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Determining When Birds Perceive Correspondence Between Pictures and Objects: A Critique

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The use of pictures in avian visual cognition research has expanded over the past few decades but understanding of how birds perceive pictures has not kept pace. Separate evolutionary pathways and distinct differences in existent avian and mammalian visual systems mean that researchers cannot assume that birds see pictures the way humans do. In this article, the authors argue that, to avoid anthropomorphic errors, researchers need empirical evidence about correspondence between perception of their picture stimuli and perception of objects. The authors review a few promising instances of correspondence. The authors further argue that closer attention should be paid to characteristics of display methodologies and their appropriateness for avian vision. Finally, they argue that the field will benefit if journal reviewers and editors provide more useful guidance to researchers about adding evidence of correspondence between the pictures and the real-life objects researchers claim or imply that their pictures represent.

Keywords: animals, anthropomorphism, avian perception, birds, natural science explanation, object perception, perceptual correspondence between pictures and objects, picture perception, pigeons, visual category learning, visual cognition

That nonhuman animals are capable of visual categorization was a landmark finding in the history of comparative cognitive science. In their classic study, Herrnstein and Loveland (1964) demonstrated that pigeons can learn to categorize pictures (e.g., colored photographic slides) according to the presence or absence of people, providing impressive evidence that pigeons have excellent visual discrimination and memory abilities. The pigeons learned to

peck at a high rate when pictures contained people, regardless of the clothing the people wore, the background scene, the number of people shown, or their location in the image. The pigeons learned to withhold pecking to various pictures that contained no people. Not surprisingly, this remarkable demonstration of categorization captured attention and stimulated research by scientists around the world.

Herrnstein (see review, 1990) and Wasserman (see review, 1995), and their respective colleagues, contributed important research and ideas to the modern view of categorization. As illustrated, for example, in the research of Wasserman and his colleagues, the main experimental criteria for categorization are as follows: First, the exemplars of a category must be discriminated one from another (Astley & Wasserman, 1992). Second, exemplars of different categories must be more easily discriminated than exemplars of the same category (Astley & Wasserman, 1992). Third, once demonstrated for a limited set of exemplars, any given categorization must transfer effectively across all novel exemplars (e.g., Herrnstein & Loveland, 1964). Finally, we add Cook's (2002) caveat that the nominal category labels ap-

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plied to sets of exemplars (e.g., color photographs of people, flowers, cars, and chairs: Wasserman, Kiedinger, & Bhatt, 1988) must be descriptive of the actual categories a species uses to classify exemplars.

Over the 40+ years since Herrnstein and Loveland's (1964) discovery, dozens of articles have enriched our understanding of visual categorization in animals (see the review by Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). Relevant to the present article, we now know much more about visual cognition in pigeons, the most typical study species for this research. In this paper we ask three questions about pigeon visual science. Do humans and birds view objects in the world similarly? Do humans and birds view objects in pictures (cartoons, photographs and video images) similarly? For pigeons and other birds, what is the relationship between their categorizations of two-dimensional pictures and their categorizations of three-dimensional objects in the real world?

The most optimistic answer to these questions is that pigeons see objects in pictures and in the world in much the same way we do. According to this view, an analysis of the features pigeons use to categorize pictures of objects tells us about pigeons' visual perception and concepts about those objects in the real world.

An alternative view, the one taken here, is that without independent evidence it is a serious error to assume that pigeons see pictures as representations of places and objects in the world: ultimately, an error that will hinder progress in the science of comparative cognition. As an example of the error, in discussing their discovery that pigeons accurately sort pictures that do and do not include fish, Herrnstein and de Villiers (1980) speculated extensively on the evolutionary history of their pigeons' discrimination of fish. Herrnstein and de Villiers (1980) even wondered when last in their evolutionary history the ancestors of pigeons had encountered fish. The authors pointed out that unlike people and trees, which pigeons also discriminate, fish do not inhabit pigeons' natural environment, yet pigeons discriminate pictures that include fish with high accuracy. These speculations about the evolution of pigeons' visual cognitions about fish leave out a crucial logical step. Herrnstein and de Villiers (1980) had no evidence that their pigeons responded to pictures of fish, people, and trees as they would have to the three-dimensional objects themselves. This brings us to the thesis of this paper: knowledge about correspondence between pigeons' representations of pictures and of real objects is crucial to understanding the results of experimental tests using only pictures.

Human and avian vision compared

Casual acceptance of correspondence between pigeons' representations of two-dimensional pictures and of three-dimensional real objects is based on the anthropomorphic assumption that because both humans and birds have good vision, both have similar vision. Here we describe the differences between mammalian and avian vision that make the anthropomorphic assumption untenable.

To understand comparisons between mammalian and avian visual cognition, it is important to know that mammals and birds diverged from two different species of reptiles (first the mammals and then the birds) some 300 million years ago. Over those millions of years, mammals and birds diverged in anatomy, physiology, and behavior. Both classes (Mammalians and Aves) are warm-blooded animals with well-developed nervous systems and brains, but the two classes differ dramatically in their characteristics--from their outer protection (fur vs. feathers) to the molecular chromosomal determinants of their sexual genotypes (in mammals, females are homozygous, XX; but in birds, the males are homozygous, MM).

Birds share many visual characteristics with reptiles, whereas mammals lost most of those characteristics and only in the primate order did some of these features reappear in vision. In other words, vision developed separately (i.e., are analogous rather than homologous systems) in birds and mammals. Differences between primate and avian vision fill articles and book chapters (e.g., see Werner & Chalupa's, 2004, massive edited book). A short summary of the comparisons we discuss here is that "anatomical, physiological, and behavioral (investigations indicate that color, depth, flicker, movement, and other aspects of vision are probably sufficiently different from humans in pigeons and other birds, enough for pictures to appear to them quite different from reality" (Delius, Emmerton, Horster, Jager, & Ostheim, 2000; also see Lea & Dittrich, 2000, who draw similar conclusions). In subsequent paragraphs in this section of the article, we summarize evidence about differences between the visual perception of humans and other higher primates and of avian species. Be aware that our summary is only a simplified version of a vast literature. Interested readers will need to read Werner & Chalupa's (2004) book and follow the literature cited here to understand what is known about avian vision.

Humans are higher primates and hence photography and video are designed for perception by higher primate eyes. (Pigeons do not buy video equipment.) Consider the issue of color vision. In both mammals and birds, the cones are responsible for color vision. Primates have three classes of cones each associated with a separate pigment. Birds have

four + classes of cones (again, each associated with a separate pigment). All of the many species of birds tested so far are sensitive to wavelengths into the UV because they possess more and different cones than primates (see Cuthill, Partridge, Bennett, Church, Hart, & Hunt, 2000; also Wright, 1972).

To complicate avian color vision further, birds' cones each contain an oil droplet which functions as a filter with the pigment in the cone to determine the spectral sensitivity of that cone. An important point in this article is that video screens produce a different pattern of color matching in pigeons than in humans (Palacios & Varela, 1992). Also, it appears that because of between species differences in oil droplets (Beason, 2003), color matching may differ even across avian species. In summary, avian and human eyes do not see the same colors or even the same number of colors. As we have noted, birds' eyes see more than three primary colors (Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998) and these colors are not centered on the same colors as seen by human eyes. Most important, because color is the result of differences in the output of receptor types, birds do not simply see additional UV colors, they perceive even human-visible spectra in different hues to those humans experience.

Differences between human and avian vision are not limited to color perception. The flicker fusion point in humans is lower than in pigeons (Hendricks, 1966) so that video images designed for humans can, for example, roll in some birds' eyes. Cues for recognizing three-dimensional objects can differ between humans and birds (Spetch & Friedman, 2006a). And finally, humans have one visual area of high cone density whereas pigeons have two separate regions of high cone density (regions of sharpest, clearest detection of objects): the projection areas of the fovea and the middle of the red area in the retina. The red area is active in binocular vision (Clarke & Whitteridge, 1976; Conley & Fite, 1980). As a consequence of researchers ignoring these important features of avian visual acuity, in many visual cognition experiments when pigeons stand close enough to peck at the touch screen, objects on the video screen can be out of focus and may lack depth cues. Using touch screens is less important than putting the video far enough behind the pecking surface to insure that birds get detailed, clear, binocular views.

Given these often ignored differences in visual perception, it is unlikely that birds ever see what humans do when looking at three-dimensional objects in nature. Difficulties multiply if one takes a step further and assumes that birds see what humans do in photographs--two-dimensional video representations of three-dimensional objects. Cautious experimentation must precede any claim about correspondence

between the visual perception of an avian species and humans or correspondence between avian visual perception of video images and of any particular object in the real world. By caution experimentation we mean direct tests of correspondence between a study species' perception of the pictures and the objects of interest in the experimentation under consideration.

A cautionary tale of anthropomorphic error

For those who might wish to dismiss our advice to exercise caution, we present a sobering example. Sexual dimorphism refers to physical differences between the sexes (excluding differences in their sex organs). In many species, the sex of individuals can be seen at a glance. For example, zebra finches (a commonly domesticated songbird) show marked sexual dimorphism. Male zebra finches (of the wild type) have bright orange cheek feathers, a red beak (as opposed to the orange beak of a female), and striking black and white patterns of feathers. What could be easier than classifying a species as dimorphic by whether the males and females look to have obviously different color markings? Then to determine whether sexually dimorphic or monomorphic avian species are more numerous all one needs to do is to count species. As it turns out, the answer depends on who is doing the looking.

It is generally thought that sexual dimorphism arises as a consequence of the powerful forces of both natural selection and sexual selection. Hence, it has been a matter of considerable interest to evolutionary biologists that despite the adaptive and sexual advantages of sexual chromatic dimorphism, some 69% of the 5,000+ known passerine bird species have been classified as sexually monomorphic in appearance (see Barraclough, Harvey, & Nee, 1995). That dimorphic species were less common had merited a special theory (see Andersson, 1994). But Eaton (2005) recently uncovered an egregious anthropomorphic error in this classification. He found that over 90% of a sample 139 avian species previously classified as sexually monomorphic by human eyes were in fact sexually dimorphic in avian eyes. Based on his comparisons of UV plumage reflectance data using an avian visual model of color discrimination threshold, Eaton now estimates that fewer than 27% of passerine species are sexually monomorphic. In other words, most avian species are dimorphic not monomorphic, as previously thought.

Not only did biologists get the proportions of dimorphic and monomorphic birds wrong, but as we have noted, they went on to concoct a theory to explain their mistaken observations (Andersson, 1994). That avian species see into the ultraviolet (UV) was well known prior to Eaton's (2005) work (see Palacios & Varela, 1992; Wright, 1972), which makes this anthropomorphic error and the ensuing development of

a specious theory even more embarrassing. The point of this cautionary tale is that biologists made an egregious scientific error by implicitly attributing human color vision to birds, well after they knew about the difference in UV perception between humans and birds. We write to ensure that behavioral biologists and comparative psychologists do not trip and fall into the same pit and then waste time, credibility, and treasure climbing out.

Differing opinions about what birds see in pictures

Researchers have sometimes uncritically assumed that pigeons see what human experimenters do when viewing two-dimensional images in photographs and on video screens. The speculations by Herrnstein and de Villiers (1980) about the evolutionary history of pigeons' discriminations of fish are a prime example. Following the work of Herrnstein and colleagues, some researchers recognized the need to provide evidence that pigeons saw pictures as representations of the real world, but were optimistic about the potential for using pictures to gain insights into pigeons' knowledge of the real world: "natural category research may provide an opportunity of communication with the pigeon. Someday, we may be able to ask the pigeon to sort through catalogs of pictures and peck those that are most like things he saw today in his travels." (Kendrick, 1992, pg. 132; see also Wilkie, Wilson & MacDonald, 1992). Indeed, the second author of the current paper was initially optimistic that digitized images of outdoor scenes could be used to study spatial memory for complex natural landmarks (e.g., Spetch & Wilkie, 1994) but subsequent work tempered this optimism (Lechelt & Spetch, 1997; Spetch, Kelly & Reid, 1999).

We are not alone in suggesting that pigeons often attend mainly to the two-dimensional features of pictures rather than to human-defined categories of three-dimensional objects. In a series of research studies, Huber and his colleagues (e.g., Huber, 1999) constructed models of human faces (perhaps with the intention of learning about human face perception in pigeons); however, over the course of their experiments (see Troje, Huber, Loidolt, Aust, & Fieder, 1999), these researchers became convinced that the features pigeons use to discriminate different categories of pictures of faces are inconsistent with pigeons having seen the pictures as faces at all. For example, Troje et al. (1999) reported good discrimination between model male and female human faces based on their surface texture but not on their shape. Huber (1999) has reviewed the progression from researchers interpreting category learning experiments in terms of human language concepts, as in Herrnstein and de Villiers's (1980) speculations about how pigeons know about fish, to more realistic interpretations of the categorization of video images, illustrated by his own feature-based explanations of

pigeons' categorizations of computer modeled two-dimensional pictures of human faces.

We note here that, once one has determined that pigeons are using two-dimensional features to categorize the pictures, it hardly matters that the pictures look like faces to humans (belong to the researcher-defined category of faces). Put simply, how pigeons and other species perceive real human faces is a very interesting scientific question that can lead to direct and compelling answers about how animals perceive their world. How pigeons perceive artificial objects derived from a researcher-defined category, such as human faces, might provide useful information about how avian species categorize artificial two-dimensional visual images, but it does not provide direct answers to questions about how pigeons perceive three-dimensional objects in the real world.

Sometimes, authors set out to use pictures to answer questions about objects in the world but their results force them to retreat from that goal. For example, several color pictures of an individual bird should constitute a category, and discrimination between several pictures of two or more birds should demonstrate individual recognition, where individual birds are represented similarly in pictures and in the world as separate open-ended categories. In experiments based on these ideas, Ryan and Lea (1994) had difficulty in training pigeons to discriminate between ten photographic slides each of two pigeons. Only one of six pigeons tested learned the operant discrimination. However, by habituating pigeons to some individual live pigeons then presenting another individual at test (a dishabituation technique), Ryan and Lea (1994) were able to show that pigeons readily discriminate individual live conspecifics.

Results using 40 moving video images each of pigeons walking and pecking were only slightly more promising (Dittrich, Lea, Barrett, & Gurr, 1998). Four of eight pigeons tested showed some evidence of discriminating among videos of walking and pecking conspecifics. The authors suggest that their results open the question of what aspects of the moving stimuli control the discrimination. The answer to this question would be very interesting if these researchers and their pigeon subjects can be shown to agree that the moving two-dimensional pictures shown on the screen represent three-dimensional live pigeons; otherwise, the answer might apply only to artificial two-dimensional moving pictures. Unfortunately, Dittrich et al. (1998) present no evidence about whether they and the pigeons hold the same category definitions.

We applaud Ryan and Lea's (1994) and Dittrich et al.'s (1998) experiments for their approach to determining what pigeons see in pictures and for comparing how pigeons discriminate among pictures of conspecifics and among con-

specifics in the real world. Despite the weak and sometimes negative findings, the results are valuable and they point to the danger of simply assuming correspondence between objects and their pictures.

In this section, we have discussed research that seemingly assumes that pigeons see more or less what human experimenters see in pictures, and other research that over time has become increasingly critical of that idea. Because these issues are difficult, it is possible to be aware of the problem and be at times appropriately cautious, but still lapse into language that suggests acceptance of the assumption that birds do see human defined objects in their pictures. For instance, Lazareva, Freiburger, & Wasserman (2004; 2006) taught pigeons to discriminate at a basic perceptual level (between chairs, cars, flowers, and people) and at a superordinate level between artificial and natural categories (chairs and cars from flowers and people). Lazareva et al. (2006) provided a disclaimer: they were "...not assuming that the pigeons actually recognize these two dimensional photographic images as depictions of real-life, three-dimensional objects. Equally noteworthy is that we use the terms natural and artificial as convenient labels for two groups of stimuli. These terms do not imply that the pigeons learn the concept of natural versus artificial or that they will generalize their discriminative responses to different basic-level categories belonging to these superordinate-level categories."

In their conclusions, Lazareva et al. (2006) appear to go back on their disclaimer: "Perhaps, the natural categories used in our studies are more coherent and less perceptually diverse in respect to their overall shape compared to the artificial categories; so, the pigeons may be able to rely on the overall shape of the object when discriminating people and flowers, but not when discriminating cars and chairs." This appeal to natural and artificial categories sounds plausible, until one remembers that the authors' do not assume that their pictures correspond to any particular real-world objects.

In a recent report, Soto and Wasserman (2010) wrote that they chose pictures of natural objects because "natural images more closely resemble the stimuli that are encountered by biological systems in the real world than the more commonly used artificial stimuli of the laboratory." How can pictures of natural objects more closely resemble objects in nature unless pigeons see the correspondence between real-world objects and their representations in pictures? Later in the same article, Soto and Wasserman (2010) proposed to "formalize a model of natural categorization". "Natural categories have the advantages of being more readily learned by pigeons" and according to Soto and Wasserman (2010) better reflect "the complexity of the task faced by animals

in their natural environment." But remember that the stimuli are just photographs, which are not natural stimuli to pigeons. They represent natural categories only when they are perceptually equivalent to real-life objects. If correspondence is not perceived, then the categories may be no more natural than those created by paintings by Monet and Picasso, which pigeons also readily categorize (Watanabe, Sakamoto & Wakita, 1995).

We want to make it clear that Wasserman, Lazareva, and colleagues' studies are experimentally sophisticated, and they are advancing our understanding of cognitive and perceptual processes underlying categorization. Our point is that although these respected researchers have never explicitly stated that pigeons can see real-world objects in their pictures, as shown here, they sometimes come very close to that claim; while at other times they describe their classifications of pictures as mere human language groupings (Lazareva et al., 2006). To avoid such conflicts, it is critical to establish by experiment whether any such correspondence between pictures and real-world categories exists in pigeons' eyes.

Subtle tests of what pigeons see in pictures

Researchers have applied logical tests to determine whether birds see real world objects in pictures. These experiments also seek to disentangle stimulus generalization based on individual features and based on the overall objects. Jitsumori and Matsuzawa's (1991) hypothesis was that animals should be able to learn that the orientation of objects in two-dimensional images matters. The experimenters trained the monkeys and pigeons on an orientation concept using 140 pictures containing full frontal views of humans against a white background. Upright presentations of the pictures were positive and upside down presentations were negative. Transfer testing included new front views of humans, new variants of human pictures (rear view, silhouettes, close and far faces only), as well as new natural categories (birds and monkeys) and new unfamiliar man-made categories (bicycles and lamps). The logic was that determining the upright orientation of the object in the picture would only be possible if the object in the picture was recognized. Thus, no transfer was expected for pictures of unfamiliar man-made objects, and none was found. Both species showed good transfer to some but not to all types of pictures of humans. The most interesting tests involved new natural categories. Transfer to these would be expected only if the animals recognized the objects in the pictures based on real world experience. One of four monkeys showed very good transfer to all new natural categories, and another monkey showed reasonable transfer to two new categories. By contrast, the results for the pigeons were variable and ranged from modest transfer

to no transfer. The authors concluded that the monkeys are capable of perceiving the representational nature of pictures, but that the pigeons likely based their classification on concrete features specific to the pictures. In this instance, monkeys but not pigeons, responded to pictures of humans as if they were representations of real world objects.

Another approach to disentangling the contribution of individual cues and the perception of objects is to test for transfer using scrambled versions of the object, which maintains the component features but destroys the configuration. The idea here is that stimulus generalization based on features might be relatively unaffected by rearrangement of the features, whereas transfer based on the object depicted in the picture should depend strongly on the spatial configuration of the features. Watanabe and Ito (1991) trained pigeons to discriminate between pictures of two pigeons and found that scrambling of the elements substantially reduced responding. But the logic of these experiments has been questioned. Wasserman, Kirkpatrick-Steger, Van Hamme, and Biederman (1993) and Kirkpatrick-Steger, Wasserman, and Biederman, (1996) found reduced discrimination accuracy when line drawings of man-made objects were scrambled. It seems unlikely that pigeons had real world experience with the objects shown in the line drawings (i.e, watering cans, irons, desk lamps, and sailboats), so in this work the effect of scrambling probably did not come from recognizing the picture as a representation of the real world object. Instead, these results might simply indicate that discrimination of complex two-dimensional stimuli may sometimes depend on both details of the components and their configuration (see Young, Peissig, Wasserman, & Biederman, 2001, for further evidence that line drawings may be a particularly poor stimulus for expecting picture-object correspondence).

A similar logic might be applicable to any experiment using scrambled images.

Watanabe (2001) investigated the effect of scrambling on pigeons' discrimination of pigeons or people shown in color photographs or cartoons. The pigeons were trained to discriminate between either (a) color images of a human cartoon character and of other cartoon characters, (b) color photographs of one person and of other people, (c) monochromatic images of a pigeon cartoon and of cartoon images of other birds, or (d) color photographs of a pigeon and of other species of birds. The pigeons were then tested with novel or scrambled images. Pigeons showed good transfer to novel stimuli except for cartoons of people. Also, pigeons showed good transfer to scrambled cartoons but not to scrambled photographs. These results suggested that pigeons attended to spatial arrangements in photographs but ignored spatial arrangements in cartoons: in particular in cartoons of people.

Overall, these results from scrambling tell us that pigeons sometimes attend to the spatial arrangement of the stimuli in two-dimensional images, but in our opinion, they tell us little about whether pigeons see the stimuli as representations of three-dimensional objects. We present more direct transfer tests in the next section of the article.

Nakamura, Ito, Croft and Westbrook (2006) explored pigeons' ability to discriminate between pictures of male and female pigeons. Most of the pigeons learned the discrimination and some generalized to new instances of the category. Further experiments in which the birds were tested with manipulations of the pictures (e.g., chimera; silhouettes, head only and body only) suggested that most birds relied on color cues and that body parts were used more than head parts for the discrimination. Nakamura et al. (2006) interpret their results as suggesting that "some pigeons are likely to have the ability to discriminate between male and female pigeons in the field without motion, auditory, olfactory, tactile, or ultraviolet cues"(pg. 337). We contend that what these results show is that, with training, pigeons can learn to distinguish between visual features that differ between pictures of male and female pigeons. The results also suggest, by inference, that real male and female pigeons differ visually in ways that are captured in photographs. It requires another step to determine whether the features that pigeons used to distinguish between photographs of males and females, are the same ones that they would use to distinguish between real male and female pigeons. That is, a study of transfer of the discrimination to live birds would be very informative here.

Recently, Aust and Huber (2006) conducted an experiment designed to test for representational insight by pigeons—actually some steps beyond picture-to-object transfer. They used a complementary information procedure to rule out the contribution of stimulus generalization in transfer to novel pictures. The training task was similar to that of Herrnstein and Loveland (1964) in that pigeons were trained, using a large set of exemplars, to discriminate between pictures that contained humans and those that did not. The clever wrinkle in Aust and Huber's (2006) study was that for one group of pigeons, humans in the images had no heads (the heads were removed or occluded), whereas for the other group of pigeons, humans in the images had no hands. This allowed Aust and Huber (2006) to test for transfer to the complementary missing parts. The authors reasoned that stimulus generalization of features would not produce a tendency to classify the missing part as human present. Instead, such a tendency would indicate recognition of the pictures as representing real humans (with whom they had years of experience). Aust and Huber (2006) found that the pigeons responded more to the body parts unseen during the discrimination than to either shapeless patches of human skin or distorted unseen

body parts. Aust and Huber (2009) have extended this research by comparing pigeons reared with and without real life exposure to humans' heads. After discriminating pictures of headless humans from pictures that did not include humans, birds with extensive real life experience with normal humans preferred pictures of humans with heads to pictures of shapeless patches of skin (a control). Birds reared without this experience showed no such preference. Aust and Huber (2009) propose their successful experimental design as an alternative to transfer from objects to pictures. Their experiment is impressive and useful but it is also an example of transfer from real life experience with a class of objects (humans) to pictures of the complete object (with heads). These are very promising results and provide the best evidence yet that pigeons can see pictures of humans as representations of humans seen in the world.

Direct transfer tests of what birds see in pictures (correspondence)

In our opinion, studies of direct transfer between three-dimensional objects in the real world and two-dimensional images in photographs or videos provide the best, most direct, evidence that birds see correspondence between a set of pictures and the objects the pictures represent. Two different sorts of methodologies, both highly effective, are reported in the literature to show transfer between pictures and objects: (a) transfer of natural responses in playback and preference testing studies and (b) transfer in operant visual discriminations.

Transfer in playback and preference testing using video of conspecifics

Playback testing involves playing recordings (audio or video) of a conspecific's behavior to a focal animal, to study that animal's responses to, and, by inference, its representations of the behaving conspecific. Playback methodology is not in common use among students of pigeon visual cognition, but in behavioral biology it is the method of choice for exploring representation of one animal's behavior by another (see McGregor, 1992).

Playback is in common use in the study of acoustic communication in birds (see Borror, 1965) where high quality recordings of songs and calls are played (hence the name playback) to conspecifics. Effectiveness of the method depends on the common finding (replicated in dozens of species and hundreds of individuals) that birds respond to audio playback recordings as if they were the actual vocalizations of a conspecific. For example, a male songbird defending its territory responds to audio playback of a male conspecific with songs, calls, and approach to the speaker, whereas a female responds with approach and copulation solicitation

postures (King & West, 1977). Most important, if the recording is altered from normal song, in any number of ways (e.g., pitch, relative amplitude, or timing) males sing and approach less and females solicit less. It is mainly from evidence of this sort that we know that birds hear correspondence between recordings and actual avian vocalizations. Correspondence is critical to the routine use of audio recordings to understand avian song perception (Sturdy, Bloomfield, Farrell, Ave, & Weisman, 2007).

Playback methodology has been extended to the study of perception and cognition for visual stimuli important to animal communication. Here we report on some highly successful extensions of the playback method to visual cognition. The first studies presented here recorded video clips and audio of courting pigeons to conspecifics (e.g., Shimizu, 1998; Partan, Yelda, Price, & Shimizu, 2005). Shimizu (1998) established the validity of the method for pigeons by playing back silent video clips of female pigeons to male conspecifics. He observed three aspects of male courtship display (i.e. bowing, tail-dragging, and vocalizations) and found that male displays were much shorter or absent to videos of a heterospecific or of an empty chamber than to video of a female conspecific. Also, courtship was increased by presenting moving relative to still video and by images of the female's heads relative to images of the female's bodies. Frost, Troje, and David (1998) obtained similar results playing back silent video of male conspecifics to female pigeons.

In a recent study, Partan et al. (2005) presented video and audio clips of courting male conspecifics to females pigeons and recorded their responses (e.g., circling and tail spreading). Although audio of male calls elicited more female responses than video images of courting males, video images were potent on their own and especially in combination with audio clips. Clearly, Partan et al. (2005) have developed useful video and audio playback tools for studying the categorization of important features of males and female courtship behaviors. Most important in the present context, this playback research demonstrates that, given the correct methodology, pigeons see correspondence between pictures and the objects they represent.

Galef (2008) and his colleagues have studied social influences on mate preferences in male and female Japanese quail for several years. Japanese quail are drably colored, terrestrial domesticated galliforms. Mate preference testing is conducted in many avian species, but like playback research, the methodology is not in common use among students of avian visual cognition. As in most mate preference tests, Galef and colleagues measured preference by accumulating time spent in proximity to one male versus a second male. A critic might comment that Galef's studies measure

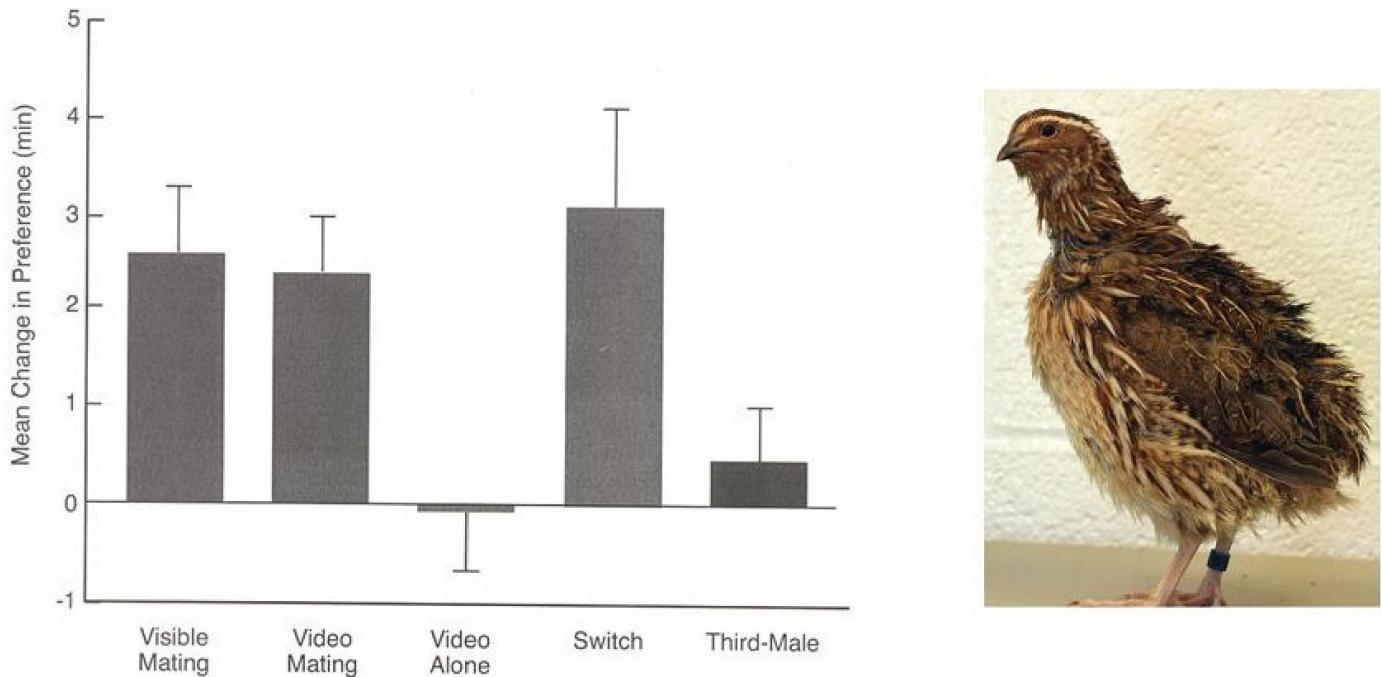


Figure 1. Left graph shows mean change in female quail's preference for a non-preferred target male quail after several viewing conditions. From left to right, bars show preference change after: 1) live viewing of the target male mating, 2) watching a video showing the target male mating, 3) watching a video of the target male standing alone, 4) watching a video of the target male mating in a different but with a switch in location from pretest to posttest, and 5) watching a video of a different male mating. The right photograph shows a male Japanese quail. (Adapted from Figures 3 and 4, p. 372-373, "Female Japanese Quail Affiliate with Live Males They Have Seen Mate on Video" by A. G. Ophir and B. G. Galef, Jr., *Animal Behaviour*, 66, 369-375. Copyright 2003 by Elsevier Ltd. with permission.)

affiliation not actual mate preference. However, White and Galef (1999) have shown that female quail mate with higher probability with the males they affiliate with (spend more time close to).

In research discussed in Galef's (2008) review, Galef & White (1998) demonstrated that female quail increase their preference for males they have observed mating with another female. Then in research more relevant in the present context, Ophir & Galef (2003) tested female quail's preferences for males they had seen mating on video. Specifically, these researchers tested focal females that had observed a video recording of either a familiar male mating, the same male alone, or an unfamiliar male mating. Only females that viewed video of the familiar male mating increased their preference for that male during the post observation test (see Figure 1). Notice that for Ophir and Galef (2003) to obtain this result, female quail had to have recognized correspondence between the male they observed live and the male they observed in the video. Clearly, female quail can identify male conspecifics they have seen live or on video. It did not escape Ophir and Galef's notice that their study was among the first to unequivocally demonstrate correspondence between pictures and objects in birds.

Ophir and Galef's (2003) study is also important because it provides strong evidence against a concern that has been raised about the interpretation of natural responses to conspecifics in pictures (e.g., Bovet & Vauclair, 2000; Spetch & Friedman, 2006a). Specifically natural responses to a pictured conspecific might possibly be elicited by some simple feature common to a video image and the real object and may not necessarily require recognition of the picture as corresponding to the whole object. In an early example of picture to object transfer, Tinbergen (1948; see ten Cate, 2009 for an update,) found that herring gull chicks direct feeding pecks at the red patch on a cardboard model of an adult herring gull's beak much as they do to obtain food from their parents. The red patch elicits the response, the adult's other features are much less important. The discovery of relatively simple releasing stimuli is useful and interesting in its own right, but uninteresting in most studies of object recognition, because object recognition is rarely controlled by a single perceptual dimension.

We believe that Galef's (2008) procedures offer much promise for researchers interested in revealing how birds recognize conspecifics. Despite serious limitations, provided the procedures of the experiment pass the correspondence

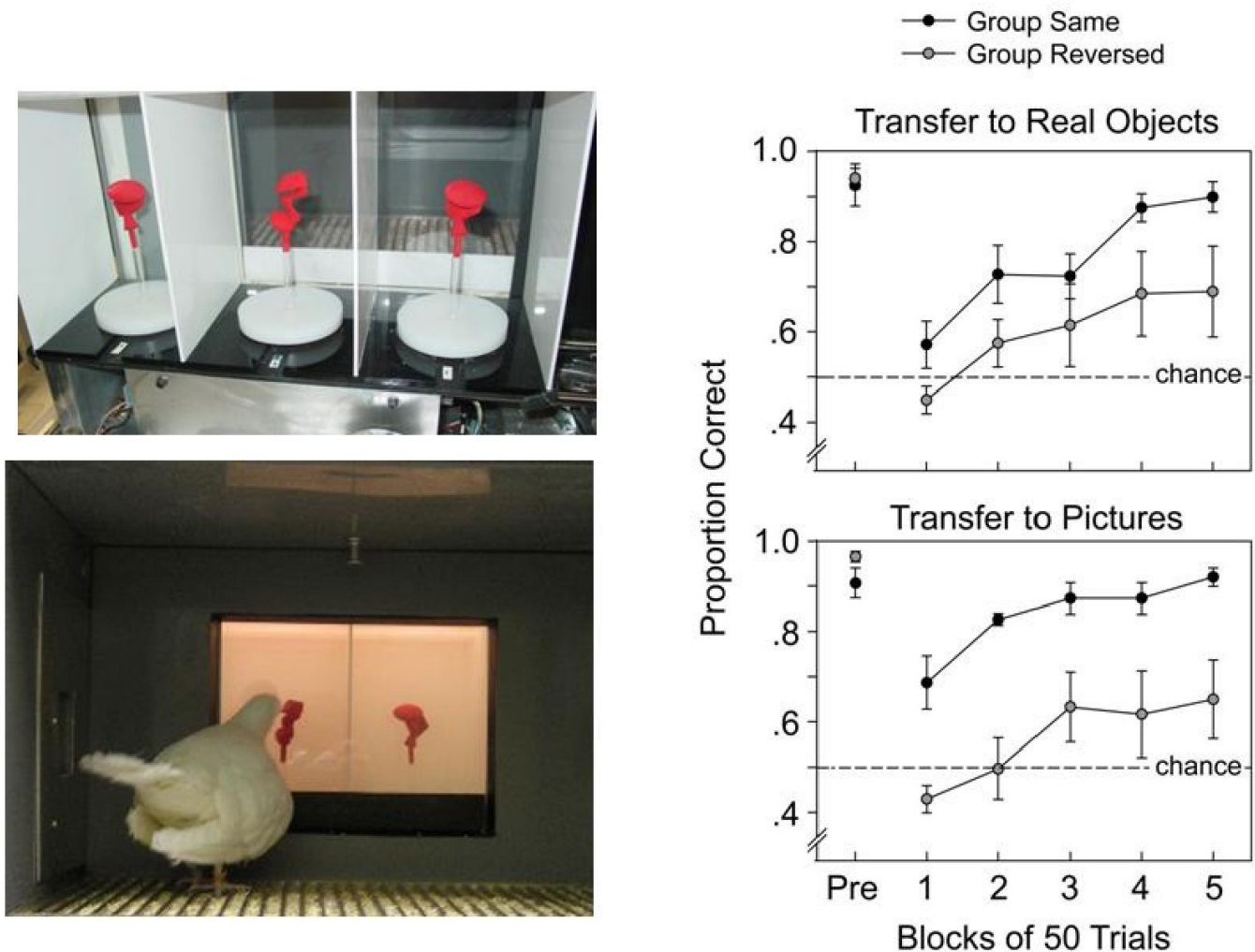


Figure 2. Objects and back view of apparatus used to display and rotate objects (top left) and front view of objects as seen by pigeons (bottom left). Right panel shows percent correct at the end of training (pre) and on the first 250 transfer trials for pigeons that were switched from pictures to real objects (top) or from real objects to pictures (bottom). For pigeons in Group Same, the contingencies between each object and reward remained the same before and after transfer; for pigeons in Group Reversed, the contingencies were reversed for transfer testing. The difference between groups Same and Different provides evidence that the pigeons saw correspondence between the pictured and real objects. (Adapted from Pigeons See Correspondence Between Objects and Their Pictures by M.L. Spetch and A. Friedman, 2006, *Psychological Science*, 17, 966-972. Copyright 2006 by Association for Psychological Science with permission.)

test, video technology can offer experimental manipulation of specific features in ways that are not possible with real animals. Using this technology, one can identify visual and movement stimuli that allow the birds to categorize pictures according to species or gender, and to differentiate between individuals. Essentially, this research can now follow in the footsteps of work on song perception in birds, but correspondence tests will be needed for each new protocol to insure that the research has referents in nature.

We have considered Galef and his collaborators' experiments in some detail, but other researchers have contributed to the growing literature showing correspondence between

pictures of conspecifics and the real world animals represented in the pictures. For example, chickens and their close relatives, red jungle fowl, give qualitatively different calls to live aerial and terrestrial predators (Collias, 1987). Evans, Evans, and Marler (1992) were able to demonstrate similar patterns of calling in the laboratory elicited by computer-generated animations of soaring raptors and raccoons. In this instance correspondence was demonstrated between behaviour elicited by live predators reported in other research and similar behavior elicited by pictures in Evans et al.'s (1992) experiments. By contrast, Patterson-Kane, Nicol, Foster, and Temple (1997), also using chickens, obtained at best ambiguous evidence of correspondence between pic-

tures and conspecifics. Researchers need to be aware that experiments demonstrating correspondence between pictures and conspecifics under one protocol does not give license to assume that correspondence will be obtained in other protocols, even with the same species. Nonetheless Evans et al.'s (1992) demonstration seems quite convincing. Provided the protocol is carefully replicated, their research points the way toward a better understanding of the referential encoding of alarm calls in birds.

Transfer of operant discriminations of objects

Another approach to determining whether birds see correspondence between objects and their pictures is to look for transfer of learned operant discriminations between video images and objects in the real world. Transfer has been tested in birds with both moving videos and stationary pictures of natural and artificial objects. Sometimes this research has produced mixed results without providing much help in deciding why some studies were successful and others failed. Both Cabe (1976) and Delius (1992) found transfer from real objects (three-dimensional shapes) to pictures of the same objects, but neither author tested for transfer in the opposite direction. Cole and Honig (1994) tested for transfer of discrimination between a real room and pictures of the room. Pigeons that learned to discriminate pictures of one side of a room from pictures of the other side transferred their discrimination to the real room. Pigeons trained in the real room did not transfer to pictures. Wilkie, Wilson, and Kardal (1989) trained pigeons to discriminate between two outdoor scenes. One of the scenes was familiar to one group of pigeons because of prior homing experiences, whereas both sites were unfamiliar to the other group of pigeons. In the first few transfer tests the familiar group showed a small but significant advantage. By contrast, Dawkins, Guilford, Braithwaite and Krebs (1996) failed to find any evidence that experience with a location in the real world facilitated discrimination between pictures of that location and another location. Also, Lechelt and Spetch (1997) failed to find transfer between pigeons' landmark-based searches of pictures and of the real room shown in the pictures. Some of the researchers that reported negative findings used CRT screens (e.g., Lechelt & Spetch, 1997), so high resolution, TFL-LCD, screens might improve transfer. However, care is required to rule out of transfer based on only a single feature of one location, e.g., a distinctly colored object on one side of a room.

To study whether pigeons can learn to recognize correspondence between objects and their pictures, Spetch and Friedman (2006b) used specially designed three-part objects identical in color, and similar in size, but different in global shape. Comparisons between these objects focused

attention on their shape. For real-object training, Spetch and Friedman (2006b) used a three-compartment apparatus first described by Friedman, Spetch, and Lank (2003). The apparatus allowed visual access to one version of each of the two shapes at a time and allowed the researchers to switch the positions of the two objects between trials to eliminate position cues to the rewarded object (see Figure 2). High-resolution digital pictures and the real objects were shown at the same orientations. Pigeons were trained with either pictures or objects using go/no-go discriminations. One object was consistently S+ (pecks rewarded with food); the other object was S- (no food reward). Each object was shown at multiple viewpoints (depth rotations) in training, which discouraged learning based on the two-dimensional shape provided by a single view. Some birds were transferred from pictures to objects and other birds were transferred from objects to pictures. For some birds the same object served as the S+ during both training and transfer (same contingency) and for other birds the training S+ served as transfer S- object (reversed contingency). The logic of the design was that if the contingency remained the same across transfer one should observe positive transfer, whereas if the contingency was reversed one should observe negative transfer.

Spetch and Friedman (2006b) observed good evidence of positive transfer in both directions: from pictures to objects and from objects to pictures. Specifically, birds transferred with the same contingency were significantly more accurate than birds transferred with reversed contingencies (see Figure 2). Most important, positive transfer occurred even when all of the object views seen during transfer testing were different from those seen during training. This argued against transfer based on memorization of specific two-dimensional shapes at each training view. Notably, however, transfer was far from perfect, indicating that, despite recognizing the correspondence, the birds noticed the change in stimuli. Several aspects of the methodology probably contributed to successful transfer (e.g., extensive pre-transfer training and elimination of cues other than global object shape) by focusing attention on aspects of the objects that were common to the pictures and real objects. These results hold promise because they indicate that pigeons can see correspondence between pictures and objects, but we cannot assume that pigeons always do so. It is important to conduct further correspondence tests with more complex and naturalistic objects.

Avian visual science without correspondence

We have left it till quite late in this article to provide dispensation to researchers with no interest in correspondence between the pictures they show to birds and any objects in the real world. We will oversimplify slightly here: research on basic sensation and perception, as in color perception,

edge detection, depth perception, motion detection, pattern recognition and shape recognition, is based on the assumption that simple visual processes apply generally in the laboratory and in nature. This assumption seems reasonable under most circumstances.

Yet, we must warn readers to be alert to anthropomorphic errors in what might otherwise be useful research on basic processes. In a study of motion perception, Mui, Haselgrove, McGregor, Futter, Heyes, & Pearce (2007) successfully trained budgerigars and pigeons to discriminate video of a woman walking a dog either forwards or backwards in the same direction. Mue et al. (2007) labeled their study one of discrimination of natural movement and discussed the work in terms of the ability of one animal to detect the movement of another. Of course, nothing of the sort was demonstrated. We have no evidence about whether or not the birds saw any kind of animal moving in Mui et al.'s (2007) video. Without evidence of correspondence in birds' eyes between the video and actual live humans and dogs, Mui et al. (2007) should have resisted the temptation to anthropomorphize about their study, and the editor and reviewers should have found this obvious error. Of course without the tantalizing reference to natural movement, the study becomes much less interesting: all the more reason to work to avoid this anthropomorphic error.

What benefits for the science are obtained when birds see correspondence between objects and their pictures? The answer depends on the goals of the science. If you believe, as we do, that comparative cognition is a natural science and the goal of the natural sciences is to explain nature (see Weisman, 2008), then there are important advantages to using objects that correspond to their pictures. The logic of inference is stronger (simpler and more direct) and researchers can begin to use pictures to determine how birds perceive conspecifics, predators, places, and common objects in their world. Without this correspondence, we can learn how the avian visual system perceives artificial two-dimensional stimuli, and we might gain some understanding of general cognitive processes such as attention, discrimination, memory and categorization (see Cook, 2001), but we will still remain far from our goal of understanding birds' perception of the natural world. A further drawback of working without proven correspondence between pictures and objects is the clear and present danger of egregious anthropomorphic errors in inference.

Is there a recipe for correspondence?

So, how can we improve our chances of obtaining good correspondence? One thing seems certain. We need to take properties of avian vision into account and pay close attention to the stimuli we are using in our research. For example,

it seems likely that correspondence between pictures and objects in birds' eyes is enhanced by using either thin-film transistor (TFL-LCD) or high-resolution 100-Hz CRT monitors, now known to improve recognition of conspecifics from video (see Galoch & Bischof, 2006; Ikebuchi & Okanoya, 1999). In recent research (e.g., Galoch & Bischof, 2006; Ophir & Galef, 2003; Partan et al., 2005), scientists have been careful to use these very high quality monitors. All that said, there are currently no prescriptions for the proper video equipment to insure successful experimental demonstrations of correspondence between pictures and objects in birds. The topic is intensely complicated (see Baldauf, Kullmann, & Bakker, 2008) and currently only careful testing for correspondence can ensure that birds are seeing the designated objects in pictures.

A second certainty is that we cannot just assume that pigeons see what we see. A recent study by Loidolt, Aust, Steurer, Troje, & Huber (2006) provides a compelling example, which complements the cautionary tale we presented earlier. Loidolt et al. (2006) trained pigeons to discriminate between pictures of human faces using either static images or movies in which the faces rotated in depth. The movies were made in two formats: (a) AVI format, which compresses the information for storage and (b) fast succession presentation of uncompressed bitmaps. Although "human observers could not see any difference between the two presentation modes" (Loidolt et al., 2006, pg. 79), pigeons most surely did. The pigeons learned the discrimination with static views and with uncompressed movies but failed to learn with AVI movies. Moreover, birds that learned the discrimination based on uncompressed movies failed to transfer to AVI movies, and birds trained with multiple static views transferred to uncompressed movies but not to AVI movies. Yet again, human and bird vision diverge.

Display and compression technology made for the human eye may not be appropriate for the avian eye. Research by Cook and colleagues introduces further complexities: these authors observed good discrimination by pigeons using AVI movies (e.g., Cook, Shaw, & Blaisdell, 2001; Cook & Roberts, 2007), suggesting that as yet unspecified differences in display equipment and compression procedure are critical to what pigeons see, even when it all looks the same to us. The lesson to be learned here and elsewhere in this review is that empirical research must replace anthropomorphic human intuition in determining when and how birds see correspondence between pictures and the objects.

A third certainty is that we must take into account where and how birds use vision. In nature, pigeons use the lateral visual field to view more distant objects and scenes. The vast majority of studies on visual cognition in pigeons, howev-

er, require them to peck at or very near to the display image. This engages the frontal visual system that is primarily used for pecking at grain. As Cavoto and Cook (2006) have noted, presenting stimuli from a close distance may encourage attention to small local features. They therefore recessed their display screen 20 cm behind the pecking screen and found good discrimination by pigeons of the depth ordering of pictured objects based on monocular cues alone. Thus, displaying pictures at a distance may enhance the perception of global scenes.

The meaning of correspondence

In this section, we pose three questions about correspondence between pictures and objects. How should we define correspondence? Is it a quality or a quantity? And, can an animal distinguish between picture and object and still show correspondence between them?

At the level of measurement, we interpret correspondence to mean transfer or generalization between pictures and objects. Transfer can be substantial, slight, absent, or anywhere in between: the greater the transfer the greater the correspondence in the birds' perception between the picture and the object. Experiments that demonstrate correspondence are necessary to draw inferences concerning the real life perceptions and cognitions of animals about objects in their world. As we have suggested a science that provides little or no information about nature is hardly a natural science at all.

Correspondence is the amount (quantity) of agreement between perceptions of pictures and the objects they represent. But can animals distinguish between a picture and an object, yet still see the object in the picture? If so, correspondence becomes just one quality of the experience of both the picture and the object. All of this sounds more like philosophy than science, but there is more science here than first appears.

Bovet and Vauclair (2000) suggested that there might be such a thing as too much transfer, because that might indicate confusion between the picture and the object. As evidence of the proper amount of transfer, Bovet and Vauclair (2000) cited an example where "the sheep stopped expressing interest in the picture of a conspecific when they realised that it was not a 'true' sheep" (See Vandenheede and Bouissou, 1994). In the lore of field biology, it is well known that songbirds eventually stop responding to a recorded song played from a speaker, and it is commonly said that the birds have learned that the song is not a 'true song'. Can animals both see correspondence and distinguish pictures from objects? There is a ubiquitous and often convincing alternative explanation for these observations of sheep and songbirds: namely, that the animals habituated to the repeated presenta-

tion of a sheep picture or a recorded song.

In one important sense whether birds know that pictures are different than objects is irrelevant. Mainly, what we want to know about is how birds represent objects; and whether birds can or cannot distinguish between the pictures and the objects is not important in that context. Yet in another sense, when a bird sees correspondence between a picture and an object, the bird's ability to discriminate differences between the two does measure something important: something we often think of as a distinctly human. We describe the phenomena here using an example from human perception. According to film critics, some of the best motion pictures have been made using black and white photography. Motion pictures are judged to be of high quality on the basis of their ability to convince humans to 'suspend disbelief' and treat the pictures as if they were the objects they represent. The paradox here is that people easily discriminate films made in black and white from nature, yet can respond powerfully to correspondence between them and objects in real life.

Some people might judge the suspension of disbelief to be uniquely human, but we are going to suggest otherwise. Readers need to know that we do not view suspension of disbelief as a conscious process or one that requires language in humans or elsewhere among animals. Now to return to our example, the main difference between a motion picture in black and white and one in color is that color photography engages the cones in human retinas. When birds view pictures, among the many disconnects with nature, they experience a partial failure of the picture to engage the cones in their retinas. Thus, it seems reasonable to propose that when birds see correspondence between pictures and objects, they can also see differences between picture and object. This nonhuman suspension of disbelief needs to be confirmed in experiments in which birds demonstrate both transfer and discrimination between pictures and the objects they represent.

Why we wrote this critique

Ours is not the first review of picture-object correspondence in animals. For example, Bovet and Vauclair (2000) published a careful review of studies of the topic, which we recommend to readers. Our purpose in offering a critique of the literature of visual cognition in birds is that, although Bovet and Vauclair's (2000) review is well-cited, curiously, few of the citations are from operant studies of avian visual cognition and even fewer are from studies that should have cited the review, i.e., those that made dubious claims about picture-object correspondence. Perhaps, our article will encourage journal reviewers and editors to provide more useful guidance to researchers about adding evidence of correspondence between the pictures they present and the real

life objects they claim or imply that their pictures represent.

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