks normally carried out visually.

4) **Blind species in the most restricted environments often show extremely reduced social behavior.** For example, blind cave fish and blind mole rats have very few social interactions, although eyed cave fish and other rodents live in groups. Further research into these species could pinpoint whether solitary behavior is linked to total vision loss or rather the confounding factors of a restricted environment.

5) **In non-fossorial mammals, where there is vision loss but animals are in a habitat that can sustain interaction between conspecifics, hearing increases in dominance, and complex social**

behavior has become more auditory. Cetaceans and bats are two groups of mammals with decreased visual demands, but specialized auditory abilities with social functions such as vocal learning. Future research could test evolutionary trends in the appearance of auditory-related behaviors such as communicative vocalizations and echolocation, in particular in less well known species such as in the microphthalmic river dolphins and other visually deprived species who live in groups. The environment, in part, constrains the senses that become dominant or that compensate. Simply lacking a particular sense such as vision need not be a disability per se (Goering, 2015), and the dominance of other senses arises in an environment that affords their use. This can give rise to a perspective of considering biologically-inspired solutions for universal or inclusive design (Lloyd-Esenkaya et al., 2020) to avoid the lack of a sense becoming disabling.

6) **Several species of mammals are considered blind, but none show complete loss of visual structures.** Visual brain structures, including V1, persist even without vision, but change in relative size. In primates in particular, visual functions integrate with audition, somatosensory, and motor functions in higher level cognitive processes. Future research could use phylogenetic comparative models to systematically investigate the diverse sensory and ecological factors, and phylogenetic constraints, guiding the evolution of visual brain structures across mammals. Further in blind mole rats it has been demonstrated that V1 does not lack functionality entirely and is used in audition. To our knowledge no one has investigated whether visual function could be "restored" in blind mole rats through alterations in development, such as by exposing the vestigial eyes to visual stimuli. Currently functional changes in vision beyond natural capacity have been imposed, and this gives insight into the process of vision restoration. Naturally dichromatic male spider monkeys can be altered genetically to produce opsins resulting in trichromacy, although in that species only females can be naturally trichromatic (Mancuso et al., 2009). Similar forms of genetic manipulation can be used not just as gene therapy but also sensory augmentation in humans to expand the perceivable color spectrum. Neuroimaging studies in humans with blindness have revealed non-visual activity in what is usually considered the visual cortex in the occipital lobe associated with tactile (Burton et al., 2012; Cohen et al., 1997) and auditory tasks (Gougoux et al., 2005; Leclerc et al., 2000). Studies in blind species could help reveal whether there are limits to such plasticity, or whether human cortical regions are eachpluripotent and can take on a variety of functions, as proposed by Bedny (2017),. For example, mammalian species with subcutaneous eyes could provide experimental models for vision restoration and its neural basis.

7) **Blind animals point to biodiverse sensory functions often overlooked since humans are such visual animals.** When the goal is not limited to being human or restricting exploration to human-specific sensory limitations, blind animals provide a special perspective in considering the impact of functional evolution and this task-based approach to perception and the wider solutions to adaptive goals.

More generally, an evolutionary approach to understanding vision and vision loss also suggests a means for linking the sensory differences between animal models and humans to bolster the benefits of translational research. For example, the increased investment in Artificial Intelligence (AI) research has led to advances in robotics and machine learning that might assist with sensory restoration or serve as assistive technology. Currently most AI work attempts to model and mimic human intelligence. However, the goals of AI do not necessitate human intelligence as a necessary precursor for most aims. For example, a goal in AI is to achieve autonomous operation in natural environments. Although many organisms can respond adaptively to the natural world in milliseconds, the computational complexity in interpreting natural images, as opposed to artificial stimuli representing single visual features, is an on-going and fundamental problem. One possible solution is to pursue research on Brain-Like Intelligence (Sendhoff et al., 2009) as a means of creating biologically-inspired solutions that might provide a generalized approach to the computational demands of multiple sensory inputs and potential motor outputs. The promising perspective to develop Brain-Like AI has been hampered by the mistaken view that intelligence is a hallmark of "highly evolved creatures". Instead, the pluralistic view reviewed here – that all organisms have evolved adaptive sensory and motor capabilities for different environments – could better endow autonomous robots with the flexibility necessary to use different computational approaches attuned to the environment or task as needed.

Phylogenetic methods that leverage species differences in evolutionary models can drive discovery in healthcare and technology. Our work illustrates how phylogenetic comparative methods can provide powerful tests of hypotheses linking structure to function (de Sousa and Proulx, 2014; Todorov et al., 2019) that can be further extended with insight from naturally blind animal species.

Author contributions

All authors had a substantial role in the conception of this review, the acquisition of references and data, the analysis and plotting of the data, and in writing and drafting the manuscript.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.neubiorev.2022.104550.

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