Review article

Picture recognition in animals and humans

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Abstract

The question of object–picture recognition has received relatively little attention in both human and comparative psychology; a paradoxical situation given the important use of image technology (e.g. slides, digitised pictures) made by neuroscientists in their experimental investigation of visual cognition. The present review examines the relevant literature pertaining to the question of the correspondence between and/or equivalence of real objects and their pictorial representations in animals and humans. Two classes of reactions towards pictures will be considered in turn: acquired responses in picture recognition experiments and spontaneous responses to pictures of biologically relevant objects (e.g. prey or conspecifics). Our survey will lead to the conclusion that humans show evidence of picture recognition from an early age; this recognition is, however, facilitated by prior exposure to pictures. This same exposure or training effect appears also to be necessary in nonhuman primates as well as in other mammals and in birds. Other factors are also identified as playing a role in the acquired responses to pictures: familiarity with and nature of the stimulus objects, presence of motion in the image, etc. Spontaneous and adapted reactions to pictures are a wide phenomenon present in different phyla including invertebrates but in most instances, this phenomenon is more likely to express confusion between objects and pictures than discrimination and active correspondence between the two. Finally, given the nature of a picture (e.g. bi-dimensionality, reduction of cues related to depth), it is suggested that object–picture recognition be envisioned in various levels, with true equivalence being a limited case, rarely observed in the behaviour of animals and even humans. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Researchers in animal and in human cognition frequently use photographs or slides in place of real objects in their studies of categorisation, face recognition, etc., but paradoxically, there are few experiments either with animals or humans that have explicitly addressed the question of the equivalence between an object and its picture. In other words, it is not obvious that animal and human subjects do really interpret the 2-D stimuli as the 3-D objects they represent. For example, the success obtained in training pigeons [40,63] or monkeys [13,80,112] to categorise photographic slides does not prove that the animals under-

stand what the pictures they categorise actually represent. In fact, as we will see in this paper, some studies have demonstrated that this is not the case, while others have shown that the establishment of some equivalence between the real object and its pictorial representation is dependent upon both the stimulus' dimensions and experimental and/or motivational conditions. The present review tries to take stock of this question by examining the available literature for humans (mostly infants) and nonhuman subjects.

This review will first examine experiments concerning humans and will subsequently consider studies with nonhuman subjects, with the latter being classified into three categories. The first category comprises of cases of convincing demonstrations in which animals are able to treat pictures like the stimuli they represent; we can assume that a picture is recognised when animals react

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to a picture as they would react, spontaneously or after some training, to the real object. Of course, such reactions may vary according to the type of presented pictures: social behaviour with pictures of conspecifics, fear with threatening stimuli, predator behaviours with pictures of prey, etc.; spontaneous responses and transfer of various acquired responses (naming, categorisation, discrimination, cross-modal matching, etc.) in other cases. The second category encompasses the experiments which could indicate the existence of picture recognition but are not really demonstrations because the experimental design is questionable (for example when only one subject is involved) or the results (subjects' preferences or time viewing, discrimination of individuals or species, or various spontaneous behaviours) are not necessarily specifically elicited by the presented stimuli. The third category includes those experiments which show that animals may have difficulties with picture recognition.

In addition, two subclasses may be distinguished among the studies that have used pictures of living or inanimate objects with animal subjects; the first class referring to the studies examining learned reactions to stimuli (as it is often the case when the subjects are primates or birds), while the second class of studies measures spontaneous or natural reactions to the stimuli (this type of study is frequently seen in experiments involving lower vertebrates or invertebrates). In this latter case, a very salient feature of the releasing stimulus can suffice to induce the reaction. For example, a male redbreast reacts to a lure (e.g. a red tuft of red feathers) as if it were a real conspecific, even if the lure does not look like a bird [61]; a colour photograph of a male conspecific may induce a similar reaction but it is not certain whether, in such cases, the whole stimulus has to be processed and recognised. However, when a subject is trained to respond to real stimuli and then transfers its response to pictures of those stimuli, or is able to use video images to acquire some information about the nature of a real object, this suggests that the most significant features of the pictured stimuli are considered and recognised. Therefore, as picture processing can differ as a function of the kind of response (spontaneous or learned), these two classes will be considered separately.

A third classificatory key concerns the issue of the stimuli presented, that is, whether the image is static (photography, slide, digitised picture) or a motion picture, which of course implies some movement and often sound and may thus greatly facilitate the subjects' reaction to the stimuli. For example, movement is well known as releasing predatory behaviour [11], or may play an important role in the courtship of many species (see for example Refs. [35,94]).

2. Studies with humans: cross-cultural and developmental studies

Even in humans, recognition of photographs or pictures is not as straightforward as it may first appear. Thus, Miller [70] showed that there are intercultural differences in picture perception, with humans who have never seen pictures having difficulty recognising what is represented in black-and-white photographs; this author gives an example originally reported by Herskovits ([41], cited in Miller [70]) who imparts that a Bush Negro woman was initially unable to recognise a photograph of her son until details were pointed out to her. Similarly, Miller cites Kidd [56] who reported that Bantus expressed difficulties in recognising objects in photographs until the details of those objects were highlighted to them and they then perceived them almost instantly. Deregowski et al. [29] encountered the same difficulties with a remote Ethiopian population, but these authors emphasised that members of this population were able to gradually recognise drawings but with considerable effort and seemingly finding the task stressful.

Kennedy [55] has suggested that the subjects studied by Deregowski and his colleagues could have initially recognised details and then progressively built up a composite structure of the picture. Miller [70] has also shown that even when people recognise objects as represented in pictures, they may experience problems perceiving the third dimension; thus, depth is often not seen. For example, objects which were represented in the background appeared to some subjects as being placed upon objects represented at the forefront of the picture. Miller concluded that the "insight that produces an overcoming of flatness cues may require very little experience with pictures, but experience in perceiving objects in the three-dimensional world is not sufficient to perceive those objects in pictorial representations and that direct experience with pictures might also be necessary for the perception of depth cues in pictorial materials" ([70], p. 148). Deregowski [28] also relied on cross-cultural studies to understand the mechanisms of the perception and representation of space; coming to the conclusion that even if people unfamiliar with 2-D representations had more difficulties with picture recognition, the same kind of difficulties could occur in pictorial and nonpictorial cultures.

An interesting experiment has presented results that contradict the preceding conclusions. Hochberg and Brooks [44] studied the behaviour of a child brought up until the age of 19 months without being exposed to pictures; when tested at the end of this period, this child was able to recognise and to name various objects from his familiar environment represented in photographs and line drawings. However, this child's environment

was not totally devoid of pictorial representations (it is impossible in the USA!), as he accidentally saw representations of objects, for example, billboards on the highway.

Even very early in life, infants are already able to discriminate between 2-D and 3-D stimuli. Thus, Pipp and Haith [76] observed that 4-week-old infants differentiated 3-D from 2-D forms, with the 2-D forms invoking shorter fixation times. This experiment was repeated with 8-week-old infants who also processed a 3-D form in a different manner than a 2-D form, not in terms of overall fixation time but in the visual scan patterns elicited; there were more eye movements in response to 3-D forms. An experiment carried out by Appel and Campos [1] may offer some insight into how infants differentiate 2-D and 3-D stimuli; results showed that 8-week-old infants could discriminate between stimuli differing only in terms of binocular disparity, that is, when they were habituated to stereograms without retinal disparity and then presented with the same stereogram with retinal disparity, heart rate increased indicating that they dishabituated.

Bower [6] studied the reaction of neonates when a real ball or its colour photograph was presented at such a distance that the ball could only be touched but no grasped. The real object was frequently contacted but the photograph not at all (it did not even elicit hand raising) although the infants attentively stared at it. In contrast, very young infants (under 23 days of age) were shown to perform a similar amount of reaching in the presence of either a three-dimensional 'graspable' object (an orange textured sphere) or a two-dimensional picture of it [32]. Slater et al. [91] showed that new-borns (mean age: 2 days and 21 h) could discriminate real objects from their photographs; all participants looked longer at the real objects, even with monocular viewing, leading the authors to suggest that motion parallax was a salient cue for this discrimination. Interestingly, there was no evidence that the new-borns were able to recognise stimulus similarity across dimensions, thus, for these new-borns, differences between objects and their two-dimensional representations seemed to be more detectable or salient than their similarities.

Other investigations indicate that human babies are not only able, with very little or no experience with photographs, to discriminate these from real objects, but also to recognise what they represent. In an experiment carried out by Rose [81], 6-month-old infants presented with various geometric stimuli were not only able, in an habituation and visual preference test, to discriminate 2-D from 3-D stimuli, but also to transfer habituation from 2-D to similar 3-D stimuli, or inversely from 3-D to similar 2-D objects. This apparent ease of processing objects and pictures in a similar way is not, however, a consistently reported result. For

example, some authors found that very young children (less than 30 months of age) did not interpret the pictures as representing current reality; when the location of a hidden toy was demonstrated using photographic stimuli, 24-month-olds did not use this information to retrieve the toy, a task which 30-month-olds readily performed [23].

Dirks and Gibson [30] have shown that 5-month-old infants, without any experience of photographs, who had previously been habituated to an unfamiliar, live face, showed no change in fixation time when presented with a slide of the same person, but dishabituated when presented with a slide of a novel person who differed in sex, hair colour, and hairstyle from the familiar face. However, if the novel person was of the same sex, and had the same hair colour and hairstyle as the familiar face, no difference in fixation time was observed, suggesting that these infants could see the similarity between a live person and their photograph using rather gross physiognomic features. Similar findings are reported in a study by Barrera and Maurer [2] who found that 3-month-old babies who had never seen photographs looked longer at their mother's photograph than at a stranger's one. Related evidence of an early sensitivity of infants to pictures of conspecifics comes from the study of the phenomenon of gaze following; for example, Hood et al. [46] showed that 3-month-olds could detect another individual's gaze shifts even when presented as digitised pictures of adult faces.

Cross-modal experiments can also be valuable in the study of transfer from objects to pictures or the reverse. Rose et al. [82] showed that such a transfer was possible with 12-month-old infants, but that it depended on familiarisation time: with a familiarisation time of 30 s, infants were only able to perform a cross-modal transfer from touch to vision (real objects), and to transfer in a visual–visual task from real objects to both their outline drawings and coloured silhouettes. With an increased familiarisation time of 45 s, subjects were able to cross-modally transfer from touch to real objects, to their outline drawings and to their coloured silhouettes. However, with a familiarisation time of 15 s, infants were no longer able to transfer in a visual–visual task from real objects to their outline drawings, or coloured silhouettes.

Streri and Molina [92] conducted another experiment on cross-modal transfer with infants of only 2 months of age. Somewhat paradoxically, these authors found that pictures were more easily recognised than real objects in a transfer from vision to touch: transfer occurred between felt objects and their 2-D visual silhouettes, but not between felt objects and their visual counterparts. The authors hypothesised that this relative ease could be explained by the fact that infants take more information from seeing stimuli than from touching them. Thus, the use of pictures could have sim-

plified and reduced visual information, consequently rendering the object more easily identifiable for the infant who had only tactile experience of the object. Subsequent experiments performed by the same authors using the habituation procedure provided some evidence that 2-month-old babies were able to perceive both the commonalties and the differences of 3-D objects and their 2-D representations.

Experiments measuring event-related potentials have reached the same conclusion as most of the experiments presented above. Recordings of ERPs in 7-month-old babies while they were watching pictures of faces showed that the active components differentiated between a happy face and a fearful face but not between an angry face and a fearful face [71], suggesting that the infants recognised what was presented on the pictures.

Perhaps the most impressive demonstration of young infants' abilities in interpreting pictorial representations can be found in a study on intermodal transfer between oral exploration of objects and visual matching. In effect, in two experiments, Kaye and Bower [52] showed that new-borns as young as 12 h old were able to match tactile shapes (pacifiers) with visual representations of the pacifiers' shafts displayed as digitised coloured or black-and-white images on a computer screen.

In summary, cross-cultural studies have demonstrated that adults who have never seen any two-dimensional representations may experience difficulties recognising pictures; these participants need some explanation and some experience with a photograph (or a drawing) before being able to perceive what it represents. However, developmental studies reveal that the ability to recognise significant information in pictures such as photographs is evident even in very early infancy (demonstrated at 3 months or even younger). This apparent paradox between adult and infant performance will be discussed in the conclusion of this article. Human babies are also able to discriminate real objects from their pictorial representations; this precocious ability does not, however, preclude infants and even toddlers from confusing an object and its referents. The methods, populations and main results of the studies discussed above are summarised in Table 1.

3. Studies with animals: convincing demonstrations

3.1. Spontaneous responses to pictures

In this section, studies that provide rather unambiguous evidence of spontaneous responses to pictures as if they were real objects are considered; studies using static and motion pictures will be presented in turn.

3.1.1. Responses to still pictures

The perception of still pictures can elicit adapted responses by monkeys. Thus, von Heusser [43] reported that a tamed marmoset displayed grabbing responses in front of photographs representing different prey (e.g. ants, butterflies) but displayed fear reactions when shown a picture of a cobra. In a similar vein, Rosenfeld and van Hoesen [83] related that naive rhesus monkeys reacted with hasty retreat, threat responses and vocalisations to the first presentation of slides of rhesus monkeys' faces. These monkeys also displayed abortive approach–retreat before touching the stimuli (i.e. the slide projector), this behaviour did not persist, however, because the subjects quickly realised that the stimuli were only pictures (i.e. unresponsive, immobile stimuli). Comparable findings were obtained with cynomolgus macaques by Kyes et al. [60], namely, that dominant monkeys produced threatening gestures when shown, for example, pictures of gorillas or humans, while subordinates gave submissive responses to these same stimuli.

Sackett [87,88] presented real-life-size coloured slides of various social stimuli to rhesus monkeys; subjects exhibited different responses to the various stimuli, many of these responses being appropriate to the situation. Moreover, the level of responses to a given slide varied according to age and rearing conditions: subjects reared in isolation showed more exploration of non-monkey pictures and pictures without any social communication content than with socially relevant pictures. Results of another experiment [59] with hamadryas baboons suggest that these monkeys were able to recognise slides of conspecifics. Subjects were given control over slide selection and viewing time, with some slides depicting individual troop members and others depicting various facial areas of a troop member; the baboons were highly reliable in their choices, with dominance status seemingly a primary factor in troop member preference and slides of full faces being consistently chosen and the eye region attracting the greatest attention.

Overman and Doty [72] have investigated hemispheric specialisation for face processing in pigtail macaques. Prior to testing, the authors examined if their subjects would react in a similar manner to real models and pictures of humans and monkeys; various emotional reactions were measured (e.g. vocalisations, lip-smacking, etc.) at the first presentation of different categories of slides and results showed that pictures of humans and monkeys were clearly differentiated from other classes of stimuli such as flowers, insects or landscapes.

The available neurophysiological evidence supports the view that nonhuman primates establish some correspondence between photographs and the individual monkeys they represent. For instance, studies with

macaques have revealed that groups of neurones in their left inferotemporal cortex are responsive to faces of other monkeys and are sensitive to the identity of the monkey [74,113]. It occurred that similar groups of neurones were firing in response to life facial stimuli, to picture stimuli and to still video [75].

In addition to nonhuman primates, it seems that sheep may also be good candidates for studying picture

Table 1
Studies with humans

Task	Nature of pictures	Age	Results	Reference
Discrimination of stimuli with binocular disparity from stimuli without binocular disparity	Stereogram or simple picture of a color drawing	Eight weeks	Increased heart rate in the dishabituation phase	Appel and Campos [1]
Mother's photograph recognition	Color slides	Three months	Preference for mother's picture	Barrera and Maurer [2]
Behavioural observations	Colour photographs	Neonates	Hand raising is elicited by a real ball but not by its photograph	Bower [6]
Event-related potentials recorded from babies watching pictures of their mother's face or a stranger's face	Two-thirds-size digitized colour photographs	Six months	ERP shows difference between observation of the mother's face and a stranger's face, but looking time does not	Nelson and de Haan [71]
Finding a hidden object when the location is demonstrated with photographs	Photographs	Twenty-four and 30 months	Failure to find the hidden object in 24-month-old children but not in 30-month-old	Deloache and Burns [23]
Behavioural observations	Color photographs	Nine months	Trying to grasp the depicted objects, despite discriminating between objects and pictures	Deloache et al. [25]
Cross-cultural studies of human picture perception	Black-and-white photographs and drawings	Adults and children with or without experience	Same types of difficulty occur in pictorial and nonpictorial cultures	Deregowski [28]
Presentation of pictures	Line drawings	Adults without experience	Difficulty recognizing what a picture represents	Deregowski et al. [29]
Habituation to a live face, then measurement of fixation times for a slide of the same and a novel face	Life-size colour slides	Five months	Perception of similarity between a live person and their photograph	Dirks and Gibson [30]
Comparison of amount of reaching to a real ball and to its picture	Color photographs	Twenty-three days	Similar amount of reaching with a real ball and with its picture	Dodwell et al. [32]
Presentation of pictures	Black-and-white photographs	Adults without experience	Difficulty recognizing what a picture represents	Herskovits [41]
Naming the represented objects	Photographs and line drawings	Nineteen months without experience	Correct naming	Hochberg and Brooks [44]
Detection of an adult's change of gaze direction	Colour digitized pictures	Three months	Correct detection	Hood et al. [46]
Intermodal transfer between oral and visual exploration of objects	Digitized colored or black-and-white images	Twelve hours	Intermodal transfer occurs	Kaye and Bower [52]
Presentation of pictures	Black-and-white photographs	Adults without experience	Difficulty recognizing what a picture represents	Kidd [56]
Review of cross-cultural research	Black-and-white photographs and drawings	Adults and children with more or less experience	Difficulty in perception and recognition of various types of pictures	Miller [70]
Recording of event-related potentials	Black-and-white slides	Seven months	Event-related potentials vary with the expression of the faces presented	Nelson and de Haan [71]
Discrimination between 2-D and 3-D stimuli	Simple black-and-white silhouettes	Four weeks and 8 weeks	Visual behavior differentiates between 2-D and 3-D stimuli	Pipp and Haith [76]

Table 1 (*Continued*)

Task	Nature of pictures	Age	Results	Reference
Discrimination between 3-D and 2-D stimuli, and transfer of habituation from 2-D to similar 3-D stimuli, or inversely from 3-D to similar 2-D objects	Black-and-white photographs	Six months	Babies are able to discriminate between 3-D and 2-D stimuli, but also to perceive similarity across dimensions	Rose [81]
Cross-modal transfer between touched objects and their pictures	Colored outline drawings and silhouettes	Twelve months	Cross-modal transfer is possible but depends on familiarization time	Rose et al. [82]
Discrimination between 3-D and 2-D stimuli, and transfer of habituation from 2-D to similar 3-D stimuli, or inversely from 3-D to similar 2-D objects	Black-and-white photographs	Two days and 21 hours	Neonates discriminate between 3-D and 2-D stimuli, but do not perceive similarity across dimensions	Slater et al. [91]
Cross-modal transfer from vision to touch	Silhouettes	Two months	Pictures are more easily recognized than real objects in this kind of cross-modal transfer	Streri and Molina [92]

recognition in animals. Thus, a study by Vandenheede and Bouissou [101] indicates that sheep recognised a 2-D stimulus at its first presentation. In this study, the fear reactions of ewes were tested when the subjects were separately presented with a full-size slide of a human, a sheep, or a control stimulus (a traffic cone); the ewes showed reduced fear reactions in the presence of a sheep's photograph, as with real conspecifics and, moreover, sniffing was primarily directed towards the anogenital region and the head, which corresponds to behaviours directed towards real conspecifics. However, the human slide failed to induce fear reactions, as they occurred with a real human or even a human-like model [101], thus suggesting the possibility that recognition of 2-D stimuli could be easier when stimuli are conspecifics. A subsequent experiment [4] showed that, in ewes, a slide of an unknown individual of its own breed significantly reduced fear reactions compared to a slide an unknown individual of a different breed, this latter result suggesting that the ewes can recognise the characteristics of their breed on the slide.

Finally, Clun Forest and Dalesbred sheep showed an ability to discriminate black-and-white photographs depicting faces of sheep versus human faces when they were tested with a procedure of spontaneous choice in a Y-maze [54]. In addition, the same study demonstrated that Clun ewes could also distinguish between the faces of male and female breed members and between a trough with and without food. Moreover, some subjects were observed displaying overt social reactions toward stimuli, such as licking the pictures (C. Fabre-Nys, pers. commun., May 1998).

3.1.2. Reactions to motion pictures

Plimpton et al. [77] showed social stimuli (for example a threatening male stimulus) to juvenile bonnet macaques

via colour videotape recordings and observed these subjects in the presence of their mother; they exhibited appropriate responses depending on the nature of the social display, that is, they behaved submissively toward the threatening male and searched for contact with their mother while they approached a passive female. Herzog and Hopf [42] showed different colour films to wild-born and laboratory-born squirrel monkeys. While the presentation of predators (cats, snakes or avian predators) caused specific alarm and flight reactions, the subjects did not emit any alarm response when nonpredator mammals were shown. Further, they reacted in the same way as they did in real situations upon seeing preparation of food or insects walking and also reacted to films of human beings as to real people. These subjects demonstrated face recognition; upon seeing in the film a caretaker who had recently removed a dead neonate, the squirrel monkeys behaved as if they were facing a real terrestrial predator. No difference was shown between wild and laboratory born-subjects.

In studies with birds, the use of predators' pictures also yielded positive indications of picture recognition. For example, in a study by Evans and Marler [34] which used video images as stimuli, domestic cockerels were shown to respond with similar alarm calls in response to an aerial predator model when either videos of hens or real caged hens were present. The use of social stimuli, notably in tasks requiring the recognition of conspecifics, can provide important insight on the ability of birds to match objects with their pictures. Shimizu [90] observed that when video images of females were presented to male pigeons, the duration of the males' social display was not significantly different from that which they performed in front of the live bird. When video images of another bird (a cockatoo)

or of an empty room were presented to the subjects, they showed much shorter, or no, display. Finally, the duration of the display was longer when video images were in motion rather than still and when only the head region was visible rather then when only the body region was visible.

An experiment carried out by McQuoid and Galef [67] with juvenile Burmese fowls provides evidence that observing feeding among conspecifics via video tapes has similar effects as observing live conspecifics on subsequent feeding behaviour (i.e. preferences for food dishes); thus, the sight of a video of a conspecific feeding before testing, even without sound, reduced the latency of the first peck. Further, a videotape of a fowl actually feeding on a food dish was more effective in reducing the latency of the first peck and in enhancing preference for that type of food dish than a videotape simply representing a fowl (either active or immobile) near a food dish.

Jenssen [49] studied the recognition of motion pictures by lizards. In this study, female lizards could choose between two films, one with males displaying the normal courtship behaviour and the other with males presenting altered displays; in most cases, the females chose the normal displays. This experiment suggests that female lizards could recognise male lizards in the film and that they could be sensitive to their behaviour. When video sequences displaying aggressive displays of their own species were shown to male lizards, these animals responded with the appropriate responses (e.g. head-bobbing, crest erection) which they would exhibit in front of live opponents. Moreover, such behaviours were inhibited when video-recorded sequences of heterospecific lizards were presented [65].

Some experiments have reported evidence of image recognition in fishes, at least when video images (implying motion) were used. Thus, Rowland [85] showed that male and female sticklebacks reacted to video images of a zigzag dancing male played at a normal or slightly faster tempo in a similar way as they would react to a live male; when the tempo was slower or much faster than the normal tempo, the animals were less attracted. In guppies, consistency of mate preference was studied by presenting females with males under three experimental procedures: live males behind clear glass, live males behind one-way glass and images of males on videotapes. Females spent significantly more time in proximity to males behind clear glass than in video and one-way glass presentations, but they spent equal time with males behind one-way glass and videotaped males [58]. In all three experiments, females responded to stimuli by displaying sexually oriented behaviours and the results show that when interaction was not possible, a videotaped male was as attractive as a real male.

Some studies suggest that even invertebrates can recognise video images. For example, Clark and Uetz [11] carried out an experiment with jumping spiders and found that in a V-maze choice, spiders preferentially chose a videotape with moving prey to a videotape without prey. In addition, the spiders did not discriminate between a live prey and its simultaneously presented video image and they behaved in a manner comparable to their reactions with life stimuli when they were presented with televised images of prey insects (attack), conspecifics (courtship) and heterospecific spider species (retreat).

3.2. Acquired responses in picture recognition

We will now turn to a consideration of studies that have attempted to test the abilities of different animal species using pictures (still and in motion) as stimuli. Although most of the experiments summarised below were aimed at investigating picture recognition, we have also considered experiments for which the explicit goal was not picture recognition as these studies also present findings relevant to this topic.

3.2.1. Reactions to still pictures

Hayes and Hayes [39] reared a female chimpanzee, Vicki, in their home, almost like a human child. While they did not specifically train her in picture perception, they did test her ability to recognise pictures depicted in books and other materials and to imitate actions illustrated in films, photographs, and line drawings. Vicki was able to recognise most of the pictures she saw, even when the pictures were presented as black-and-white drawings. Nevertheless, those authors reported that Vicki did not confuse photographs with real objects; Vicki did not try to grasp 2-D objects and when she pointed for example to pictures of beverages, she said 'cup', and let the person who was with her go to the kitchen and get a drink. Gardner and Gardner [38] showed that four chimpanzees that had been familiarised with pictures could also recognise and name in American Sign Language various objects represented on new slides.

Sarah, an adult chimpanzee experienced with films and photographs was shown videotaped scenes of a human actor struggling with one of eight problems and then presented with two photographs that could constitute a solution to the problem [78]. Sarah chose the correct photograph on seven of the eight problems suggesting that she recognised both what happened in the films and the objects as depicted in photographs and as films. Furthermore, Savage-Rumbaugh et al. [89] trained chimpanzees to categorise various objects into the two categories 'tools' or 'foods'; when the objects were replaced by photographs (the subjects were already familiarised with pictures), the two chimpanzees tested were still able to categorise (and thus to recognise) them.

An interesting study on the recognition of pictures of individual faces by chimpanzees was carried out by Bauer and Philip [3]. The authors found that three chimpanzees initially trained to match photographs of faces of the same individuals were able to later match different vocalisations to facial portraits of the familiar individuals.

Experiments on cross-modal perception can also provide us with useful indications concerning the question of picture recognition in nonhuman primates. For example, Davenport and Rogers [16] trained three apes, one orang-utan and two chimpanzees, who were unfamiliar with photographs, to match a visual sample (the real object) to an haptically presented object. When the visual sample was a photograph, subjects' responses were clearly above chance (80% or more) from the beginning. Further, there was little difference in accuracy between colour and black-and-white photographs, and no difference between real objects and their colour photographs. Thus, it seems that apes are able, even without any familiarity with photographs, to recognise them and treat them like real objects. In another experiment [17], five chimpanzees trained only in a haptic to visual cross-modal experiment with real objects were submitted to the same sort of problems with photographs or drawings; four of the subjects performed significantly above chance with full-size colour photographs, with full-size or half-size black-and-white photographs and with full-size line drawings. However, cross modal-perception was better with photographs than with line drawings.

An experiment of cross-modal matching of objects with their photographs was conducted by Malone et al. [66] with two adolescent male rhesus monkeys. One of the monkeys was trained on visual to haptic matching to sample, and the other on haptic to visual matching to sample (the visual stimuli were full-sized colour photographs of the haptic objects). While both monkeys succeeded on the task, they needed prior training to do so and the authors highlighted that it was unclear whether training was necessary because subjects had difficulty mastering the matching-to-sample procedure, or if they had to learn first the equivalence between photographs and objects. In a subsequent experiment [97], the same subjects were required to perform the same task but with black-and-white photographs, silhouette photographs, and outlines drawings of the objects, that is, forms of stimuli with which they had had no prior training; the monkeys were still able to perform the task when visual stimuli were black-and-white photographs and silhouette photographs, but not with outline drawings.

Zimmermann and Hochberg [114] trained infant rhesus monkeys (5–150 days of age) to discriminate between flat and solid objects (e.g. squares and cubes) and then tested the transfer to photographs and outlines figures of these objects. The results showed that these subjects were able to make consistent responses to pictorial representations of the stimuli (photographs or drawings) and that while the presence of shadow facilitated transfer, this feature was not necessary.

Dasser [14] showed that two Java monkeys were able after a few trials, to identify novel views (full face or full animal) of a familiar conspecific presented on slides, and that another subject could match different body parts of the same familiar group members. In a subsequent experiment, Dasser [15] showed that two adult female Java monkeys, first familiarised with slides of their conspecifics, were able to identify mother–offspring pairs or to match views of offspring to their mother, a task which requires the recognition of group members on the slides.

In a recent study by our group [5], olive baboons were trained on the natural category of food versus non-food with real objects. After categorical transfer with novel items, subjects were trained again with one pair of cut-out pictures each of which belonged to the two previously learned categories; after this limited training, categorical transfer was high in both baboons for cut-out photos of the food and non-food objects. Results of the experiment and of additional control situations involving various modes of picture presentations further demonstrated the abilities of the baboons to relate real objects to their pictorial representations.

A consideration of studies using nonprimates reveals that most of these experiments have been conducted with birds, especially pigeons, but studies with other zoological groups will be considered subsequently. One of the first studies concerned with the question of picture recognition in animals addressed the ability of pigeons to recognise a conspecific shown in a picture [62]. The authors used three pigeons with experimental histories of attacking a mirror target, but not pictures, and submitted them to an intermittent schedule of reinforcement for key pecking; they found comparable results for both temporal pattern and locus of attacks (the head region) to that reported in studies with live, taxidermally stuffed pigeons or mirror targets. Subsequent experiments demonstrated that an upright silhouette, white-on-black silhouette of a pigeon, with or without eye, was more effective in controlling attack than an inverted silhouette, an outline of a pigeon, or a piece of coloured paper.

A study of transfer of discrimination from solid objects to pictures by pigeons was carried out by Cabe [10]. The pigeons, which were naive with respect to pictorial stimuli, were first trained to discriminate two objects, and then four groups of four pigeons were tested in reinforcement reversal with objects, black-and-white photographs, silhouettes or line drawings of those objects; negative transfer was expected in all cases if the pigeons recognised the pictures. In fact, negative trans-

fer occurred with objects (for all four pigeons), with photographs (for three of the four pigeons) and with silhouettes (for all four pigeons), but not with line drawings (none of the four pigeons). Four birds tested only with objects were then re-tested without reversal using black-and-white photographs and showed a positive transfer and, in addition, subsequent training to discriminate objects from their photographs showed that this was fairly easily obtained. These results suggest that the birds did not confound objects and their pictures and, altogether, these experiments also attest that prior experience is not necessary for picture recognition.

Delius [26] trained eight pigeons to discriminate spherical objects from nonspherical objects and following this training, seven birds out of eight were able to transfer to black-and-white photographs, colour photographs, or drawings of these objects, as well as to photographs of novel objects; the overall transfer to black-and-white photographs was best, that to drawings intermediate, and that to colour photographs worst. The author suggested that the pigeons did worst with colour photographs because their colour vision is at least pentachromatic and the colour photography was matched to the trichromatic colour vision of humans. Watanabe [105] trained 12 experimentally naive pigeons to discriminate, for one half, between real objects (edible and nonedible objects) and their photographs, and for the remaining half between food and non-food objects in the same set of stimuli (real objects and their photographs). The pigeons performed high on either task and showed generalisation to novel stimuli for the two tasks, hence demonstrating that pigeons were able to treat photographs like real objects, and to discriminate between them, according to their training and categorical judgement.

Jitsumori and Ohkubo [51] found that four experimentally naive pigeons trained to discriminate right-side-up and upside-down orientations of colour slides of natural scenes depicting humans, transferred this discrimination to new slides of the same kind. Both the orientations of the human figures and of the background scenes controlled this discrimination, but when these slides were oriented in the opposite direction, the background orientation cue was the dominant feature. The birds were also able to categorise by orientation natural objects (humans, apes, monkeys and birds) on a white background, indicating that the subjects recognised the objects presented.

3.2.2. Reactions to motion pictures

Infant chimpanzees [68] and even baboons [102] were able, after limited experience, to match what they observed on a television screen to events occurring elsewhere in order to determine the location of a hidden goal object in a familiar outdoor field. Along similar lines of research, Menzel et al. [69] showed that two chimpanzees could use mirrors or live video images to move their hands in the appropriate direction and make contact with target (food) objects.

It has been demonstrated that fear reactions can also be learned by use of videotaped demonstrators. For example, naive rhesus monkeys acquired a fear of snakes through watching videotapes of conspecifics reacting fearfully to snakes; note however, that the monkeys did not acquire a fear of flowers through watching videotapes of monkeys reacting fearfully to flowers [12].

To summarise, it appears that the experiments presented in this section reveal that picture recognition is possible by animals, even without previous experience. Thus, spontaneous adapted responses were displayed to significant stimuli photographs (prey, predators, or conspecifics) by monkeys. Other mammals (sheep) showed adapted responses to slides of conspecifics and similar responses to pictures of conspecifics were also evident in other species (birds, lizards, fishes and even in some invertebrates) when the pictures were presented in motion; such spontaneous responses to these stimuli did not require any previous training with pictures.

Apes, monkeys and pigeons were also able to transfer acquired responses from objects to pictures in various tasks, however, it is difficult to know in such cases whether familiarisation with the pictures is necessary for their recognition. The methods, species and main findings of the papers that have reported some evidence of picture recognition in animals are outlined in Table 2.

4. Studies with animals: experiments that could indicate picture recognition

This section reviews those experiments which provide some cues indicating the presence of picture recognition but that may not constitute real proof of such an ability.

4.1. Spontaneous responses to pictures

As in the previous section, studies that used still and motion pictures will be considered in turn.

4.1.1. Reactions to still pictures
Humphrey [47] used visual stimuli, either plain fields of light colour, or photographs or films, and a simple choice procedure with two adolescent rhesus monkeys; subjects could push two buttons to choose one of the two stimuli presented on a screen. Humphrey interpreted rhesus monkeys' preferences in terms of 'interest' (determined by the information content in the stimuli) and 'pleasure' (determined by features such as colour and brightness), with these two factors determining the

Table 2
Convincing demonstrations of picture recognition in animals

Task	Nature of pictures	Species	Results	Reference
Matching vocalizations to facial portraits of familiar conspecifics	Black-and-white photographs	Chimpanzee	Correct matching	Bauer and Philip [3]
Behavioural observations	Life-size colour slides	Sheep	Appropriate spontaneous responses to images of conspecifics	Bouissou et al. [4]
Categorization of objects and their pictures into food and non-food categories	Colour photographs	Olive baboons	Correct transfer occurs from objects to pictures	Bovet and Vauclair [5]
Discrimination transfer from two objects to their pictures	Black-and-white photographs or drawings	Pigeon	Correct transfer occurs from objects to pictures	Cabe [10]
Behavioural observations	Black-and-white video images	Jumping spider	Appropriate spontaneous responses to images of conspecifics, prey and heterospecific spiders	Clark and Uetz [11]
Acquisition of fear of snakes or of flowers by observation of conspecifics	Colour video images	Rhesus monkey	Fear of snakes acquired but not fear of flowers	Cook and Mineka [12]
Matching various novel views of a conspecific	Colour slides	Long-tailed macaque	Correct matching	Dasser [14]
Categorization of mother–offspring pairs or matching mother to offspring	Colour slides	Long-tailed macaque	Correct categorization or matching	Dasser [15]
Matching a touched but unseen object to its photograph	Black-and-white and colour photographs	Chimpanzee	Correct cross-modal matching	Davenport and Rogers [16]
Matching a touched but unseen object to various 2-D representations	Black-and-white and colour photographs (life-size and half-size) and line drawings	Chimpanzee	Correct cross-modal matching	Davenport et al. [17]
Categorization of objects and pictures as spherical and non-spherical objects	Black-and-white and colour photographs or drawings	Pigeon	Correct transfer occurs from objects to pictures	Delius [26]
Behavioural observations	Colour video images	Domestic cockerel	Appropriate spontaneous responses to predators	Evans and Marler [34]
Naming the represented objects in American Sign Language	Colour slides	Chimpanzee	Correct naming	Gardner and Gardner [38]
Matching pictures and imitating actions illustrated in pictures	Black-and-white films, photographs, and line drawings	Chimpanzee	Correct matching and imitation	Hayes and Hayes [39]
Behavioural observations	Colour films	Squirrel monkey	Appropriate spontaneous responses to predators, food, and humans	Herzog and Hopf [42]
Behavioural observations	Kodachrome II indoor films (BW or NB unspecified)	Lizard	Female choice of normal male displays	Jenssen [49]
Discrimination of right-side-up and upside-down orientations of scenes	Colour slides	Pigeon	Correct discrimination transfer to novel views	Jitsumori and Ohkubo [51]
Spontaneous choice in a Y-maze between pictures	Life-size black-and-white photographs	Sheep	Discrimination between human and sheep faces, between male and females conspecifics and between a trough with and without food	Kendrick et al. [54]
Behavioural observations	Life-size colour video images	Guppy	Appropriate spontaneous responses to images of conspecifics	Kodric-Brown and Nicoletto [58]
Spontaneous choice between slides of conspecifics	Colour slides	Hamadryas baboon	Choices consistent with social context	Kyes and Candland [59]
Behavioural observations	Colour slides	Long-tailed macaque	Appropriate spontaneous responses to pictures of gorillas and humans	Kyes et al. [60]
Reinforced attack of a pigeon target	Colour photographs and drawings	Pigeon	Attack of the target picture comparable to attack of a live target	Looney and Cohen [62]

Table 2 (*Continued*)

Task	Nature of pictures	Species	Results	Reference
Behavioural observations	Life-size colour video images	Lizard	Appropriate spontaneous responses to images of conspecifics	Macedonia et al. [65]
Cross-modal matching of objects and their photographs	Full-size colour photographs	Rhesus monkey	Correct cross-modal matching	Malone et al. [66]
Behavioural observations	Life-size colour video images	Burmese fowl	Acquisition of preferences for food dishes by observation of conspecifics	McQuoid and Galef [67]
Finding a hidden object with video images used to demonstrate location	Black-and-white video images	Chimpanzee	Correct transfer from video images to real situation	Menzel et al. [68]
Moving their hands to make contact with target objects shown on video	Colour live video images	Chimpanzee	Correct hand movements	Menzel et al. [69]
Behavioural observations	Colour slides	Pigtail macaque	Spontaneous choice and appropriate spontaneous responses to slides of humans and conspecifics	Overman and Doty [72]
Discrimination transfer between various hens and objects to their pictures	Colour video images	Domestic hen	Transfer occurs only when the two stimuli to discriminate have different colours	Patterson-Kane et al. [73]
Electrophysiological recording	Drawings and still video images	Rhesus monkey	Similar neuronal responses to images as to life facial stimuli	Perrett et al. [75]
Behavioural observations	Colour video images	Bonnet macaque	Appropriate spontaneous responses to pictures of conspecifics	Plimpton et al. [77]
Choice of a photograph as the solution to a problem presented in a film	Photographs and film	Chimpanzee	Correct choice	Premack and Woodruff [78]
Discriminations of conspecifics faces and behavioural observations	Slides	Rhesus monkey	Correct discrimination and appropriate spontaneous responses to conspecifics' faces	Rosenfeld and van Hoesen [83]
Behavioural observations	Colour video images	Stickleback	Appropriate spontaneous responses to images of conspecifics	Rowland [85]
Measurement of visual and tactile responses	Colour slides	Rhesus monkey	Visual and tactile responses vary consistently with the nature of stimuli, and with the subjects' age and experience	Sackett [87]
Behavioural observations	Colour slides	Rhesus monkey	Appropriate spontaneous responses to pictures of conspecifics	Sackett [88]
Categorization of objects and their pictures into food and non-food categories	Photographs	Chimpanzee	Correct transfer occurs from objects to pictures	Savage-Rumbaugh et al. [89]
Behavioural observations	Motion and still colour video images	Pigeon	Courtship display to images of conspecifics	Shimizu [90]
Matching an object touched but unseen to various 2-D representations	Black-and-white and colour full-size photographs, silhouettes and outline drawings	Rhesus monkey	Correct cross-modal matching for photographs and silhouettes, but not for outline drawings	Tolan et al. [97]
Behavioural observations	Colour slides	Sheep	Reduction of fear and appropriate spontaneous responses to images of conspecifics	Vandenheede and Bouissou [100]
Finding a hidden object when the location is demonstrated using video	Colour video images	Guinea baboon	Correct transfer from video images to real situation	Vauclair [102]
Behavioural observations	Photographs	Marmoset	Appropriate spontaneous responses to prey and predators	von Heusser [43]
Categorization of objects and their pictures into food and non-food categories, and discrimination between objects and pictures	Colour slides	Pigeon	Correct transfer from objects to pictures, and correct discrimination between objects and pictures	Watanabe [105]
Discrimination transfer between squares and cubes to their pictures	Black-and-white photographs or drawings	Rhesus monkey	Discrimination transfer occurs	Zimmermann and Hochberg [114]

strength and direction of preferences; when the two factors are set against each other, interest overrode pleasure in determining the preference. When naive monkeys were tested for preferences for coloured photographs paired with plain fields of light, they first showed negative preferences and signs of fear. However, as they became more experienced, the signs of fear dropped away and they showed positive preferences for colour photographs (the same pattern of response change was observed when films were introduced instead of photographs). The photographs were divided into six classes, and the rank order of preferences exhibited by the monkeys was 'other animals', 'monkeys', 'men', 'flowers', 'abstract paintings' and 'foods'. In a further experiment, Humphrey [48] used novelty preference for slides to investigate how rhesus monkeys could differentiate between individual animals of the same species; the finding was that monkeys to which domestic animals were unfamiliar treated individual domestic animals of the same species as being closely similar, but treated individual monkeys as being different from each other. However, monkeys who had been exposed for 6 months to many pictures of animals, treated all individuals as different from each other. Demaria and Thierry [27] conducted a rather similar experiment with female stumptailed macaques. These females were submitted to slides displaying individual primates or non-primates and the results showed that subjects looked longer at slides of individuals of their own species than at slides depicting other macaques species; moreover, they looked more at adult females carrying infants than at adult females alone. With pictures of non-primates animals, subjects looked most at slides of felids. However, spontaneous social responses, like facial expressions, were very rare.

Fox [36] observed the responses of young and adult dogs (the breed was not given) presented for the first time with a life-size dog painting. The young dogs sniffed more at hind leg and inguinal regions, while adults sniffed more at ear and anal areas; as all these areas are normally investigated by conspecifics, we can infer that the subjects had perceived the correspondence between the painting and a real dog.

In sheep, Kendrick and Baldwin [53] recorded responses of cells in the temporal cortex of awake subjects and demonstrated that some of these specifically responded to slides (photographs and drawings) of faces (but not to upside-down faces or profiles). Moreover, different groups of these cells were influenced by relevant social factors, such as dominance, breed, familiarity, and facial expression. Franklin and Hutson [37] investigated the reactions of sheep to full-size colour photographs of one sheep and to colour films of moving sheep and found that the sheep reacted to 2-D images as if they were real animals: subjects were slow to approach a sheep facing them, but they approached

without hesitation or followed a sheep displayed in profile; reactions which were heightened when the image was moving. The most attractive stimulus was the film of sheep moving across the screen towards the exit.

Several studies are available concerning the ability of birds to spontaneously display adapted responses to pictures of biologically relevant situations. For example, dark-eyed juncos which could choose between slides of their winter and summer habitats spent more time in front of the pictures that were consistent with their season of capture and laboratory photoperiod conditions compared to the inconsistent habitat [79]. Klopfer [57] performed imprinting tests with Peking ducklings, using various decoys or images and demonstrated that the ducklings followed both decoys and images. However, the images elicited responses that were not strictly equivalent to the three-dimensional decoys; in effect, the ducklings reacted differently to different decoys (according to their colours, and according to those they were accustomed to follow) but not to different two-dimensional representations of ducks. One aspect of the task is particularly interesting in this experiment: the comparison between decoys and images, because the only difference between those two representations is the presence or absence of the third dimension, that is, the lack of three-dimensionality was sufficient to cause a decrease in attention or in responses to feature differences.

4.1.2. Reactions to motion pictures

Rosenthal et al. [84] presented green swordtail females with video-recorded sequences of the same male which was either engaged in an active courtship display, or which performed similar levels of feeding activity, or which remained inactive (control sequences showed food particles in movement or an empty aquarium). Female behaviour patterns differentiated between the pre-stimulus, stimulus and post-stimulus periods for the three stimuli showing a male, but not for the two controls; courtship displays elicited more activity than any other stimulus, and there were no significant differences between the responses to the feeding and inactive sequences.

4.2. Acquired responses in picture recognition

We will now examine studies of acquired reactions which fall into the category of responses that could possibly be evidence for the ability of picture recognition in animals.

In an experiment conducted by Tomonaga et al. [98], a sample of students and a language trained female chimpanzee (called Ai) were trained to recognise video still pictures of individual faces of humans or chimpanzees, presented at various orientations. The experiment yielded two main findings indicative of picture

recognition in the chimpanzee; firstly, it was more difficult for Ai to recognise human faces than chimpanzee's faces, while the opposite was shown for human subjects (they had more difficulty recognising chimpanzee's faces than human faces) and, secondly, it was more difficult for her to recognise inverted faces or horizontal faces than to recognise upright faces (a similar, but more pronounced effect being obtained with human participants). It must be noted that experiments conducted with macaque monkeys [8,83] failed to show this inversion effect, but this could be due to differences in processing rotated complex visual stimuli. For example, monkeys and some apes could be more suited to doing this type of rotation because they live in an environment in which they often hang upside-down [103], the above findings do not, therefore, necessarily imply that subjects were unable to recognise the pictures presented. Nevertheless, Swartz [93] showed, with a visual fixation habituation–dishabituation paradigm, that infant pigtail macaques (3 months old) could discriminate between colour photographs of faces of three macaque species (pigtail, cynomolgus, and stumptailed) when they were presented upright, but not when the faces were displayed upside-down.

Other experiments using schematic drawings of monkeys' bodies indicate that longtailed macaques were able to discriminate one monkey from other monkeys, basing their recognition on the limited information provided by the black-and-white shape and texture of their body characteristics [31]. Such findings, however, do not present any obvious interpretation regarding picture recognition. Firstly, as stated by the author of the above study "it remains questionable whether the monkey has a knowledge of the representational nature of the image" (Dittrich [31], p. 150). Secondly, we know from other studies that monkeys can correctly categorise images of different classes of stimuli by using some absolute cues which are not constitutive of the to be categorised stimuli. For example, D'Amato and van Sant [13] have shown that their monkeys used an irrelevant red patch to form the 'person versus non-person' category. Thus, caution is in order before concluding that seemingly appropriate classification skills mean that the animal realises the relationship between a picture and the real object.

Watanabe and Ito [106] trained pigeons to discriminate between colour slides of two pigeons' faces. While discrimination was apparently effortless for two stimuli easily discriminated by human observers, it was difficult with the stimuli which humans also struggled to differentiate. When the S+ stimulus was replaced by its scrambled parts, subjects did not respond; such a reaction seems to indicate that the birds recognised that the stimuli depicted on the slides represented conspecifics (which could be recognised only when the faces were not scrambled).

Lumsden [64] conducted an experiment with one pigeon; the bird was trained to discriminate one geometric object from two others, after which transfer was examined when the object, its cut-out photograph, or its line drawing was shown at various orientations. Response curves were the same for photographs and for three-dimensional objects: generalisation was good at 0, 45, and 135°, poor at 180°, and was absent for 90°. Although the line drawings were responded to at the lowest rate, the pattern of responding was similar. In a subsequent experiment, the pigeon was trained to discriminate between the object and its photograph displayed at 45°: the bird then generalised that discrimination to photos presented at other orientations. We should note however that there was only one subject involved in this experiment.

Wilkie et al. [108] trained four pigeons to discriminate between pictures taken in the vicinity of the loft to which they had been raised and other areas they had not visited, with four other pigeons that were not trained to home being tested as a control. The results showed that after training with only eight slides, both groups were able to transfer and then to discriminate the two categories of slides, but homing pigeons were better than nonhoming pigeons. In the same paper, the authors mention the experiment of Honig and Ouellette [45], in which eight pigeons were taught to discriminate colour pictures of various views of two ends of a long room. Following this task, the pigeons had to discriminate between the two ends of the real room; a feeder was placed at each end of the of the test room but only one feeder contained food: for the congruent group, it was in the same location that had been positive during the previous slide discrimination procedure, while for the incongruent group, it was the opposite end of the room. The subjects in the congruent condition took consistently less time to find the correct feeder than the incongruent subjects. In a similar study, Wilkie et al. cited an unpublished study by Willson et al. [109] in which eight pigeons were placed outside the laboratory for 20 min prior to each training session in a picture discrimination task; for four of the pigeons the place they had seen outside was presented as the positive stimuli ('relevant place'), whereas for the other four pigeons, the visited place was not pictured at all ('irrelevant place'). The 'relevant place' birds acquired the discrimination more quickly than did the 'irrelevant place' subjects. Such experiments suggest that pigeons can perceive the correspondence between pictorial stimuli and the place they represent.

The above findings provide further information regarding the issue of picture recognition. In some experiments, animals showed differential preferences for pictures and appeared to be able to discriminate between them. However, they did not treat them as the conspecifics they represented: for example macaques

did not display social behaviour toward pictures of conspecifics [27,47] and ducklings did not react to the pictures in exactly the same way as they did with decoys [57]. In other experiments, behaviours were indicative of picture discrimination [79,84] but were not specifically directed toward the stimuli. While visual experience with real locations can facilitate the discrimination of photographs by pigeons, and vice versa, it is not yet clear how this facilitation occurs.

Table 3 summarises the methods, species and main results of the studies that could be indicative of picture recognition in animal species.

5. Difficulty with picture recognition

This section reviews those studies which show a difficulty or failure of the subject to react to 2-D stimuli as if they were meaningful or 3-D stimuli.

5.1. Spontaneous responses

It is important to note that socially salient stimuli presented as pictures do not always elicit overt responses in birds or even in monkeys. Butler and Woolpy [9] studied visual attention in rhesus monkeys submitted to various slides or motion pictures of other rhesus monkeys but their results are not easy to interpret because they appear to be quite contradictory; the amount of visual attention given to slides of conspecifics was not different from attention devoted to an homogeneous illuminated screen. Such a result seems to imply that the monkeys did not recognise the slide as representing one of their conspecifics although viewing behaviour (and thus attention) was more important (i.e. monkeys looked longer) when motion pictures were projected in the normal orientation than when they were projected upside-down.

Table 3
Experiments which could indicate picture recognition in animals

Task	Nature of pictures	Species	Results	Reference
Behavioural observations	Paintings	Dog	Sniffing the areas normally investigated on conspecifics	Fox [36]
Behavioural observations	Life-size colour slides and films	Sheep	Following images of conspecifics	Franklin and Hutson [37]
Transfer of discrimination of two ends of a room from pictures to real places	Colour slides	Pigeon	Transfer occurs	Honig and Ouellette [45]
Choice between two visual stimuli (plain field or various stimuli)	Colour slides and films	Rhesus monkey	Consistent choice	Humphrey [47]
Novelty preference	Slides	Rhesus monkey	Discrimination of individuals depends on subjects' experience	Humphrey [48]
Electrophysiological recording	Colour slides and black-and-white drawings	Sheep	Specifics cells in the temporal cortex respond to faces	Kendrick and Baldwin [53]
Behavioural observations	Colour film	Pekin duckling	Spontaneous following of moving ducks	Klopfer [57]
Transfer of discrimination between objects at various orientations to pictures	Cut-out photograph and line drawing	Pigeon	Same type of curve depending on object orientation, but overall level of responding considerably less	Lumsden [64]
Measurement of time spent in front of slides of habitats	Colour slides	Dark-eyed junco	Spontaneous choice of appropriate habitats according to the season	Roberts and Weigl [79]
Measurement of female interest	Colour video images	Green swordtail	Frequency of behavior patterns in females depends on the male courtship	Rosenthal et al. [84]
Discrimination between faces of three macaque species	Colour photographs	Pigtail macaque	Difficulty recognizing inverted faces	Swartz [93]
Discrimination between faces of chimpanzees and humans individuals	Colour video still pictures	Chimpanzee	Difficulty recognizing inverted faces	Tomonaga et al. [98]
Discrimination between pictures of locations	Colour slides	Pigeon	Discrimination between pictures facilitated by prior experience with the location	Wilkie et al. [108]
Discrimination between pictures of locations	Colour slides	Pigeon	Discrimination between pictures facilitated by prior experience with the location	Willson et al. [109]

Social recognition experiments which used pictorial stimuli with hens, failed to indicate any transfer of discrimination from live birds to photographs [19]: hens preferred flock-mates rather than unfamiliar conspecifics (even when they saw only their heads and necks) when presented with live stimuli, but they failed to show any preference with photographic stimuli. Similar findings were observed in a study of hens shown video sequences [21]: hens neither took longer to eat near unfamiliar conspecifics than near flockmates, nor near high-ranking flockmates than near low-ranking flockmates, as they usually did when they saw live stimuli behind a clear screen. Pigeons also failed to exhibit any natural social response when they were presented with life-size moving video images of conspecifics [86].

5.2. Acquired responses

5.2.1. Reactions to still pictures

Winner and Ettlinger [110] trained two chimpanzees with no prior experience with photographs in a matching-to-sample task. First, the subjects had to match real objects to real objects and subsequently had to match objects with their photographs. Initially, they were unable to perform the task successfully with performance remaining at chance levels for the first 4 days and then rising moderately, but not consistently, above chance. The second experiment of Winner and Ettlinger attempted to replicate the results obtained by Davenport et al. [17] (see above); in their experiment, two chimpanzees with no prior experience with photographs were required to transfer a discrimination between pairs of objects that were felt but not seen to their photographic representations or vice versa. The new subjects responded significantly above chance when tested only with objects and at chance level when required to transfer a learned response from a felt object to a photograph or from a photograph to a felt object. The authors suggest that in Davenport et al.'s experiment the objects were not paired by size: consequently, subjects might have succeeded by choosing the bigger one.

Jitsumori [50] has also demonstrated that picture recognition is difficult for untrained animals. The task consisted of training four monkeys (two of them had prior experience with discrimination problems between pictures containing or not containing monkeys) and four experimentally naive pigeons to discriminate between normally oriented displays and top–bottom reversals. If the monkeys saw meaningful objects in these slides, then transfer was supposed to occur with various novel slides; subjects were trained with a go/no-go discrimination task with colour pictures of full humans, and then tested with other pictures of humans, monkeys, birds, mammals and man-made objects. Both monkeys and pigeons showed good transfer to novel human pictures but when tested with other pictures, levels of performance revealed considerable interindividual variation, namely, in pigeons and in nonexperienced monkeys transfer was relatively good for some pictures but not for others. Thus, the overall performance was inconsistent and successful transfer might be explained by perceptual similarities among the slides presented in a fixed orientation. In this study, only one of the experienced monkeys produced results suggestive of the perception of meaningful objects in pictures.

Another experiment [19] attempted to establish whether or not transfer between geographical locations and photographs of those locations occurred in homing pigeons. Eight pigeons were trained to discriminate photographs of two geographical locations, having been given visual experience of a real geographical location beforehand. Half of the birds were transported to one of the two locations that appeared in the photographs, while the remaining subjects were transported to a third, 'irrelevant' location. Although there was no significant difference in acquisition or transfer to novel stimuli between the two groups, the authors suggest that this might be due to their methods (inadequate amount of experience outside or lack of immediate reward for learning about the environment), but also to differences between human and bird vision (see above). Moreover, it is possible that the pigeons were processing the far-distance views and the near-distance views in different manners.

A study with laying hens by Bradshaw and Dawkins [7] attempted to replicate the experiment performed by Dasser [14] (see above) with macaques. Hens were trained to discriminate between slides of either familiar or unfamiliar conspecifics and were then presented with novel views of these birds; during training, the right-hand side of a hen's head was presented, whereas the novel stimulus set was composed of pictures of left-hand side of the corresponding hen's head, a frontal view, or a view of the tail or feet. The birds failed to generalise discrimination from training slides (both familiar and unfamiliar) to novel view categories and the authors concluded that their study provided no evidence that the hens perceived the slides presented as representations of their group members. Ryan and Lea [86] obtained somewhat comparable results in a study in which pigeons and chickens were trained to discriminate between slides of two individuals (two pigeons or two chickens). For both species, the chicken slides were learned faster and better than the pigeon slides, with the pigeons' performances being much worse than chickens' on both chicken and pigeon stimuli. Moreover, only one pigeon out of six was able to discriminate slides of pigeons, and none learned to discriminate between two different stuffed pigeons, even though a subsequent experiment proved that they readily discriminated individual live pigeons.

Table 4
Experiments showing difficulties recognizing pictures in animals

Task	Nature of pictures	Species	Results	Reference
Discrimination between pictures of familiar or unfamiliar conspecifics	Color slides	Laying hen	Discrimination not facilitated by familiarity	Bradshaw and Dawkins [7]
Behavioural observations	Black-and-white and colour slides and motion pictures	Rhesus monkey	No spontaneous responses; no more attention to slides of conspecifics than to a homogeneously illuminated screen	Butler and Woolpy [9]
Spontaneous discrimination between familiar and unfamiliar conspecifics, either live or presented on photographs	Life-size colour photographs	Domestic hens	Discrimination occurs for live hens but not for photographs of hens	Dawkins [18]
Discrimination between pictures of locations	Colour slides	Pigeon	Discrimination between pictures of locations is not facilitated by experience	Dawkins et al. [19]
Spontaneous discrimination between familiar and unfamiliar conspecifics, either live or presented on video	Life-size colour video sequences	Domestic hens	Discrimination of live hens but not for those presented on video	D'Eath and Dawkins [21]
Discrimination of right-side-up and upside-down orientations of scenes	Colour slides	Monkey and pigeon	Difficulty transferring discrimination to various classes of slides	Jitsumori [50]
Discrimination transfer between various hens and objects to their pictures	Colour video images	Domestic hen	Transfer occurs only when the two stimuli to discriminate have different colours	Patterson-Kane et al. [73]
Discrimination of individual pigeons and chickens and behavioural observations	Colour slides and moving video images	Pigeon and chicken	Great difficulty in identifying novel views of an individual, no spontaneous responses	Ryan and Lea [86]
Categorization of objects and their pictures into food and non-food categories or into arbitrary categories	Colour slides	Pigeon	Correct transfer from objects to pictures occurs only for a natural category (food)	Watanabe [104]
Matching an object touched but unseen to its photograph	Black-and-white and colour full-size photographs	Chimpanzee	Failure to match objects with their photographs	Winner and Ettlinger [110]

A study by Watanabe [105] is particularly interesting in the discussion of picture recognition because it suggests that object–picture equivalence can be performed relatively easily when there is some functional basis. Twenty-four pigeons were divided into four experimental groups: two object-to-picture groups and two picture-to-object groups; one of the object-to-picture groups and one of the picture-to-object groups were trained on a natural concept (food objects were S + for half, and non-food objects were S −, and it was the opposite for the remaining half) while the other two groups were trained on a pseudoconcept (an arbitrary grouping of edible and nonedible objects as positive and negative stimuli). When tested with the natural concept, the subjects showed a good transfer of discrimination in both object-to-picture and picture-to-object conditions, but no transfer was observed with the pseudoconcept. Such a result indicates that picture recognition can depend on the consistency of the task.

5.2.2. Reactions to motion picture

Attempts to train domestic hens to transfer from real stimuli to video images generally produced negative results, although, depending on experimental conditions, the birds could use some features of the patterns (e.g. the colour) in their discrimination [73]. It was concluded from this study that complex video images, such as those required to recognise social stimuli, are not equivalent to the real stimuli. In addition, some pigeons did not transfer a learned discrimination from live conspecifics to their photographs and had great difficulties in discriminating between slides of individuals (although they easily discriminated live conspecifics).

The results of the studies reported in this section are somewhat contradictory to the findings summarised in Sections 3 and 4. In effect, they demonstrate that picture recognition in animals is not obvious and is dependent on experimental factors. In several experiments, monkeys and birds (such as pigeons and chicken) failed to display an interest in photographs of conspecifics. Moreover, different tasks involving picture recognition have reported a failure to demonstrate such an ability; thus chimpanzees failed to realise a cross modal matching and only one monkey (out of four), which was

already familiarised with photographs, was able to discriminate the orientation of photographs. In addition, it was shown that experience with a particular place did not facilitate the discrimination between that location and another. Finally, it was shown that when tested with a natural concept (food), pigeons transferred a discrimination from object to picture and vice versa, but they did not demonstrate such transfer when they were tested with an arbitrary pseudoconcept. In brief, the experiments summarised in this section highlight the importance of biological relevance in picture recognition tasks.

Table 4 presents an outline of the investigations that demonstrated a failure to recognise pictures in animals.

6. Conclusion

One of the main conclusions of this survey is that visual stimuli presented as pictures (either as black-and-white photos, colour photos, slides, or videos) are not necessarily immediately recognised by non-human and even human subjects. In this final section, we will summarise the principal results concerning picture recognition in the much-studied species and attempt to identify some of the factors which may be responsible for the apparent difficulties in recognising pictorial stimuli. Finally, we will suggest some possible steps which could be useful in describing picture processing; ranging from feature discrimination, to correspondence, and ultimately, to strict equivalence between a 3-D object and its pictorial representation and a consideration of the issue of confusion between pictures and the objects they represent.

6.1. Summary of main findings

Very young humans appear to be able to recognise photographs from 2 or 3 months of age and at an even earlier age they are likely to discriminate real objects from their pictorial representations. Paradoxically, picture recognition seems to present greater difficulties for adults who are unaccustomed to seeing photographs and drawings. Thus, it could be hypothesised that such an ability is innate but that this ability diminishes if the person has grown up without opportunities to see 2-D representations. In this case (which is less and less likely to happen in contemporary societies), such individuals are accustomed to seeing the world of objects around which are inevitably characterised by the presence of features like colours, depth, and motion parallax; when presented with pictures, these people, who have lived in an exclusively 3-D environment, would experience difficulties and some familiarity and/or training with pictures would then be required in order to recognise the stimuli which lack those features.

The available literature is quite convincing concerning the abilities of several animal species familiar with pictures to recognise such 2-D stimuli. In mammals in general (but with most evidence coming from experiments conducted with monkeys and apes), it also seems that picture recognition is possible for both adults and young even if the animals have never been exposed to any picture prior to the experiment. In this latter case, recognition seems to be more difficult and appears to depend on the nature of stimuli and on the experimental conditions (see below). Some experiments, in which subjects have to transfer what they have learned with real objects to the pictures of these objects (e.g. in cross-modal transfer between touch and vision), have shown that these tasks present serious difficulties for the subjects. Furthermore, because some training is often necessary in order to perform picture recognition tasks, the training phase probably allows subjects to get familiarised with pictures prior to testing; this requirement implies that subjects are rarely naive with respect to viewing pictures or their discrimination.

The studies reporting spontaneous responses to pictures are interesting because they can provide useful indications on the perceptual and cognitive processes involved in picture recognition performed by truly naive subjects. These studies have shown that monkeys and other mammals (sheep and dogs) can, at first sight, adaptively respond to various animals or foods (although pictures of conspecifics seem to be responded more easily to than pictures of other categories of stimuli) presented on slides. We can speculate that this ease presumably expresses the fact that these animals confuse the real objects and their pictures; nevertheless, this recognition can be quite precise, if we consider that some animals are able (e.g. [4]) to differentiate individuals from their own breed from individuals belonging to other breeds. It is also worth noting that transfer is generally better for pictorial stimuli which better match (at least for a human viewpoint) real objects, that is, motion films are more easily recognised than still pictures, slides are better recognised that colour photographs, the latter leading to better performance compared to black-and-white photographs and line drawings.

It may be an interesting observation that in the first section of our review (convincing demonstrations), studies concerning mammals are more numerous than studies concerning birds, and that the opposite is true of the third section (difficulties with picture recognition). Actually, the pattern of results obtained with birds is quite different compared to other zoological groups; a divergence which may be explained in part by the fact that bird vision is different from mammal vision. With regard to pictures, photographs used in experiments with these animals are usually matched for human vision and lack some critical features of birds'

vision, such as UV light [111], and offer false colour representations for these subjects because the stimuli are based on the trichromatic colour vision of humans and not on the pentachromatic vision of birds (e.g. [33]). Motion pictures are also matched for human vision. In motion pictures, still images are shown in succession to produce the impression of a continuous moving image. But the frequency at which a flickering stimulus starts to appear continuous is higher in birds (notably in pigeons and in chicken) than in humans [20,107]. Further, chickens are myopic (they can recognise a conspecific only at a very short distance [18]) and it is possible that they process far-distance views in a manner distinct from that used for near-distance views. The above considerations may thus explain some of the problems encountered by birds in interpreting pictures and why, for example, transfer is sometimes better for black-and-white photographs than for colour photographs. Nevertheless, some of the experiments reported earlier showed a good transfer from objects to pictures or confusion between the slides or films and the animals they represented.

Finally, a handful of studies have convincingly demonstrated that responses to pictures are not limited to birds and mammals; reptiles, fishes and even invertebrates reacted strongly to video images depicting biologically significant stimuli (conspecifics, prey or predators, for examples). It is, however, not surprising that animals of different phyla respond to salient visual cues in similar ways, i.e. as they would respond to real objects; for many years, experimental ethology's techniques have used visual lures for identifying the stimulus characteristics of social and aggressive behaviour in animals (e.g. the pioneering and now classic studies employing cardboard models of a Herring gull's head by Tinbergen and Perdeck, [95]).

6.2. Factors influencing picture recognition

The experiments reported in the section on acquired responses to pictures fail to provide a clear and definitive answer to the question of capacities of different animal species for processing pictorial representation of objects. Given that the most advanced and detailed studies have been conducted with birds, it may be useful to list some of the factors that authors have highlighted as playing a determining role in the extent and limits of picture recognition. Some of these factors have been summarised in the discussion of d'Eath and Dawkins' [21] article reporting a failure of domestic hens to discriminate between familiar and unfamiliar conspecifics on videos and are thoroughly described in the review by d'Eath [20]. A first and obvious factor has to be mentioned: pictures, being still or in motion, are abstractions from the reality they represent. Thus, even if birds predominantly use visual cues to identify social

stimuli, auditory and olfactory information are also present in encounters with real conspecifics but absent in pictorial stimuli. Moreover, viewing a real conspecific involves an interplay and exchange between the pair of animals; this aspect of social interactions is also lacking when the animals are presented with pictures. Thus, because the picture cannot duplicate any interaction between the viewer and the stimuli, a discrepancy between the real object and the picture quickly becomes apparent and renders the picture unrealistic and unchallenging for the viewer.

Further, the experimental context of picture recognition presents subjects with stimuli which are reduced along physical dimensions, such as the size (sometimes), the colour and stereoscopic and motion parallax cues used for perceiving depth. It should not be forgotten that pictorial stimuli are abstract objects, which, because of their bi-dimensionality and because of the other factors just mentioned, do not show all the visual cues provided by real objects; such a reduction in the informational content prevents the establishment of a strict equivalence between real objects and their representations.

A crucial factor in facilitating picture recognition is related to the nature of the stimulus object; experiments with animals have clearly demonstrated that categorisation of biologically relevant objects, such as food, is readily generalised to photographs depicting the same objects (see Ref. [105] for an example with pigeons and [5] for an example with monkeys). Conspecifics and predators also appear to be good stimuli for picture recognition as shown by the evidence gathered with birds [34], sheep [54] or macaques [14]. It is apparent that interest for 2-D images, given their relative poverty compared to real objects, can be reinforced if those objects represent significant stimuli that belong to the animal's natural and/or social environment. To formulate the latter point in more general terms, it can be stated that the value of the stimulus (e.g. familiarity or/and experience with the to be recognised object) will shape and facilitate discrimination and recognition based on pictures (e.g. [48]).

Another factor, which seems obvious but is not always considered, is the complexity of the pictures presented, for example, very simple stimuli, like geometric shapes or animals' silhouettes (like those used by Cabe, for example, [10]), might be more easily perceived than complex photographs. This feature could explain why the transfer observed in the preceding study was better than that obtained with photographs of complex scenes, such as those used by Dawkins et al. [19].

It is also important to note that the actual features of the 2-D stimuli used by the subjects to solve a pictorial task often remain unknown. In birds, such features can be very different from those employed by humans. For example, Troje et al. [99] tested pigeons in a categorisa-

tion task of human faces according to sex; the birds solved the task by using textural information, i.e. surface properties (average intensity of images, and other properties not yet totally identified, such as colour of the skin, vertical intensity gradient, local contrast, etc.) rather than by using shape. The pigeons chose the textural information despite the fact that the shape contained information more useful for this task than texture (a preference which is reversed in humans).

When considering the factors influencing picture recognition, some experiments can be particularly interesting, such as those in which the only difference between the presented stimuli is the presence or absence of the third dimension. For example, Klopfer's experiment [57] (and see above) compared the effect of 3-D decoys and 2-D images of ducks: the lack of the third dimension was sufficient to cause a decrease in attention or in responses to variation in features. The same was true for Vandenheede and Bouissou's [100,101] experiments; ewes showed fear reactions to a real human or a human-like model but not to a colour full-size human slide. Thus, the absence of the third dimension appears to be the unique factor which could explain the lack of fear in ewes. In contrast, Ryan and Lea [86] showed that pigeons could easily discriminate individual conspecifics when the stimuli were live pigeons, but not when they were photographs or stuffed pigeons; what seemed to be important for the pigeons for recognising individuals was not the third dimension, but the presence of movement or/and vocalisations. Similarly, Kodric-Brown and Nicoletto [58] presented female fish with three conditions: (1) live males, (2) live males behind one-way glass (to prevent any interaction), and (3) images of males displayed on videotapes. The results indicate that a live male was more attractive only when interactions were possible; when interactions were not possible, a videotaped male was as attractive as a real male. However, this type of experiment (allowing the comparison between two situations with or without 3-D) is quite rare and it is generally more difficult to detect a single factor which could influence the subjects' behaviour.

At this point, it might be useful to envision that at least three stages could be considered with respect to the level of precision and the nature of the relationship between the object and its picture.

6.3. Stages in the relations between real objects and their pictures

One can postulate that the first and minimal step for picture perception implies an ability on the subject's part to discriminate one or a few salient visual feature(s) on the picture (e.g. a form, a colour or any other relevant information) which is necessary and sufficient to assess its recognition. Many examples were provided

in this review to indicate that animals belonging to different phyla may react to a picture as they would react to the real object (for example by displaying adequate social responses). Given the very nature of pictures (e.g. their bi-dimensionality, the fact that they do not necessarily show all visual cues provided by real objects, such as depth or motion), the next step would imply that the subjects establish some correspondence between objects and their photographed representations. A criterion for assessing such a correspondence was suggested by Wilkie et al. [108] (and see above), in their study on perception and memory for places in pigeons; this criterion is called 'transfer of influence' and refers to the fact that knowledge gained with the real stimulus (or its picture) affects subject's reactions with the picture (or the real object). Again, several cases were mentioned in this survey in favour of the existence of such a correspondence and let us now consider a final example. In an investigation of individual recognition in budgerigars, Trillmich [96] trained one bird with colour slides of other budgerigars as sample stimuli and this discrimination showed generalisation to live bird models. Further, discrimination transfer was also found in the other direction; namely, with live budgerigars serving as sample stimuli and picture slides of those same birds as test stimuli.

The final level to be considered is that of the equivalence; in this case, subjects might form a true equivalence between the real object and some or all of the dimensions presented on the picture. Some criteria can be proposed to differentiate object–picture correspondence from object–picture equivalence. A quite obvious criterion for equivalence refers to the ability demonstrated by a subject for bi-directional discrimination transfer from real objects to their pictures and from pictures to real objects. A second and more stringent criterion would be met if the subject showed an ability to acknowledge some identity between an object and its picture when the picture carries only some visual dimensions of the real stimulus, or/and that the visual information is altered in some ways; cross-modality matching experiments (see above) using not only photos but drawings, outlines, etc. of the real objects, offer valuable approaches to test the stability and the limits of the equivalence established between these connected aspects of objects.

6.4. The problem of the confusion between objects and their pictures

An important question related to the issue of picture recognition concerns the interpretation of the data as revealing either true recognition or a mere confusion between a stimulus and its picture. This issue of deciding between the two kinds of processing is especially relevant in the context of the experiments that investi-

gate subjects' spontaneous reactions to biologically significant stimuli. Some empirical evidence for distinguishing between the two interpretations can be found in the studies with sheep cited above, in particular, when the sheep stopped expressing interest in the picture of a conspecific when it realised that it was not a 'true' sheep [100]. In the experiments involving some sort of training (e.g. our category of acquired responses), the same difficulty arises in deciding whether responses express merely the confusion between the pictures and their referents or true recognition. For example, the pigeons tested by Watanabe [105] were able to differentiate food versus non-food, or real objects versus pictures, but these same subjects were unable to simultaneously perform both kinds of discrimination. Similar interpretation problems occur concerning successful cross-modal matching performance by nonhuman primates; it is by no means obvious that these subjects know that the picture they see is not the real object (e.g. [16]).

Even for human infants and children, the distinction between objects and pictures can be unclear. Deloache et al. [25] showed that 9-month-old infants (from two very different cultures regarding their familiarity with pictures) were quite similar in their manual investigation of colour photographs: they touched them and tried to pick them up off the page as if they were real objects. However, a subsequent experiment clearly demonstrated that the infants were able to discriminate between pictures and real objects, in the sense that they preferentially grasped real objects. A possible explanation is that the infants investigated the pictures to try to understand their two-dimensional nature and their properties; pictures appear like real objects in some ways, but they are not. As concluded by the authors, "physically grasping at pictures helps infants begin to mentally grasp the true nature of pictures" ([25], p. 210). This manual investigation is gradually replaced by pointing at the pictures, which constitutes the predominant behaviour at 19 months of age. The question of equivalence between an object and its picture can also be raised regarding young children who had to retrieve a hidden toy from a location shown on a picture. Deloache and Burns [23] (and see above) showed that 24-month-olds were unable to perform such a task, although children of the same age and even infants can recognise pictures of familiar individuals (e.g. their mother). Moreover, an experiment with 30-month-old children has shown that they could retrieve an object whose location was shown to them on a picture but, perhaps surprisingly, these same children could not solve this task when the information was provided using a scale model; a task which might appear easier given the high degree of iconicity that exists between the symbol (the model) and the reality [22]. It seems that this surprising difference comes from the perception of the model; for the children of this age group, the

model is an interesting object per se, not the image of another thing. In the same way, when 2-year-old children could see a video of a demonstrator hiding an object, they retrieved the object if they thought that they were looking through a window but not when they knew that they were watching the same scene on video. For the authors, the children did not treat the televised information as real information, although they could perceive and understand that information [24].

An important point concerning picture recognition is illustrated by the above examples and it is emphasised by the expression used by Deloache et al. [24]: the development of pictorial competence involves three 'Rs', namely representation, referent, and relation. In effect, it is not enough to see a picture only as a piece of paper or as the object represented because real pictorial competence requires understanding the relation between pictures and their referents. Such an understanding is observed when 19-month-old children, instead of trying to grasp pictures, will point and try to name them [25].

It is also possible for some animals to establish object–picture correspondence and at the same time to show evidence that the two are not perceived as being the same. In fact, a clear case of a possible recognition of the difference between an object and its picture can be found with a linguistically trained chimpanzee (e.g. the example of Vicki mentioned above) who showed an ability to refer to objects represented on pictures (by using a token) without confusing them with real objects (see also Ref. [89]). A related instance is provided in our study with olive baboons [5]; upon seeing cut-out pictures of food objects shown to them in rotation, the baboons never attempted to grab them (as they did with real food), although they were still able to adequately categorise them with respect to the food versus non-food categories.

In any case, the decision concerning the nature of the relationship perceived by animals between real world stimuli and their pictorial representation (being a photograph, a digitised picture or a video) will remain problematic. In his recent review of the use of video images in animal behaviour experiments, d'Eath [20] observed that even if an animal responds adequately upon viewing biologically relevant video stimuli, a further demonstration that such a response is produced as a specific reaction to the particular stimuli used by the experimenter has to be provided. In this respect, some studies (e.g. [86]) have shown that an unrelated class of visual stimuli, and even the screen itself, can elicit a seemingly adapted response! In other words, systematic controls are required before concluding that the presentation of pictorial stimuli has the same behavioural effects as would the objects they represent.

A final remark is in order; namely, that it is surprising to observe that the questions we have addressed in this review have received relatively little attention in the

literature concerned with perceptual processes in both animals and humans. Moreover, the evidence at hand, which is summarised in this paper, is fairly controversial and by no means presents a definitive explanation regarding the process of picture recognition. It is, therefore, our hope that the present review will contribute to launching additional investigations towards a better understanding of the nature of the cognitive representations which underlie picture recognition both in animals and in humans.

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