



Categorical learning in pigeons: the role of texture and shape in complex static stimuli

Nikolaus F. Troje^{a,*}, Ludwig Huber^b, Michaela Loidolt^b, Ulrike Aust^b,
Martin Fieder^b

^a *Max-Planck-Institut für biologische Kybernetik, Spemannstr. 38, 72076 Tübingen, Germany*

^b *Biocenter, Universität Wien, Althanstr. 14, 1090 Wien, Austria*

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Abstract

Pigeons are known to be able to categorize a wide variety of visual stimulus classes. However, it remains unclear which are the characteristics of the perceptually relevant features employed to reach such good performance. Here, we investigate the relative contributions of texture and shape information to categorization decisions about complex natural classes. We trained three groups of pigeons to discriminate between sets of photorealistic frontal images of human faces according to sex and subsequently, tested them on different stimulus sets. Only the pigeons that were presented with texture information were successful at the discrimination task. Pigeons seem to possess a sophisticated texture processing system but are less capable in discriminating shapes. The results are discussed in terms of the possible evolutionary advantages of utilizing texture as a very general and potent perceptual dimension in the birds' visual environment. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Ethologists and psychologists have long pondered the riddle of how animals can categorize stimulus classes containing instances so variable that we cannot physically describe either the class rule or the underlying capacity. Pigeons have demonstrated their capacity to categorize a wide variety of stimuli, for example, people, pigeons, man-made objects, trees, water, oak leaves, fish, landscapes, artificial faces and even paintings by Monet and Picasso (Herrnstein & Loveland, 1964; Siegel & Honig, 1970; Lubow, 1974; Herrnstein, Loveland & Cable, 1976; Cerella, 1979; Herrnstein & De Villiers, 1980; Honig & Stewart, 1988; Watanabe, Sakamoto & Wakita, 1995; Huber & Lenz, 1996). However, the fact that pigeons also fail to learn certain categorization tasks is evidence that they are not limitlessly malleable by reinforcement on the stimulus side (Lea & Ryan, 1990; Ryan & Lea, 1994).

Categorization can be conceptualized as grouping discriminable objects or events together in order to respond similarly to them. According to the standard terminology (Keller & Schoenfeld, 1950), categorization involves both generalization within and discrimination between classes. Categorization is the basis for any identification and classification task and accordingly, has an enormous biological relevance. It is involved in identifying locations, food, prey and predators, as well as distinguishing conspecifics from other animals, males from females and recognizing individuals. The ability to recognize individual conspecifics is a particular prerequisite for the evolution of any social system involving hierarchies within the group and bonding between individuals.

Pigeons can perform complex classification tasks on the basis of purely visual cues. In a seminal experiment, pigeons readily discriminated between pictures in which a particular person was visible and pictures that did not contain this concept (Herrnstein & Loveland, 1964). In that early period, research on animal concept discrimination has been largely influenced by concepts from human cognitive psychology (Poole & Lander, 1971;

* Corresponding author. Present address: Department of Psychology, Queen's University, Kingston, Ontario K7L 3N6, Canada. Tel.: +1 613 5456000; fax: +1 613 5452499; e-mail: niko@psyc.queensu.ca.

Lubow, 1974), often leading to a questionable interpretation of the original findings in terms of human language concepts.

When Greene (1983) repeated and slightly modified the original experiments of Herrnstein & Loveland (1964), she could show that the birds' performance was not based on the concept of a person being present or not. In contrast, the results of Greene's experiments indicated that the birds had memorized features of individual stimuli by rote. In fact, behavior was mainly controlled by the background of the images, that is, by features that were irrelevant to the concept imposed by the experimenter.

Such results emphasize the need for a more ecological approach, sought to study classification from the bird's eye view. In the spirit of Brunswik (1956), Garner (1974), Shepard (1984), and Gibson (1966), perception should be studied as it occurs in the natural environment, focussing on the basic aspects of the stimulus to which the pigeon is preadapted (see Fetterman (1996) for a recent review).

The methodological problem is, however, as Herrnstein (1985) has already acknowledged, that pigeons can categorize at levels of abstraction that defy both explanation and simulation, but they do not have to. Despite the huge body of work with this bird species and the ambitious surveys through this literature—see reviews in Herrnstein (1984), Lea (1984), Herrnstein (1985, 1990), Watanabe, Lea & Dittrich (1993); Fetterman (1996) see also several chapters in Commons, Herrnstein & Wagner (1983); Commons, Herrnstein, Kosslyn & Mumford (1990); Honig & Fetterman (1992); Zentall (1993)—we are far from completion of a list of the perceptually important features in the pigeons' discrimination performances.

One reason for this is the difficulty of compiling a list of features occurring in the perceptual environment and the lack of reasonable concepts to classify and sort them into a handy framework. Almost any stimulus aspect can be regarded as a feature. Features are nowadays no longer considered as the atoms of the stimuli, i.e. constant stimulus elements that could serve as the building blocks of more complex objects that compose the natural world (Fetterman, 1996). Features can vary with the context and tasks in which stimuli are presented (Blough, 1985). What is extracted from the environment depends on learning and experience, leading to the view that features are a product of the perceiver. A further complicating fact is that natural categories are typically polymorphous in nature; no single stimulus aspect is likely to be a necessary or sufficient condition for category membership (Herrnstein, 1985). Therefore, it is often difficult to specify, on the basis of the subjects' response patterns, the exact array of stimulus properties exploited, let alone the underlying perceptual or cognitive mechanisms (von Fersen & Lea, 1990).

Recently, a very basic subdivision of stimulus attributes has been made in the context of describing the information contained in the images of human faces by addressing the spatial arrangements of stimulus features on the one hand and their particular appearance on the other hand (Beymer & Poggio, 1996; Vetter & Troje, 1997). Consistent with Vetter & Troje (1997)—see also Troje & Vetter (in press)—we will use the terms 'shape' and 'texture' to address these two parts. Note, that usage of the term 'texture' is in accordance with its meaning in computer graphics where the texture of an object is meant to be its color or gray-level map. This differs slightly from the common usage of this term in visual perception and pattern recognition¹.

The role of an object's shape for recognition and classification has been subject to innumerable investigations in different species. There is also a number of investigations on texture perception in birds and other vertebrates, but most of them inquire into the role of texture in the context of segmentation tasks (Cook, Cavoto & Cavoto, 1995; Wasserman, Hugart & Kirkpatrick-Steger, 1995), the ability to acquire an abstract concept of an oddity in same-different experiments (Cook, Katz & Cavoto, 1997a; Cook, Cavoto, Katz & Cavoto, 1997b; Cook & Wixted, 1997c) and two-alternative forced choice experiments, e.g. in fish, (Bando, 1991, 1993). However, in none of these investigations has texture been treated as a major part in complex, natural stimuli: the information that remains if a stimulus item is normalized with respect to its shape. Consequently, none of these investigations has contrasted the pigeons' capability to perform classification on the basis of texture information or on the basis of shape information.

It is surprising that, despite the impressive progress physiologists and psychologists have made in understanding the pigeon's visual capacities, few have endeavored to investigate the relative roles of these most fundamental stimulus properties. One reason for this may be the difficulty of using appropriate stimuli. On the one hand they should be complex enough to contain both shape and texture information relevant and diagnostic for class membership. On the other hand,

¹ There exists no generally accepted definition of the term 'texture' in the literature. Probably due to its origin in the tactile appearance of a surface (i.e. its roughness), the term 'texture' as used in visual perception and pattern recognition often stands for repetitive visual structures similar to the ones resulting from the pattern of light reflected from rough three-dimensional surface structures. Used in this latter sense, first-order statistical properties, such as average luminance or average chromaticity are not necessarily considered to be 'texture' properties. In contrast to this intuitive usage of the term 'texture', some authors do treat average intensity as a texture property (e.g. Julez, 1981). The way the term 'texture' is used in computer graphics (and also in this paper) does include color and luminance too.

they should be manageable such that the experimenter can control and quantify the amount of shape and texture information.

We chose human faces as stimuli and the concept ‘sex’ as class definition, for three reasons:

(1) The two categories, ‘male’ and ‘female’, are natural categories that are consistent with natural stimulus variation and are assumed to be evolved to be classified correctly. Although it is not easy to quantify the differences between them, they provide enough differences to be easily discriminated by humans (96% correct, (Bruce, Burton, Hanna, Healey, Mason, Coombes, Fright & Linney, 1993)) as well as artificial neural networks (98% correct, (Troje & Vetter, in press)).

(2) Pigeons are probably naive with respect to the task of classifying human males and females. Training is thus completely under the control of the experimenter. We don’t expect them to understand something about or even respond to the semantic contents of the images a priori.

(3) Human faces provide complex variations in both shape and texture. Vetter & Troje (1997) have developed a representation of human faces that provides a straightforward way of separating these two aspects.

In the experiments reported here, we compared the classification performance of three groups of pigeons. The three groups were confronted with different versions of the same set of stimuli, differing according to the amount of shape and texture information they contained. In Experiment 1, we measured learning curves in a go/no-go learning paradigm. The first group (Group O) was presented with the original set of images showing frontal views of male and female human faces. These images contained both shape and texture information. For the second group (Group T) we used the same set of images, but with the shape of the faces normalized, so that all faces had the same average shape and only texture information could be used for classification (‘texture-only’ images). The faces shown to the third group (Group S), contained the same average texture and thus provided only shape information (‘shape-only’ images). In Experiments 2–4, pigeons were tested by interspersing single test stimuli into the series of training stimuli. In Experiment 2, we tested the pigeons’ performance in generalizing to a novel set of stimuli of the same type as experienced during training. Experiment 3 tested the amount of texture and shape information used by the animals of Group O that had access to both types of information during training. Experiment 4 was designed to verify whether the pigeons used particular image attributes, such as average intensity or size of the heads. Group T was tested with images normalized for their shape (as in Experiment 2) and also for their overall intensity. Group S was tested with images normalized for their texture (as in Experi-

ment 2) and also for their overall size. In Experiment 5 we measured learning curves from pigeons of both Groups S and T using the same training paradigm as in Experiment 1. However, this time, all animals had to learn to discriminate between images that were normalized for their shape and overall intensity.

2. Methods

2.1. Subjects

We obtained 24 pigeons (*Columba livia*) of a local race (‘Strasser’) from an Austrian breeder. The pigeons were randomly divided into three subgroups that we will call Groups O, T and S. Each group was kept in a separate compartment of a large (54 m³) outdoor aviary. Water and grit were freely available in the aviary, but food was provided only in the learning boxes during and after the experimental sessions. The birds were maintained at a slightly lower rate of their free-feeding weights. All pigeons were experimentally naive at the onset of Experiment 1. The experiments were run sequentially. Pigeons of Group O participated in Experiments 1–3. Pigeons of Groups T and S participated in Experiments 1, 2, 4 and 5. One pigeon of Group T had to be removed from Experiment 5 due to illness.

2.2. Stimuli

The stimuli were derived from laser scanned three-dimensional models of faces of 100 men and 100 women. The faces were free of any kind of accessories like glasses or earrings. Men were shaved and the hair of the head was digitally removed from the models (Troje & Bülhoff, 1996). The 200 face models were randomly subdivided into two groups (Set A and Set B), each containing 50 male and 50 female faces. For each single pigeon, one set served as training set and the other as test set.

Images were rendered in frontal view using only ambient light and a black background (Fig. 1a). Viewing as well as illumination conditions were held constant. Any variability in size and luminance was due to natural differences in head size and in skin complexion of the subjects.

From the original images, we derived different stimulus sets for the different experiments. We used a technique described in Vetter & Troje (1997), to create image sets providing only texture information and image sets providing only shape information to be used for sex classification. We refer to these image sets as ‘texture-only’ and ‘shape-only’ stimuli, respectively. The separation was done by using a correspondence based image description that allows for the subdivision of the



Fig. 1. Examples for the different types of stimuli used. (a) A male and female face as rendered from the 3D faces models. These images contain both their original texture and shape. (b) Texture-only stimuli. They are derived from the original images by combining the original texture of the face with the average shape of the whole data base. The images thus differ only in texture. (c) Shape-only stimuli derived by combining the original shape of the face with the average texture. (d) Texture-only stimuli with ambiguous intensity information. The male face is somewhat lighter than the female face. (e) Shape-only stimuli with ambiguous size information. The male face is somewhat smaller than the female face.

information contained in the image into ‘texture’ and ‘shape’ (Vetter & Troje, 1997). Then, the original texture of each image was combined with the average shape of the whole database to yield a set of images which differed only in texture but not in shape (texture-only, Fig. 1b). Similarly, we produced a set of images differing only in shape by combining each face shape with the average texture of the whole database (shape-only, Fig. 1c).

For Experiments 4 and 5, we needed texture-only image sets with a defined average image intensity. The intensity of the image was multiplied by a scaling factor to achieve the desired average intensity. For Experiment 4, image intensity was rescaled such that female faces now had the average intensity of the original male faces and vice versa (Fig. 1d). For Experiment 5, the intensity of all images was rescaled such that all had the same, namely the overall average intensity of the whole data set.

For Experiment 4, we also needed a set of shape-only images with defined size. The original size of each face was given by the expansion term of the deformation field transforming the average shape into the shape of the exemplar face (Vetter & Troje, 1997). Image size was rescaled such that all female faces now had the average size of the original male faces and vice versa (Fig. 1e).

2.3. Apparatus

We used three experimental indoor chambers, each connected through a passage-way system with one outdoor aviary compartment (Huber, 1994). The experimental chambers were standard one-key operant chambers for pigeons. The interior size of the wooden chambers was 50 × 30 × 40 cm. The front panel was equipped with a pecking key and a food hopper. The oversized, clear perspex, pecking key (5 cm diam, ENV-125M, MED Associates, USA) was mounted in the center of the panel 28 cm above the floor. A 6 × 6 cm aperture for the food hopper was directly below the key (8.5 cm above the floor). The pigeon grain feeder (ENV-205M) featured a 28 V DC solenoid activated hopper designed to ensure reliable delivery of grain to the bird. A hopper light illuminated the receptacle area whenever grain was accessible. During the experiments, the chamber was weakly illuminated by a 2 W house-light (ENV-215) located in the rear part of the chamber. All images were presented at a size of 64 × 64 pixels ($\approx 2 \times 2$ cm) in full color against a black background on a 15 inch (38 cm, diagonal) PC monitor (Panasonic PanaSync 4G) at a distance of 5 cm behind the clear pecking key. The stimulus presentation procedure was controlled by three Pentium PCs, one for each chamber, running a Delphi program that selected the patterns according to a pre-specified sequence. The

MED behavioral control package, including a computer interface card (DIG-704) inside a Pentium PC, a modular interface (SG series, DIG-711, DIG-721) and the behavioral control software (MED-PC for Windows), was used to control events in the operant chambers, to signal onset and offset of presentation to the presentation PCs (via separate communication interfaces) and to register responses.

2.4. Procedure

Pigeons were first trained to enter the box voluntarily (a description of this voluntary training method can be found in Huber (1994)), to find food in the hopper and finally were autoshaped by standard methods to peck at the illuminated key. The widely used go/no-go procedure (Vaughan & Greene, 1984), required the birds to peck in the presence of positive stimuli and to withdraw from pecking in the presence of negative stimuli. Each animal ran one session per day consisting of 40 trials. A trial started with the presentation of a stimulus and finished with the fulfilment of the response requirement. Pecks were counted only in the first 10 s of a trial. The images remained visible at least during a further variable interval (mean: 10 s, range: 1–20 s) and then until the response requirement was accomplished. If the stimulus was positive, the first response to occur within 2 s of a previous response produced 5 s of access to food. In contrast, responding to a negative pattern caused a continuation of the trial which terminated only if 8 s had passed without a response occurring. In such trials no reinforcers were delivered. Trials with neutral contingency were terminated immediately after the first 10 s, during which the pecks were counted. Each trial was followed by a 4-s intertrial interval, during which the houselight was turned on. The intertrial interval ended with a short dark phase that signalled the presentation of the next stimulus.

The pigeons of each group were arbitrarily assigned to the two different stimulus subsets (A and B) and the two possible reinforcement conditions (male + /female – and male – /female +). Experiment 1 was a pure training experiment consisting of two training phases. In Training I, a subset of ten pictures was presented four times in each 40-trial session. On consecutive days, different images were shown so that a pigeon completed a whole cycle of the 100 images from either Set A or Set B within 10 days. We ran four of these cycles. In Training II, the same 100 pictures were used, but now 40 different images were shown only once per session. This phase lasted for at least ten sessions and was then continued until the subject performed five consecutive sessions in which significant discrimination was demonstrated ($P < 0.05$, Mann–Whitney U-Test). If this criterion was not fulfilled within 30 sessions, Training II was terminated.

Experiments 2–4 were transfer experiments in which the pigeons were confronted with randomly inserted test images. In Experiment 2, each of the ten sessions consisted of the presentation of 30 training stimuli and ten novel stimuli from the test set. Each test stimulus was shown only once. Reinforcement conditions were as in Experiment 1 for both training and transfer stimuli. The experiment was completed after ten sessions.

In Experiments 3 and 4, only four test stimuli were inserted into each 40-trial session. Reinforcement to the training stimuli was similar as in Experiment 1 except that the test trials came with neutral contingency. As such trials led neither to a positive nor a negative consequence, there is no reason to assume that subjects would update their classification strategy. In Experiment 3, both the 100 texture-only and the 100 shape-only stimuli were tested with the same animals. During a single session, however, all four test stimuli were either texture-only images or shape-only images. Texture and shape sessions were intermixed randomly. Experiment 3 lasted for 50 sessions. In Experiment 4, each bird saw only the texture-only stimuli or the shape-only stimuli. This experiment thus lasted for 25 sessions. Experiment 5 was again a pure training experiment and followed exactly the same scheme as Experiment 1.

2.5. Data evaluation

The pecking rate in response to each stimulus was automatically registered during the first 10 s of stimulus presentation. For each pigeon, each pecking rate was then divided by the average over all pecking rates measured from that bird during the current 40-trial session. All further calculations were based on these normalized pecking rates. To evaluate the discrimination performance of the pigeons, we used the ρ (rho) discrimination measure introduced by Herrnstein, Loveland & Cable, (1976). This value equals the probability that the rank for the response to a positive stimulus is above that to a negative. The ρ -value is derived from the Mann–Whitney U-statistic, by dividing the value of U by the product of the numbers of positive and negative stimuli contributing to its calculation. We use the ρ -value on two different levels. First, ρ -values were computed for each animal and each session ($n = 40$) to describe the temporal course of learning of a whole group in Experiments 1 and 5. Second, we computed ρ -values based on responses to the whole stimulus set ($n = 100$) to evaluate the final discrimination performance of single pigeons at the end of Experiments 1 and 5 and also to quantify the performance in the other experiments. In the case of Experiments 1 and 5, we used the pecking rate emitted to the last presentation of each image as a score when ranking

the images in order to calculate the ρ -value. The ρ -values in the other experiments were based on the pecking rate emitted to the single presentation of each test stimulus and on the pecking rate emitted to the first presentation of each training stimulus.

In Experiments 2–4, we also compared the normalized pecking rates to positive and negative stimuli and to training and test stimuli. Analyses of variance were used to compare the means.

3. Results

3.1. Experiment 1: training

The three groups of pigeons were trained to classify different sets of images by means of the sex of the faces shown. Group O was presented with the original images, Group T with texture-only images and Group S with shape-only images.

Classification learning produced a strong behavioral differentiation in an early stage of training: Groups O and T learned very quickly and accurately, while Group S was significantly worse. Fitting hyperbolic functions to the data to model the learning behavior revealed very steep curves in the two former cases but a very flat curve in the latter case (Fig. 2). Half-maximal performance was reached after < 5 sessions by Groups O and T but was still not achieved by the end of the 40th session by Group S.

The final performance at the end of Training II, as given by the mean ρ -value computed by ranking all 100 stimulus images, is shown for each single animal in Table 1. The subjects of groups O (mean ρ -value: 0.86) and T (mean ρ -value: 0.78) were able to distinguish perfectly male and female faces. With a single exception, all birds reached ρ -values whose corresponding P -values were below 0.001 (Mann–Whitney U-Test). Group S performed much worse (mean ρ -value: 0.62). Only four of the eight pigeons in this group achieved ρ -values with corresponding P -values smaller than 0.05.

Experiment 1 revealed that the pigeons exploit texture, but not shape, as the main source of information to learn the association between the images and reinforcement. One important question is to what extent the acquired knowledge can be generalized to novel stimuli. The very steep learning curves for the pigeons of Groups O and T are already indicative of the ability to generalize to new stimuli even at a very early stage. However, since each single image was shown four times in each session, the results could also be based on a very proficient ability to learn each single image by rote (Vaughan & Greene, 1984). To investigate generalization performance more explicitly, we tested the trained pigeons with 100 novel images from the complementary set of faces.

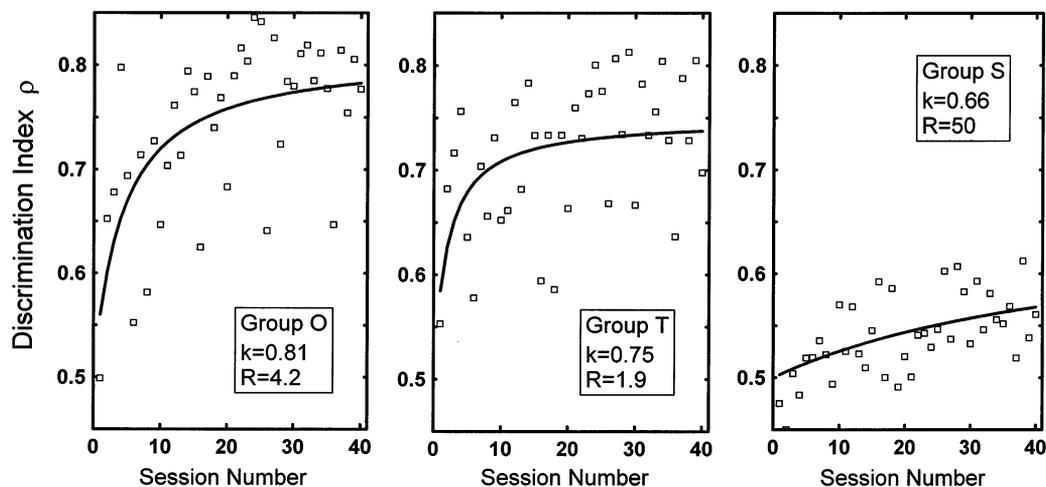


Fig. 2. ρ -values as a function of session for the three groups during Training I in Experiment 1. Group O was provided with the original images containing both texture and shape information, Group T with texture-only images and Group S with shape-only images. Lines fitted to the data plot the hyperbolic equation $\rho = 0.5 + n(k - 0.5)/(n + R)$, a convenient description of many negatively accelerated learning curves (Mazur & Hastie, 1978). n denotes the session number, k stands for the asymptote for performance and R is the learning rate expressed by the number of sessions needed to reach half-maximal performance.

3.2. Experiment 2: generalization to new faces

For all three groups, there was no difference between the pecking rates emitted to training and test stimuli (Fig. 3). Generalization seemed to be perfect for Groups O and T, whereas Group S showed poor performance with both the test and the training stimuli. We computed a repeated measures, two-way analysis of variance (ANOVA) with class (positive vs negative) and stimulus (training vs test) as variables for each group separately. For Groups O and T, this revealed a significant effect of the factor coding for stimulus class (Group O: $F(1,7) = 177$, $P < 0.001$, Group T: $F(1,7) = 32.3$, $P < 0.001$) but no effect for the factor coding for training versus test stimuli nor any interaction between the two factors. For Group S, the class factor had a marginal effect ($F(1,7) = 5.6$, $P = 0.05$) and there was also no effect for the second factor nor any interaction between them.

We also analyzed the performance of single pigeons. Pigeons that classified the faces with ease in Experiment 1 also performed well in Experiment 2 (Table 1). With only two exceptions, classification in this transfer test was significantly beyond the $P = 0.001$ level (Mann–Whitney U-test) for all animals of Groups O and T. Response rates to the test images were nearly identical to those to the training patterns shown in these sessions. Although taken as a group, the S subjects failed to show good transfer, this was different for some individuals. Three of the four subjects that eventually reached reasonable performance in Experiment 1 did also succeed in generalizing to novel patterns.

3.3. Experiment 3: transfer from original images to texture-only and shape-only images (Group O)

In Experiments 1 and 2, animals of Group T performed much better than animals of Group S. This indicates that texture information is used more readily than shape information by the pigeons. Based on this finding, we predicted that the pigeons in Group O that were presented with stimuli containing both texture and shape information also relied primarily on texture information. To verify this prediction, we tested Group O with both the 100 texture-only test images that were shown to Group T in Experiment 2 and the 100 shape-only test images that were shown to Group S in Experiment 2.

The results of this experiment are illustrated in Fig. 4a. The pigeons performed much better with the images providing texture information (mean ρ -value: 0.749) than with those providing shape information (mean ρ -value: 0.587). Discrimination performance on the training stimuli was about the same as in Experiments 1 and 2 (mean ρ -value: 0.842). Discrimination performances on the test images are comparable to those obtained from Groups T and S in Experiment 2 and worse than those obtained from Group O in Experiment 2.

Although, for the shape-only images, the mean ρ -value of the whole group was not significant, four of the eight animals did show significant ($P < 0.05$) discrimination. This is also comparable to the behavior of Group S in Experiments 1 and 2.

The results of this experiment also supports our hypothesis that the information contained in the texture of the stimuli is more accessible to the pigeons than the

Table 1
 ρ -values ($n = 100$) for single birds of Groups O (first block), T (second block) and S (third block) in Experiments 1–5

Pigeon	Experiment 1	Experiment 2		Experiment 3		
		Training	Test	Training	Test T	Test S
O-71	0.86	0.86	0.87	0.85	0.84	0.67
O-72	0.83	0.91	0.77	0.90	0.76	0.63
O-75	0.91	0.90	0.84	0.85	0.74	0.68
O-76	0.87	0.84	0.80	0.91	0.75	0.52
O-73	0.90	0.96	0.88	0.85	0.79	0.64
O-74	0.78	0.72	0.80	0.78	0.68	0.58
O-77	0.88	0.82	0.81	0.73	0.67	0.48
O-78	0.82	0.88	0.83	0.87	0.77	0.49
Mean	0.86	0.86	0.82	0.84	0.75	0.59

Pigeon	Experiment 1	Experiment 2		Experiment 4		Experiment 5
		Training	Test	Training	Test	
T-60	0.80	0.75	0.67	0.72	0.56	0.86
T-63	0.78	0.75	0.75	0.73	0.44	0.76
T-66	0.63	0.67	0.69	0.78	0.59	—
T-67	0.81	0.78	0.78	0.73	0.64	0.88
T-64	0.71	0.61	0.58	0.70	0.42	0.56
T-65	0.85	0.78	0.80	0.78	0.60	0.85
T-68	0.81	0.95	0.88	0.85	0.69	0.80
T-69	0.82	0.77	0.71	0.82	0.43	0.80
Mean	0.78	0.76	0.73	0.76	0.55	0.77
S-01	0.54	0.49	0.55	0.58	0.41	0.59
S-02	0.63	0.68	0.73	0.68	0.54	0.86
S-51	0.64	0.52	0.53	0.47	0.46	0.52
S-52	0.79	0.63	0.76	0.72	0.45	0.79
S-03	0.56	0.46	0.53	0.50	0.45	0.72
S-54	0.69	0.55	0.71	0.56	0.48	0.83
S-04	0.48	0.51	0.41	0.46	0.54	0.58
S-50	0.59	0.52	0.56	0.49	0.40	0.65
Mean	0.62	0.54	0.60	0.55	0.47	0.69

All data are based on a single presentation of each stimulus. ρ -values larger than 0.60, 0.64 and 0.68 correspond to significance levels of $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively (Mann–Whitney U-test). ρ -values larger than 0.64 ($P < 0.01$) are given in bold face.

information contained in the shape. However, both seem to be used at the same time. The discrimination performance of Group O, as measured in Experiment 2, in which the pigeons had both sources of information available is approximately equal to the sum of the performances measured in response to texture-only and shape-only stimuli in this experiment supporting a linear feature integration model as used by Lea & Ryan (1990), Huber & Lenz (1993) and Jitsumori (1993).

3.4. The role of average intensity and size

The distinction between shape and texture is important but coarse. Which stimulus parameters within the texture domain did the pigeons use and which parameters within the shape domain were used by the

few successful S subjects? Male and female faces differ on average in both size and average intensity. The average male face is larger and darker than the average female face. Whereas size is a shape attribute, average intensity is a texture attribute. In order to find out whether the pigeons used these cues, we computed the rank correlation between pecking rates to individual faces and either the size or the average intensity of the faces. The pecking rates associated with each single image used for this calculation was the mean of the normalized pecking rates emitted to the last 16 presentations of each stimulus in Experiment 1. To exclude the partial correlation between pecking rate and sex which is not due to the parameter under investigation, we computed the correlation separately for only the male and for only the female faces (Table 2). Pecking rates of almost all animals of

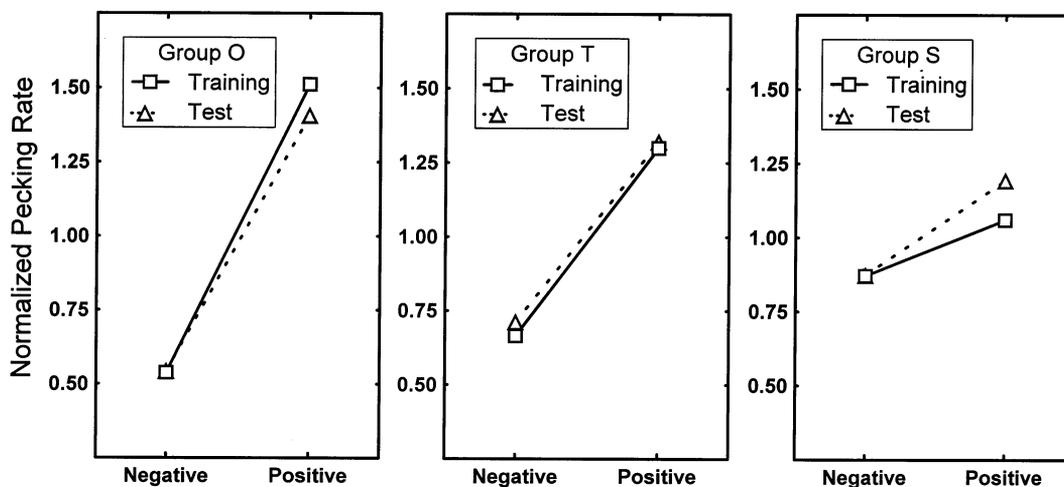


Fig. 3. Normalized pecking rates emitted to positive and negative training stimuli as well as positive and negative test stimuli in Experiment 2. Normalized pecking rates were computed by dividing the pecking rate by the average over all pecking rates measured from the same bird during the current 40-trial session. Each data point contains the averaged data of eight subjects.

Groups O and T showed significant correlations with intensity, but no correlation with size. Pecking rates of S-subjects did not correlate with average intensity, but for the four animals with reasonable classification performance there was a weak correlation with size. Pigeons of Groups O and T thus seemed to use the intensity of the face as a cue to discriminate between male and female faces. In Group T, however, there was one interesting exception: The pecking rate of the pigeon that generally showed the highest ρ -value of all T-subjects (T-68) did not at all correlate with intensity.

To what extent can average intensity be responsible for the good performance of Groups O and T? To answer this question, we ranked the images by their average intensity. The ρ -value ($n = 100$) corresponding to the resulting order is 0.787. If pigeons relied only on average intensity of the stimulus, even this value could only be reached if the pecking rates were perfectly correlated with image intensity. However, correlations between pecking rates and image intensity are much smaller than 1. The ρ -values, on the other hand, are often larger than the value of 0.8 (Table 1). The good performance of the O and T subjects cannot be explained by assuming that pigeons used average image intensity as a cue exclusively.

A similar analysis was used to determine to what extent size differences between male and female heads accounted for the performance of the few S subjects that managed to reach reasonable levels of discrimination. The ρ -value corresponding to the images ranked by the size of the faces is 0.924. Size thus provides a very efficient cue. Half of the S subjects appeared not to be able to use this cue at all. However, for the animals that did reach significant ρ -values, size may have been an important cue.

3.5. Experiment 4: transfer to stimuli with ambiguous intensity (Group T) or size (Group S) information

Average intensity is a major component contained in the texture and overall size is a major component contained in shape. In order to investigate explicitly the role of average intensity and size, we subjected the pigeons of Groups T and S to a second test measuring their spontaneous response to images with ambiguous information. The average intensities of texture-only images were rescaled such that female faces now had the average intensity of the original male faces and vice versa. If pigeons from Group T had classified the images by means of their average intensity then the performance should break down completely and pecking rates should even show a reversed tendency. Likewise, the size of the faces shown in the shape-only images was rescaled such that all female faces now had the size of the original male faces and vice versa. Male heads were now smaller than female heads and if the S-pigeons had used size as a cue, their pecking behavior should now be reversed.

The results are illustrated in Fig. 4b and c. The ρ -values are listed in Table 1. A 2×2 repeated measures ANOVA was performed separately for Groups T and S. Pecking rates of Group T were higher on training stimuli than on test stimuli ($F(1,7) = 13.08$, $P < 0.01$) and higher on positive than on negative stimuli ($F(1,7) = 14.86$, $P < 0.01$). The interaction between the two factors was highly significant ($F(1,7) = 26.24$, $P < 0.005$), indicating that the very good performance on the training stimuli (paired t -test: $t = 4.85$, $P < 0.005$) decreased to a level at which the difference was no longer significant ($t = 1.50$, $P > 0.1$) for the test stimuli. However, there was still slightly more pecking on the positive than on the negative stimuli. Group S

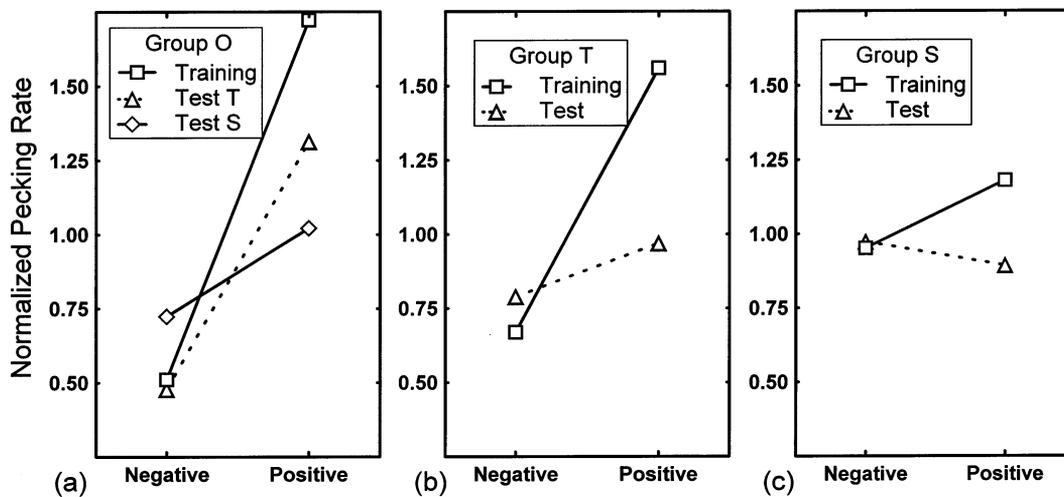


Fig. 4. (a) Normalized pecking rates to positive and negative stimuli of the eight pigeons of Group O participating in Experiment 3. Training: training stimuli; Test T; texture-only test stimuli; Test S: shape-only test stimuli. (b), (c) Normalized pecking rates emitted to positive and negative stimuli as well as to positive and negative test stimuli of pigeons from Group T and Group S in Experiment 4.

pecked slightly more frequently on training stimuli than on test stimuli ($F(1,7) = 5.69$, $P < 0.05$), but there was no difference between the responses to positive and negative stimuli, on average. A significant interaction between the two factors ($F(1,7) = 6.32$, $P < 0.05$) indicates the tendency to reverse the pecking behavior on the test stimuli. Size differences apparently played a major role in the classification strategy of the successful animals of Group S.

3.6. Experiment 5: learning intensity-normalized texture-only stimuli

So far, the experiments have shown consistently that pigeons use texture rather than shape to solve the discrimination task. At this point, we want to consider which kind of information contained in the texture is used. Experiment 4 already showed that performance dropped, if the average intensities of the images of male and female faces were exchanged. Average intensity obviously was used as a cue, but it could not have been the only one. The pigeons' behavior was not reversed as would have been expected if intensity had played such an important role. Furthermore, we have shown that the maximal ρ -value that theoretically could be reached by exclusively employing average intensity information is considerably smaller than those that were actually reached. We assume that pigeons used average intensity among other cues because it was offered as a cue during training. How good would they perform after a complete training cycle with images lacking any differences in average intensity?

Pigeons in this experiment were trained to classify intensity-normalized texture-only images. Pigeons of Groups T and S participated (one pigeon of Group T had to be dropped because of illness).

Learning curves are plotted in Fig. 5. The animals of Group T performed even better than in Experiment 1. The animals of Group S performed worse than Group T but still much better than they did with the shape-only images in Experiment 1. This becomes even clearer from the classification performed at the end of Training II (Table 1).

As both groups were trained on the same stimuli, the difference between their performances has to be due to their previous experience with the faces. The fact that the animals of Group T reached slightly better performance than in Experiment 1, although less information was provided this time, also argues for long term learning effects. Pigeons are well known for having a very efficient long-term memory (Vaughan & Greene, 1984). The average performance of the S pigeons is still poor but the variability within this group is large (Table 1). Three animals were unable to learn the task at all. This is probably due to the long and unsuccessful experience in the course of the other experiments that may have affected their motivation. An impairment in learning due to an experience of 'helplessness' is well described in the literature (Overmier & Seligman, 1967; Seligman, 1975). Note, that the S Group pigeons at this stage had been trained continuously on shape-only stimuli (not containing any texture differences) for several months without managing to solve the task. However, the other five animals performed very well and even those that couldn't learn to discriminate the shape-only stimuli did pick up the cues in the texture and finally reached discrimination rates comparable to those reached by the T animals.

The most important result of this experiment is the fact that all the pigeons of Group T, with one exception and at least some of the pigeons of Group S, were able

to discriminate the textures of male and female faces even without being able to use average intensity as a cue.

4. Discussion

Pigeons performed exceptionally well in classifying human faces by their sex. The present results suggest that the classification scheme that develops during training is predominantly based on information contained in the texture of the faces rather than in their shape. In the few cases where shape information was sufficient, the main cue used was apparently the size of the face.

One cue that pigeons were able to use within the texture domain was the average intensity of the images. However, deprived of this cue, pigeons were still able to

Table 2

Spearman rank correlations between normalized pecking rates and either average intensity or size of the images for individual pigeons

Pigeon	Intensity		Size	
	Positive	Negative	Positive	Negative
O-71	-0.57	-0.56	-0.07	0.27
O-72	-0.51	-0.52	-0.10	0.13
O-75	-0.61	-0.44	0.20	0.19
O-76	-0.41	-0.41	0.22	0.13
O-73	0.40	0.67	-0.28	-0.04
O-74	0.65	0.78	-0.05	0.18
O-77	0.59	0.42	-0.00	-0.23
O-78	0.69	0.66	0.02	-0.03
T-60	-0.73	-0.74	-0.25	0.11
T-63	-0.77	-0.76	-0.23	0.08
T-66	-0.59	-0.65	-0.19	-0.06
T-67	-0.76	-0.66	-0.13	0.20
T-64	0.58	0.75	-0.17	0.20
T-65	0.68	0.87	0.07	0.20
T-68	0.21	-0.10	0.07	-0.05
T-69	0.73	0.38	-0.12	0.08
S-01	-0.14	0.04	0.11	-0.09
S-02	0.11	-0.15	0.53	0.45
S-51	0.05	-0.03	-0.29	-0.08
S-52	0.18	0.23	0.32	0.06
S-03	0.00	0.06	-0.19	-0.03
S-54	0.06	-0.23	-0.24	-0.41
S-04	-0.02	-0.04	-0.13	-0.02
S-50	0.07	-0.06	0.11	0.02

The pecking rates used to compute the correlations are normalized pecking rates for individual images averaged over the last 16 presentations of each stimulus in Experiment 1. Average intensity was computed in terms of the average pixel intensity of the texture-only images. Size was given by the expansion term of the deformation field transforming the average shape into the shape of the exemplar face (Vetter & Troje, 1997). Correlation coefficients larger than 0.24, 0.33 and 0.45 correspond to significance levels of $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively. Correlation coefficients larger than 0.33 ($P < 0.01$) are given in bold face.

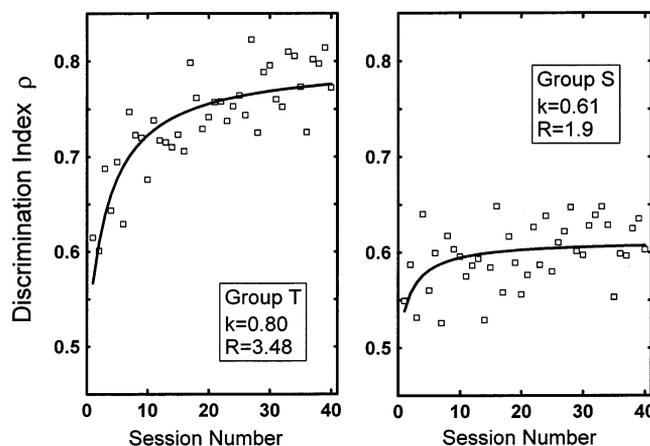


Fig. 5. Learning curves as measured in Experiment 5. The upper curve shows the performance of the seven animals of Group T in response to intensity-normalized texture-only stimuli during the first 40 sessions, the lower curve the performance of the eight animals of Group S presented with the same images. The lines fitted to the data plot the hyperbolic function $\rho = 0.5 + n(k - 0.5)/(n + R)$.

solve the task. Further experiments have to be designed to reveal the nature of the relevant stimulus attributes within the texture domain. Pigeons might have used simple cues such as the color of the skin (that seems to differ slightly between men and women) or differences in the vertical intensity gradient caused by beard shadows in male faces, or more complex cues based on a comparison between color distributions in different parts of the face. Texture attributes such as the local contrast, homogeneity and entropy are further candidates to be subjected to a more detailed investigation.

The experiment was an exercise in animal visual categorization. Considered from a purely behavioral standpoint, the present outcome fits seamlessly into the list of pigeons' complex concept formation (Herrnstein, 1985; Watanabe, Lea & Dittrich, 1993). Presented with the proper stimuli, the pigeons learned quickly and generalized widely. Although pigeons have strong resources for learning specific exemplars (Vaughan & Greene, 1984; von Fersen & Delius, 1989) and have also displayed surprising cognitive capacities (Emmer-ton & Delius, 1993), neither categorization in terms of exemplar memorization nor in terms of abstract concept formation is plausible to explain the results of our experiments. Common to both these approaches is the underestimation of the pigeon's ability to instantaneously adopt a perceptual description of visual classes that are corresponding to natural categories (Cerella, 1979). Interestingly, there have been many unsuccessful attempts to teach pigeons man-made classes (e.g. bottles, chairs and wheeled vehicles; reported in Herrnstein (1985)). Evidently, these and probably other such failures have never been published.

The surface properties of objects establish a feature domain that provides enough possibilities for a code to

reflect the actual distribution of reinforcement in the environment (Haralick, 1979; Pentland, 1984). Unfortunately, such image aspects have never been seriously considered as providing the appropriate descriptors of seemingly complex stimulus classes. Much effort, in contrast, has been made in constructing artificial categories out of simple forms like line-drawings to control for feature content (Morgan, Fitch, Holman & Lea, 1976; Cerella, 1980; Lea & Ryan, 1990; Huber & Lenz, 1993, 1996). Even in the recent case of pigeons classifying photographs of human faces according to their facial expressions (Jitsumori & Yoshihara, 1997), performance was controlled by an additive integration of simple salient form aspects like open or closed mouths. As the authors admit, the separability of these features implies that the findings can hardly be generalized to the categorization of natural stimuli. In fact, employing the more natural class structure in the present experiments showed that surface properties are not only sufficiently informative for pigeons to easily classify a particular complex natural category but are, at least for this species, superior to shape attributes.

Support for our conclusion can be found in two studies on budgerigar conspecific recognition (Brown & Dooling, 1992, 1993). The authors investigated explicitly the perceptual salience of several stimulus attributes using a same–different paradigm in which photographs of real birds and schematic drawings were shown. The features that were most important for discrimination were color of head, pupil and cere as well as the stripe pattern on the birds' neck. These are all features belonging to the texture domain. In contrast, features such as size of pupil, number of spots on the chin or spot size, that are features belonging to the shape domain, were not employed by the birds.

The predominance of texture compared to shape is an unexpected result, because shape contains more information useful for sex classification than texture as had been shown by training artificial neural networks using different types of information (Troje & Vetter, in press). Furthermore, data from our lab have shown that humans are more sensitive to shape differences than to texture differences (Troje, unpublished). In these experiments, human subjects performed a same–different face recognition task using frontal views of faces that differed either only in shape or only in texture. Performance on the shape-only faces was better than performance on the texture-only faces. Using non-facial objects, Biederman & Ju (1988) showed that surface characteristics play only a secondary role in human recognition of an intact object when its edges can be readily extracted.

A sophisticated texture analyzing system, on the other hand, might be of great value for recognition of objects without concrete boundaries and for the recognition of degraded or partially occluded objects. Fur-

thermore, it makes viewpoint independent recognition very easy. Any system that relies on shape has to compensate for the complex changes occurring to the two-dimensional projection of an object viewed from different viewpoints (Ullman, 1996).

There is still another possibility that we want to mention. We are aware that we excluded an important stimulus attribute using static images of faces; they did not contain any motion. It may be that motion is much more important to the pigeon than to the human visual system. Coherent motion might be needed to integrate isolated image features into the percept of a single object. Parallax motion might be essential to extract shape. Pigeons may well be able to see and use shape under natural conditions, but may not be able to derive it from a static image. Further experiments using motion stimuli may give more insight into the differences between the visual systems of pigeons and humans.

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