



Animal visual perception

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Perception processes can be investigated at the physical (concerning the stimulation from the environment to the receptors), physiological (the processes taking place in the neural system), and psychological (the 'sense' of perception, the outcome produced by the physical stimulation and the physiological processes) level. The present paper focuses on visual perception, mainly from a psychological level of investigation, and revises comparative literature, highlighting both similarities and differences in the visual structures and functions in different animal classes. For this purpose, the structure of the current eyes is described in a comparative perspective, as well as perceptual organization and object recognition processes, color perception, three-dimensional structuring of the image, and motion perception. Finally, the literature about comparative susceptibility to various visual illusions will be discussed, as illusory perception has been revealed to be a most useful tool to unveil the perceptual algorithms shared by the different species. In spite of major differences between animal species in the structures in charge of perception and in the adaptations to specific ecological niches, experimental data presented here will lead to the conclusion that a number of basic perceptual principles of organization and functioning are shared between species. © 2010 John Wiley & Sons, Ltd. *WIREs Cogn Sci*

Historically, the starting point for the comparative investigation of animal perception has been to acknowledge the existence of individual perceptual worlds, which differ greatly between species. In 1934, Jacob von Uexküll stressed the distinction between the 'Umwelt', those stimuli of the external world which are effective (i.e., those that can be detected by an animal's perceptual system), from the 'Innenwelt', the inner world of the neural and physiological processes which respond to such stimuli, and from the 'Gegenwelt', the sense of perception that arises in the mind of the beholder. The classical example made by von Uexküll¹ is the case of the tick, a totally blind Arachnid which can sit on the top of a blade of grass for months or years, waiting for its host to walk by. The only two stimuli the tick can respond to (and therefore represent its Umwelt) are the odor of butyric acid that emanates from mammals and the temperature of around 37°C: A rather awkward and nearly impossible world to be imagined by us, humans, who rely on vision as the primary sensory modality. Vision, though, is not the predominant sense for all animal species. Sensory abilities have been selected

as a response to the specific needs and ecological niches of each species. Rodents and other nocturnal mammals, for instance, are primarily oriented by smell and hearing and other species take advantage of senses which humans do not possess at all, such as the echolocation system of bats and dolphins or the infrared detectors of certain snakes.

Comparative studies of perception, therefore, are faced with the fascinating but extremely challenging task of trying to understand Umwelts, which can be different, even completely different, from our own. One way to tackle such a difficulty, however, would be to focus on some virtually identical or remarkably similar solutions, which several species have been shown to develop in response to certain crucial perceptual problems.

Focusing on the visual modality, the present paper is intended to highlight how the general principles of perception would be plausibly shared between species because of environmental regularities and general needs, which are relatively independent from the specific ecological niches.

For this purpose, following a first section about the *natural history of the eye*, a review of the scientific literature on the main topics of visual perception will be provided, such topics being *color perception*, *perceptual organization*, *three-dimensional (3D)*

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structuring of the visual image, motion perception, and animals' susceptibility to *visual illusions*.

NATURAL HISTORY OF THE EYE

The structure of the eye has been regarded as one of the crucial instances of biological structures supporting creationism. Darwin himself was well aware that such a unique and sophisticated device as the eye would make a favorite target for criticism. He though had already identified a possible answer to how it could have evolved according to natural selection: 'if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certainly the case; if further, the eye ever varies and the variations be inherited, as is likewise certainly the case; and if such variations should be useful to any animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, although insuperable by our imagination, should not be considered as subversive of the theory'.² Nowadays, the evolution of the eye remains just an historical debate. Natural selection favors mutations, no matter how fine, which benefits exceeded the costs, and this process has gradually led up to the current eyes. In fact, eyes corresponding to every stage in the evolutionary sequence have been found in both fossils and existing living species.³ Moreover, the inherited nature of eye

features has been extensively shown, for example, the same genes (*Pax* genes) were shown to be responsible for the development of the different types of vertebrate and invertebrate eyes.⁴

Several differences have been found in the structure of the eyes of different species (Figure 1), ranging from single photosensitive cells, through more complex camera or compound eyes, to exotic morphologies such as parabolic mirror eyes.³ The simplest form of 'eye' (the proto-eye) consists in a flat patch of light-sensitive cells (as present, e.g., among unicellular organisms). This eyespot allows sufficient vision for daily synchronization of circadian rhythms and phototaxis. Several selective forces moved in the direction of increased spatial resolution, by forming a depression in the light-sensitive patch and constricting the aperture. The eyespot was therefore deformed into a cup, shaping the so-called pit-eye, allowing to the determination of the direction of light according to which cells the light is falling on. Pit-eyes were found in ancient snails and are present in some invertebrates living today. As the pit deepened into a cup, the size of the opening was reduced, and the pinhole eye was developed (such as in the Nautilus). By reducing the amount of light entering the hole, the acuity improved, allowing for shape perception. The increase in resolution is obtained by narrowing the hole, at the expense of the amount of light entering, therefore the image, although quite detailed, appears rather dim. This is plausibly the reason why a transparent layer of skin over the pinhole pupil (possibly developed

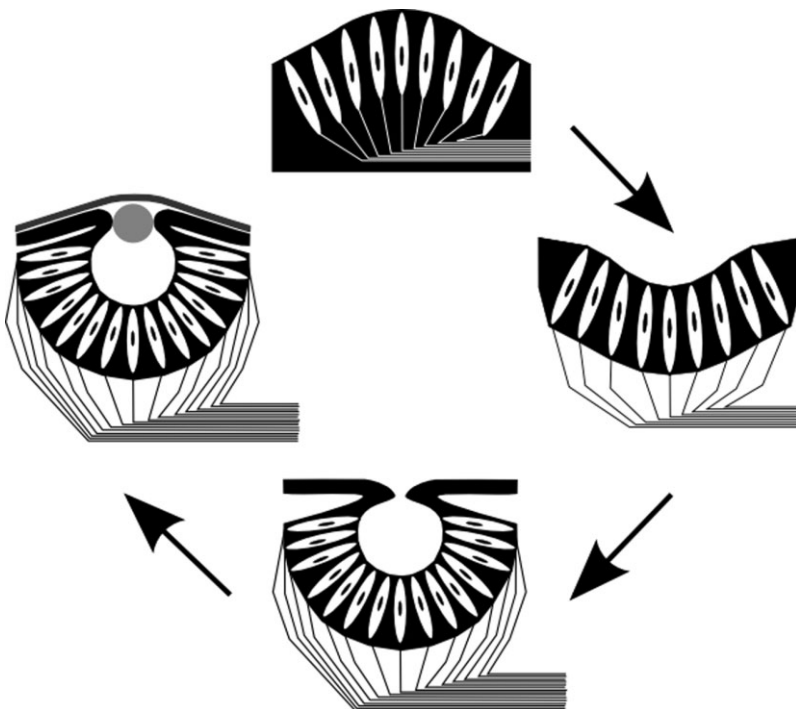


FIGURE 1 | Eye evolution. Clockwise from top: the photosensitive patch of the proto-eye; eye with a cup-shaped photoreceptor layer; the pinhole eye; the camera-like eye with primitive lens.

for protection) grew gradually to form the primitive light-focusing structures, allowing for a bigger hole and increasing the resolution obtainable. The lens-furnished eye (called a 'camera-like eye') is found in fish, cephalopods other than Nautilus, some annelid worms, and at least one copepod.⁵

The camera-like eye is not the only complex eye developed by animals. Superposition eye and mirror eye are two examples, and the compound eye is probably the most known alternative, evolved by invagination of several pigmented cups. The precursor of the compound eye, in fact, is the basic eye with photoreceptors in pigmented tubes, such as are found in starfish and sabellid tube worms.⁵ The most common compound eye is the apposition eye. It consists of an array of ommatidia, columns usually hexagonal in cross-section and located on a convex surface (and thus pointing in different directions). Each ommatidium is an independent sensor, composed of a lens focusing light on the rhabdom. It is innervated by one axon that provides the brain with one pictorial element. The compound eye can typically be found in arthropods such as flies and bees and although it does not allow for high visual resolution, it can detect fast movement and usually the polarization of light.

Further differences in visual mechanisms regard, for example, the size of the visual field and the number of areas with increased density of photoreceptors in the retina, which are responsible for differences in sensibility and visual acuity.

COLOR PERCEPTION

The basic mechanisms by which all animals perceive color are the same. Two types of photoreceptors are present on the retina: rods, which have a high sensitivity but are color blind, and cones, which vary in types of photopigments and are responsible for color perception. Cones are generally classified into four groups: SWS1, very short wavelength-sensitive [i.e., ultraviolet (UV)]; SWS2, short wavelength-sensitive (i.e., blue); MWS, medium wavelength-sensitive (i.e., green); and LWS, long wavelength-sensitive (i.e., red). Different degrees of color vision depend on the spectral separation of the photopigments, the number of such types of pigments, and the proportional distribution of the types of cones on the retina.⁶

The interesting feature of color vision is that there is a direct and feasible link between variations in the number of types of cone pigment in the retina and color perception as revealed by behavioral tasks. Comparative studies showed the fundamental differences in color perception both within and between animal species. In fact, primates are known

to have three types of cone (trichromats); other species have two (squirrels, rabbits, cats; dichromats); fishes, turtles, and some insects have four (tetrachromats), and some birds have five (pigeons; pentachromats).

With regard to insects, the honeybees, as the majority of hymenoptera except ants, have three spectral types of photoreceptor.⁷ They are sensitive to UV light (having a cone photoreceptor sensitive to the UV wavelengths) and also to the light polarization pattern; this is the least capability that is fundamental for aerial navigation. Butterflies instead possess a considerable variety of photoreceptor spectral sensitivities.⁸

Color vision is quite well developed also in vertebrates. Fishes have highly developed color vision, which has been investigated both by microspectrophotometry and behavioral tasks.⁹ The goldfish, for example, is a tetrachromatic species,¹⁰ in fact each of its four different types of cones¹¹ contributes to color vision.

A remarkable uniformity in the visual pigments has been shown for several species of birds,⁷ and avian color vision is in most species tetrachromatic: each of the four types of cones contains one photopigment and an oil droplet with carotenoid pigments, which seem to act as filters shifting the maximum absorption to longer wavelengths.^{12,13} Sensitivity to the UV dimension has been found in many species of diurnal birds.

Many species of mammals have poor color vision: rats, rabbits, cats, dogs, and the majority of nocturnal species (their visual system, in fact, evolved to see at very low levels of illumination and is usually very rod-rich). Whereas ground squirrels,¹⁴ and the majority of primates, have a well-developed color sensitivity.

Human-like trichromatic vision has been shown in both Apes and Old-World monkeys, for which color vision capacities were found to be quantitatively indistinguishable both between and within genera.¹⁵ Color perception in New-World monkeys is more heterogeneous and characterized by intraspecies variation.¹⁴ For example, female squirrel monkeys can be either dichromats or trichromats, whereas all males are dichromats.¹⁶

Many hypotheses have been put forward about the biological function of color vision. For insects, for example, color perception seems to allow for the detection of flowers and orientation to light polarization patterns in the sky, and sometimes detection of conspecifics.⁷ For birds, color vision is exploited for aerial navigation.¹⁷ The evolution of trichromatic color vision in primates has been supposed to allow for a rapid identification of yellow-red fruits on the background of green leaves in the forest.¹⁴

Differences between species could depend on the coevolution of color perception and animals' main foraging target or communication signals. However, empirical data (derived by a comparison between sensitivities of the receptors and the spectral reflectance properties of target objects) do not seem to support this hypothesis,⁷ except for butterflies.¹⁸ It seems more likely that color vision developed for general purposes, not directly related to the specific ecological niches of a given species.

PERCEPTUAL ORGANIZATION

Perceptual organization refers to the process by which several visual elements are grouped in a coherent scene by the relationship among them.¹⁹

In spite of conspicuous variations in the mechanisms of vision, it is plausible that the general principles of perceptual organization are common between species because of environmental regularities, which are relatively independent from the specific niche of each species. The most relevant case is the segmentation of a visual scene in biologically relevant units, the objects.

This process seems to be regulated both in human and nonhuman animals by the tendency to order experiences in a manner that is regular, symmetric, and simple (*prägnanz*²⁰). This is achieved on the basis of some general laws, known as Gestalt principles (i.e., closure, similarity, proximity, continuity, symmetry, and common fate²⁰).

These principles have been exploited whenever an animal's survival depended on it being conspicuous or indiscernible from the surrounding environment.

The first case is typical of releaser stimuli. The most known example is that of the stickleback fish, exhaustively studied by Tinbergen.²¹ During the breeding season, the male of this species turns a bright red color on its throat; this noticeable feature both attracts females and triggers other males' aggression.

The opposite case is provided by camouflage (the capability of some organisms to appear indistinguishable from the background); this widespread strategy must have coevolved with the mechanisms of perceptual organization in order to counteract them. Cryptic coloration is the most common type of camouflage: the animal's color is similar to the background, making it very hard to perceptually segregate its body; this occurs both with homogeneous (polar animals whose fur is the same hue and average brightness of the ice) and with uneven backgrounds (the best strategy in this case is to disrupt segregation through a textured pattern of camouflage that enhances similarities with the background and prevails onto the grouping

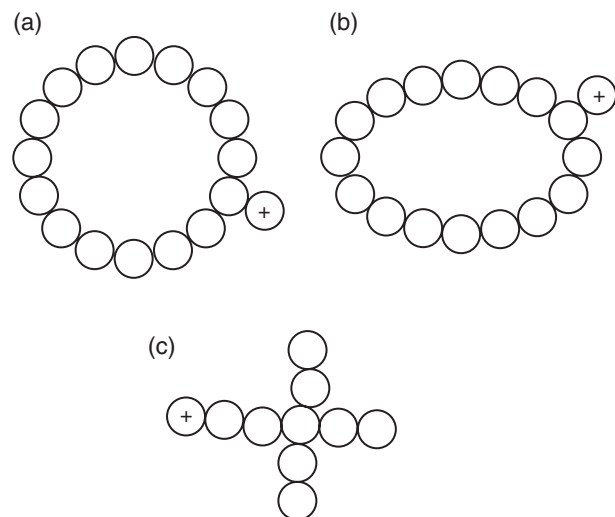


FIGURE 2 | Herz experiment with jays. Birds were trained to identify the X-labeled element within a configuration of identical elements. The X-labeled elements in (a) and (b) were easier to learn than that in (c).

by proximity within the body parts). The coevolution of the prey camouflage capability and the visual abilities of its predator are clearly detectable in some prey–predator pairs, such as described by Cuthill and Bennett.²²

Few studies investigated experimentally nonhuman animals' capability to respond to the Gestalt Laws, all obtaining positive evidence.

Herz, in 1928,²³ investigated figural perception in jays trained to find food hidden beneath one of a set of identical cups disposed to form different complex shapes (a circle, an irregular cross, ...). In some of those configurations, the correct target would be easily distinguishable from the whole configuration by the proximity and closure laws (Figure 2). The jays behaved as humans would do: the perceptual organization processes of jays were similar to our own. Similar key evidence has been reported by Tinbergen on the digging wasp.²⁴

Overall, for a comparative understanding of animal perceptual organization the Gestalt Laws provided a good descriptive tool. They may work because they reflect a set of effective assumptions about the world: a perceptual visual system employing such assumptions would probably reach correct solutions to perceptual organization.

STRUCTURING THE VISUAL IMAGE FROM 3D CUES: THE CASE OF AMODAL COMPLETION

Visual information received by the eye is in most cases fragmented: objects are mostly opaque and often

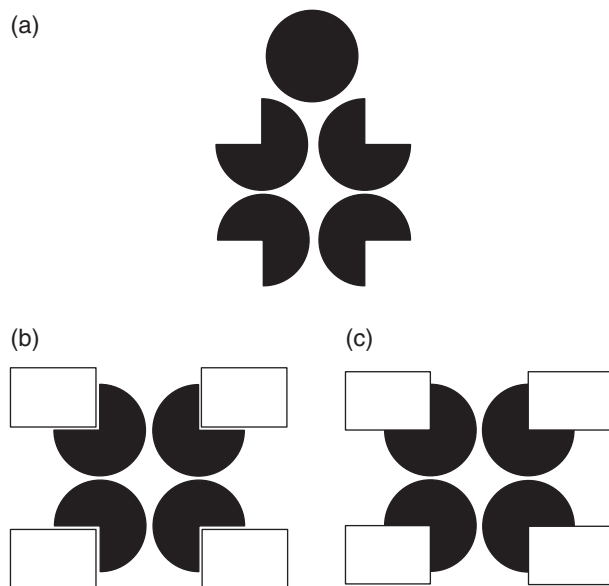


FIGURE 3 | Stimuli employed by Kanizsa et al.²⁷ with mice. Training stimuli (a) and testing stimuli (b and c).

partly occlude one another. Nevertheless, we do not perceive the world as made up of fragments, the visible parts allow for the recognition of the whole object. The process by which it is possible to perceive partly occluded objects in their entirety is highly adaptive and it is deemed ‘amodal completion’ due to the absence of any visual stimulation from the occluded parts.²⁵

Amodal completion was at first explained as a top-down inference, the outcome of a learning process due to experience. A mental integration made on the basis of previous knowledge certainly operates in certain situations, such as when inferring the features of a dog’s head by looking at the body. Amodal completion has, though, been shown to be there in a variety of animal species,²⁶ including rodents, primates, and birds, and to have a truly perceptual nature, the hidden parts of the object would in fact have a ‘genuine phenomenal presence’.²⁷ Kanizsa et al. in 1993 obtained some evidence in mice. Trained to discriminate between completed and amputated discs, subjects were tested with stimuli in which squares were juxtaposed or only placed close to the missing part of the disc (Figure 3). Mice were shown to behave as if they perceived the phenomenon of amodal completion, although alternative explanations could be provided.²⁷

In 1997, Sato et al. showed for the first time amodal completion in a nonhuman primate: an 18-year-old chimpanzee was able to perceive two fragments of a rod and an occluding bar as a complete rod behind the occluder.²⁸ The capability to complete a partly occluded object has been successfully tested also in monkeys.^{29–32} Similar perceptual rules are

crucial to amodal completion in all those species, such as common motion and global regularity³⁰; another crucial two-dimensional (2D) cue would be provided by ‘T-junctions’.

Even chicks³³ and fishes are susceptible to amodal completion.³⁴

Different strategies can be used to identify a partly occluded object in nature, such as responding to specific features of the object or reconstructing the whole shape by the object’s fragments; which strategy is used depends on several factors, such as genetics and the adaptation to the specific ecological niche. Unlike chicks, for example, studies on pigeons reported controversial evidence concerning amodal completion. Pigeons trained to discriminate a complete shape from others, in fact, did not seem to recognize it in a partly occluded shape.^{29,35,36} Fujita hypothesized that the capability to perceive a partly occluded object in its entirety would be specifically developed for birds which are ‘predators and extractive foragers’,²⁹ such as owls³⁷ and domestic chicks.^{33,38} If special training is provided, though, it seems that at least some pigeons would respond to the occluded stimuli.³⁹

Occlusion is suggested by both monocular and binocular cues,⁴⁰ allowing for the perception of the 3D relation between the occluding and the occluded object. 3D features suggested by occlusion are clearly perceivable by humans, and at least by two other species, the domestic hen⁴¹ and the baboon.^{31,32} Forkman and Vallortigara trained adult hens to peck at the highest pattern over two placed on a pictorial depth display. When presented with the two objects partly overlapping, the hens pecked significantly above chance at the object which would have been perceived as ‘behind’ the other one by a human observer, showing themselves to be susceptible to the 3D cues of both occlusion and pictorial perspective.⁴¹ Such cues were even more important for the perception of occlusion in baboons, as this was only possible with stimuli which were real overlapping objects that could be manipulated, rather than computer-designed stimuli.³¹ Similarly, occlusion depended on the use of a background facilitating depth perception (i.e., if stimuli were presented on perspective lines³²).

The capability to perceive the 3D component of occlusion, moreover, clearly highlights the key question in visual perception regarding how the visual system extracts 3D information about both objects and space from a 2D stimulation (i.e., light on the retina). The empiricist theory of vision suggests that this capability would be learned rather than a consequence of the physical properties of the objects. Comparative studies, however, support a different conclusion, as data on infant pigtailed macaque monkeys⁴² as well

as human infants,⁴³ horses,⁴⁴ domestic hens,^{41,45} and pigeons⁴⁶ coherently suggest that depth perception by linear perspective is a fundamental feature of space perception shared between species.

Although we cannot say whether nonhuman animals perceive 3D features of the world just the same as humans do, comparative data suggest that several nonhuman species are sensitive to the 3D features of both objects and space.

MOTION PERCEPTION

Motion constitutes a crucial source of information regarding several aspects of the surrounding world, providing cues about possible object collisions, image segmentation, and the 3D structure of a scene. Studies over several years have shown that the basic mechanisms of motion detection are shared between species.

The first experimental studies on motion detection investigated the optomotor response of insects. Reichardt⁴⁷ showed that an insect, suspended in a rotating striped drum (Figure 4), flies turning in the same direction of the drum, with a strength of torsion proportional to the temporal frequency of the stripes. The optomotor response system underlying this process, hence, was shown to be a motor-detector sensitive to the temporal frequency and not to the angular velocity of the drums *per se*. The direction of motion could be judged by a mechanism comparing the signals from two adjacent photoreceptors (A and B). Such a system has been hypothesized to act by selectively delaying and comparing the two signals (A versus delayed B; B versus delayed A): The pair with the strongest correlation would indicate the direction of motion.⁴⁷ Nowadays, it has been shown that insects' motion detection systems take advantage of temporal filters, while pure delay mechanisms are not commonly found.

Up-to-date perception of motion has been studied in several species of insect, as it is fundamental in a variety of ecological tasks, such as to estimate the range of a target by peering behavior (i.e., moving the head from side to side; locusts use it to estimate the power of jumping needed to reach the target^{48,49}; mantes use it to judge whether the target is within its jumping range⁵⁰; bees use it to segregate objects from the background⁵¹), to guide the centering response during flying through a narrow gap (in bees⁵²), and to visually regulate the speed of flight (for a review, see Ref 53).

Motion detection in other animal classes has been mostly studied through behavioral research on the basic ability to discriminate simple motion

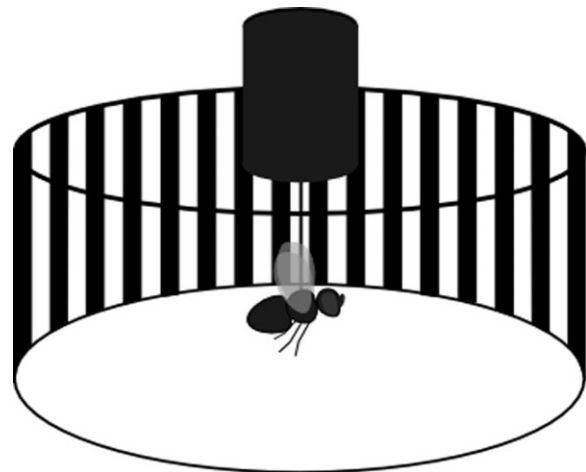


FIGURE 4 | In the apparatus employed by Reichardt⁴⁷ to study the optomotor response in insects, a fly suspended in a rotating drum adjusts its direction of flight according to the striped pattern.

features. The most widely used species has been the pigeon, which was shown able to discriminate two successively presented cyclic trajectories of a single moving dot and also the axis orientation of a moving dot or a moving-outline pattern.⁵⁴ Pigeons succeeded in this task, recognizing a moving gestalt in the absence of any figural information. Moreover, when previously trained to discriminate video images of conspecifics on the basis of movement, pigeons were shown to be able to generalize the discrimination performance.⁵⁵ Although such discrimination was based on visual features of the stimuli, it was invariant against changes in size, brightness, perspective, and color and also against different viewing angles. The authors argued that discrimination of movement in pigeons is based on motion concepts and high-order generalization across motion categories.⁵⁵ Other basic motion detection abilities in pigeons are the discrimination of stimulus velocity⁵⁶ and the perception of apparent motion.^{57,58}

Motion is also used to infer 3D shape of objects. This is the case, e.g., of discrimination between different objects on the basis of their moving shadows or of a random-dot display depicting them (in domestic chicks⁵⁹). One very compelling example of shape recovery from motion is the case of biological motion perception. Biological motion, the typical motion of vertebrates, has been studied using point-light animations generated by placing a few markers on some key joints of the moving organism. Humans are very good at perceiving and discriminating such displays⁶⁰ and the same capability has been shown in several animal species such as cats,⁶¹ pigeons,^{62,63} monkeys,⁶⁴ apes,⁶⁵ domestic chicks,⁶⁶ and dolphins.⁶⁷ The use of point-light displays allows for the investigation

of motion processing in the absence of any other objectual cue (shape, color, texture, etc.). Animals' discrimination of displays depicting biological from nonbiological types of motion supports the hypothesis that this is a basilar skill shared by all vertebrates, which enables animals to attend to the presence of other animals.

VISUAL ILLUSIONS

In visual illusions, the image perceived visually differs from or even contradicts the physical reality of the source of stimulation. Visual illusions always attracted much curiosity *per se*, and have therefore long been studied, both in humans and other animals. Moreover, such phenomena showed to be very useful in understanding how the visual system integrates the physical visual stimulus to obtain a complex representation of the environment. Visual illusions also allow for a direct comparison of the active role played by the nervous system of different species in perceptual organization.

In a class of visual illusions, the geometrical optical ones, the perceived figure undergoes distortions induced by the context in which it is inserted, an example being the Müller-Lyer illusion. It usually consists in two identical straight lines mistakenly perceived of different length because of the arrow ends pointing in or out (Figure 5). When asked to judge the length of the two lines, subjects typically perceive the line with the inward arrow end as longer than the other one. Pigeons trained to discriminate between lines of different length (some having two brackets of the same orientation, i.e., not changing the perceived length of the lines as in humans) and tested with Müller-Lyer figures behaved as if they perceived the Müller-Lyer illusion, regarding the inward-pointing stimuli as longer than the outward ones.⁶⁸ Susceptibility to the Müller-Lyer illusion has been recently shown also in capuchin monkeys⁶⁹ and at least in a gray parrot.⁷⁰ Those data together with data regarding other geometrical optical illusions, such as the Corridor illusion (perceived by baboons⁷¹ and chimpanzees⁷²) and the Ponzo illusion (perceived by pigeons,⁷³ chimpanzees, and rhesus monkeys⁷⁴), showed striking similarities in the distortions induced by context on the visual perception of animal species.

A typical case of perception of objects and contours which are not physically there is the case of subjective contours, which are edges not present in the physical distribution of luminance but nevertheless 'quasi-perceptive' (the most known example is the Kanizsa's triangle²⁰). Behavioral experiments have showed that several animal species are able to perceive

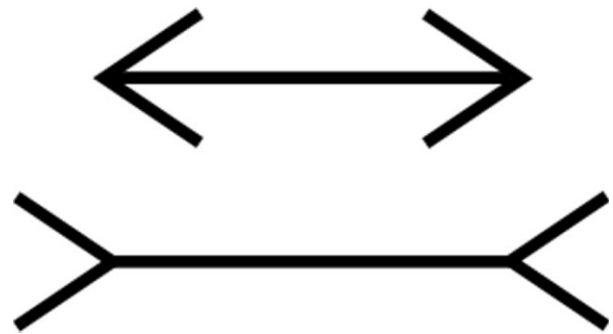


FIGURE 5 | The Müller-Lyer illusion consists in the fact that the length of the upper horizontal bar is estimated as shorter than that of the lower bar, due to the orientation of the brackets.

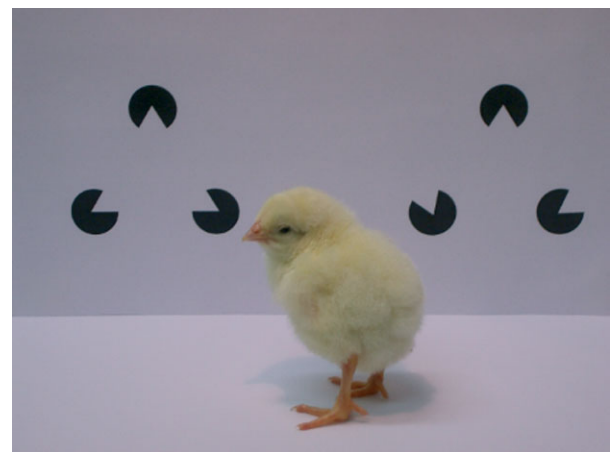


FIGURE 6 | In the experiment by Zanforlin,⁷⁶ chicks had been trained on a triangle as the positive stimulus, then recognized as positive the figure to the left, which produces the perception of a triangle through illusory contours.

those kind of figures,⁷⁵ probably because of the adaptive value of this capability, which allows for object detection under conditions of low illumination levels, camouflage, etc. Domestic chickens were trained with a triangle as a reinforced stimulus, then identified such a shape also when it was produced by anomalous contours⁷⁶ (Figure 6). Barn owls³⁷ were shown to perceive anomalous contours exactly as a real edge, as the neural response in the Wulst of the birds was the same for both types of edges.³⁷ Subjective contours perception has also been shown in cats,⁷⁷ monkeys,⁷⁸ fish,⁷⁹ and honeybees.⁸⁰ All those findings support the hypothesis that perception of subjective contours would be an adaptive capability underlain by mechanisms shared between different animal species.

Only few studies have been conducted about motion illusions in animal species. In recent years, the susceptibility of both domestic chickens⁸¹ and

common marmosets⁸² to the so-called stereokinetic effect was shown. In this effect, a 2D stimulus, placed in slow rotation in front of an observer, is eventually perceived as a solid 3D object, although that object does not actually exist.

The existence and the peculiar features of animals' susceptibility to visual illusions indicate that coherent rules hold for very different species irrespective of their visual perception machineries, so that the visual space and the objects are structured by the different systems according to a very similar constraint.

CONCLUSION

Comparative studies have provided a key contribution to the understanding of visual perception phenomena. No matter the differences between the variously and diversely shaped currently existing types of eyes: striking similarities have been described among species for what concerns the main topics of vision processing, from color vision to perceptual organization, image structuring, and motion perception. The reason being that all creatures dwelling this planet undergo, to different degrees, similar constraints.

Dealing successfully with the actual world, in fact, is crucial to animal survival and therefore a number of identical and invariant rules (most of them being available very early in life, even at birth, and requiring little or no learning) are imposed on how the world can be effectively perceived. As the evidence reviewed above suggests, an insight on the nature underlying such shared phenomena can be gained only in an evolutionary perspective of investigation, exploiting the comparison between the peculiarities of the Umwelts of the different species. The most interesting set of evidence can be obtained by looking at the shared 'mistakes' of the visual systems (e.g., visual illusions): when two different systems operate and result in a similar though unexpected outcome, much information can be gathered regarding the underlying common principles of functioning. Let us take two examples. Amodal completion of stationary displays

was described as available to human infants not earlier than few months of age.^{83,84} Its presence at birth was first shown in a different species, the newborn chick. Chicks were reared with a red triangle partly occluded by a black bar, which they soon imprinted onto and regarded as a social partner. On day 3 of life, each chick was presented with a choice test between either isolated fragments of the imprinting stimulus or a whole red triangle. Chicks consistently preferred approaching the complete triangle rather than the fragmented one (control experiments ruled out the role of differences in the area or perimeter of the two shapes), hence they behaved as if they experienced amodal completion.^{33,38} Years later developmental research has reconsidered this issue, suggesting that amodal completion is available, under certain circumstances, also to human newborns.⁸⁵ The second example concerns the perception of biological motion from point-light displays, which origin had long been debated.⁶⁰ Its presence at birth was again shown first in chicks. When asked to choose between a biological (i.e., a walking hen) and a nonbiological motion display, newly hatched and visually naïve domestic chicks were shown to prefer the biological stimulus.^{66,86} Such preference holds even when the biological stimulus depicts a walking cat, supporting the idea that the biological motion perception would represent a general and nonspecies-specific mechanism for the detection of other animals. Recently, newborn babies tested in the same paradigm and with the same stimuli used for chicks also were shown to discriminate and to prefer the biological to the nonbiological motion stimulus,⁸⁷ supporting Johansson's original claim⁶⁰ that perception of biological motion represents an intrinsic capacity of the visual system.

In the case of both phenomena described, comparative research provided first a set of convincing evidence for understanding their nature. Moreover, data from nonhuman animal species were produced at a time in which evidence in our species was either scanty or negative: animal results therefore prompted developmental scientists, often sharing comparable methodologies and interests, to further investigation.

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