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Familiarity in the Pigeon (*Columba livia*): Does a pigeon know who he knows?

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1 ABSTRACT

Pigeons were asked to categorize photographs on the basis of familiarity using a two-choice touch screen procedure. Two groups of birds were presented with photographs of conspecifics. For the experimental group half of the pictures were of familiar pigeons with whom they shared an aviary, the other half were of unfamiliar pigeons who they had never seen. The control group were unfamiliar to both sets of birds. The pigeons mastered the task, and tests revealed that most could generalize to novel views of the training stimuli. A second, critical, test presented photographs of pigeons that had not been used as training stimuli. Two were aviary-mates of the experimental group and two were unfamiliar. Two of the five experimental birds were able to classify these stimuli correctly whereas the control group could not. Further tests revealed that none of the subjects could categorize visually familiar but socially unfamiliar stimulus birds in terms of familiarity; however one subject transferred the learned discriminative behavior to photographs of familiar and unfamiliar objects. The results suggest that pigeons possess the ability to categorize on the basis of familiarity.

2 INTRODUCTION

Categorization is a cognitive operation that allows individuals to deal with the enormous quantity of information in their environment. By simplifying the surrounding world, which offers a high degree of complexity and change, categorization represents an economical way to reduce cognitive demand on the system. The formation of categories requires a subject to detect common invariant features or properties shared by objects or events and to find points of contact between them in different situations. The identification of a new object as member of one category, of which the properties are known, allows animals to apply this knowledge about the category to an unfamiliar stimulus. The consequence of this ability is an appropriate response to a novel instance of a class without having to be conditioned to each specific stimulus (Zayan & Vauclair, 1998). Categorization, thus, plays a crucial role in a variety of contexts in nature as it serves as prerequisite for recognizing food, prey, predators and locations.

As a fundamental aspect of information processing, categorization is also a central issue in cognitive science. Research examining the animals' ability to visually categorize objects started in 1964 with the seminal experiments of Herrnstein and Loveland. In this pioneering study pigeons were trained to discriminate photographs containing humans from any other photographs. The birds sorted the pictures into different classes according to their content and transferred the learned discriminative behaviour to novel pictures of the same categories. This study was followed by a number of operant conditioning experiments that demonstrated the pigeon's capacity to sort images according to a variety of categories. Examples of these studies included photographs that were distinguished according to whether they did or did not picture birds, or other animals (Roberts & Mazmanian, 1988), bodies of water, trees (Herrnstein, Loveland, & Cable, 1976), chairs, cars, humans, and flowers (Bhatt, Wasserman, Reynolds, & Knauss, 1988), different human faces (Troje, Huber, Loidolt, Aust,

& Fieder, 1999; Huber, Troje, Loidolt, Aust, & Grass, 2000) or even colour slides of paintings by Monet and Picasso (Watanabe, Sakamoto, & Wakita, 1995).

In nature, categorization plays a decisive role in animals' social lives, as it allows discrimination between the natural classes of individuals of different species or between classes of conspecifics (Zayan & Vauclair, 1998). Under natural conditions numerous members of a particular category need the same response, not only conspecifics, but also predators or food need to be considered as natural categories. If an animal needs to reliably identify a certain conspecific regardless of distance, orientation or posture an individual itself can also be considered as natural concept (Watanabe & Ito, 1991). Social interactions mostly require the ability to recognise others in terms of gender and familiarity or even on the basis of the individual identity. As soon as repeated contact between several individuals that differ in their intentions takes place, it becomes valuable to recognize them. Prominent examples for the importance of recognition in social contexts are territoriality, competition and parental care as well as pair-bond formation. The benefits of recognition are numerous, ranging from the avoidance of aggressive interactions over status to the improvement of mating success. Therefore, it is not surprising that this capability is widespread in animals (Tibbetts & Dale, 2007).

The pigeon's ability to sort images into different categories as well as the relevance of category formation in social contexts, led researchers to the idea of using the category discrimination method for the investigation of individual recognition in this species. Poole and Lander (1971) were the first to train pigeons with photographs of conspecifics. The birds were presented with images which they had to sort according to whether they contained a pigeon or not. The subjects mastered the task and transferred to slides showing different breeds, while other bird species elicited only a weak response. This finding led to the overall interpretation that pigeons can form a representation of their own species.

Watanabe and Ito (1991) trained pigeons with pictures showing the head region of different conspecifics in an operant setting. They reported that the birds learned the discrimination between two pictured heads and responded appropriately to novel views of a stimulus bird in a generalization test whenever the depicted conspecifics were easily identifiable by humans. Interestingly the pigeons' ability to discriminate an individual pigeon did not seem to be superior to that of humans. Therefore the authors concluded that pigeons do not possess the ability to precisely recognize individuals on the basis of static visual features. Similar difficulties regarding the recognition of individual conspecifics were found by Ryan and Lea (1994). Their attempt to train pigeons to discriminate between slides of conspecifics was only successful with one subject out of six. In three successive experiments the authors examined the necessary information for making the discrimination based on the identity of the individual. By using a dishabituation technique they showed that pigeons can easily distinguish between live conspecifics, however moving video images of conspecifics and stuffed pigeons did not elicit any response from the subjects. The authors concluded that purely visual information is not sufficient for this species to detect a pigeon as conspecific.

In contrast to the above experiments, Jitsumori, Natori, and Okuyama (1999) were successful in showing that pigeons can discriminate two-dimensional representations of conspecifics using video images of different pigeons as stimuli. They concluded that visually mediated recognition of others in this species is based on motion cues. This claim was disproved by Nakamura, Croft, and Westbrook (2003), who demonstrated the pigeon's ability to discriminate between static images of individual pigeons. Subjects were trained to distinguish between photographs of two groups of unknown pigeons, each consisting of five birds that were shown from different views. After the birds learned the discrimination, a transfer test was conducted, including novel images that presented the stimulus pigeons from novel perspectives that were not shown during the training. Subjects transferred their learned discriminative behaviour to the photographs showing stimulus birds from unknown views. In later experiments, the authors demonstrated that pigeons can also discriminate photographs of unknown conspecifics on the basis of their sex (Nakamura, Westbrook, & Croft, 2006). By testing the subjects with modified photographs, they examined the information on which the discriminative behaviour of the pigeons was based. It was reported that the discrimination between females and males was mainly controlled by the body region of the stimulus pigeons, however the head region also had some influence on the discriminative behaviour. Pigeons maintained the discrimination when black and white photographs were used as stimuli, but failed when only information about the shape was present. The exact features used for the visual discrimination, however, are still unknown. The findings of these experiments above provide strong evidence of the pigeon's ability to use static visual cues for the discrimination between conspecifics.

Overall, a large number of research investigating a variety of species have been conducted to examine the role of vision in the important ability of recognizing conspecifics and discriminating between individuals of the own species. By using still or moving images of conspecifics, it has been shown that several bird species principally possess the requirements to visually distinguish between different individuals of their own species (e.g., Brown & Dooling, 1992; Candland, 1969; Ryan & Lea, 1994). But even in highly chemosensory species like lizards, visual traits may contribute to the discrimination of conspecifcs (Van Dyk & Evans, 2005). Experiments conducted with mammals indicate that vision plays a role in conspecific and individual recognition in a number of species (e.g., McLeman, Mendl, Jones, & Wathes, 2008). Linked to the issue of visual recognition of conspecifics the face represents an important body part especially in primates but also in other animals. Presentations of pictures of the face region alone allowed rhesus monkeys and chimpanzees to discriminate strangers of the own species (Parr, Winslow, Hopkins, & de Waal, 2000). This capability was also evident in sheep (Kendrick, Atkins, Hinton, Heavens, & Keverne, 1996). Furthermore, the facial cues may also contribute to visually mediated kin recognition in chimpanzees (Parr & de Waal, 1999). Chimpanzees were shown to be able to match photographs of the faces of adult females with the picture of their sons. Therefore, it was concluded that the subjects perceived a similarity between the pictures of related conspecifics.

In the previously mentioned studies, the subjects were obviously able to sort pictures of different conspecifics into distinct categories. This, however, does not mean that the target individuals were recognized as conspecifics. The discriminative behaviour can be explained by simple feature generalisation that does not require any understanding of the representational state of the pictures.

It seems to be reasonable to assume that a variety of species including pigeons reliably discriminate and classify conspecifics to same extend in their real social life. However, it is essential to consider when using images as stimuli that subjects may not understand the representational content of the pictures. Two-dimensional representations of conspecifics, thus, may be seen as just a complex pattern, lacking any social relevance. However, Aust and Huber (2006) reported strong evidence for the pigeon's ability of recognizing the representational state of pictures. By using the so called *complementary information procedure* the authors trained pigeons to distinguish between pictures according to whether they do or do not picture a human. As training stimuli photographs of persons were used that missed a body part. Images of this unseen body region served as stimuli in a subsequent transfer test. The subjects responded significantly more to stimuli showing the previously missing part than to pictures devoid of a person.

Another way of getting more information about the animal's capability to connect images with real items may be the use of pictures showing unfamiliar and familiar items in a visual discrimination task and the comparison of the subject's performance on both stimulus types (Zayan & Vauclair, 1998). In domestic hens (*Gallus gallus domesticus*) several studies were conducted to clarify if this species regards slides of other hens as representations of real conspecifics (e.g., Bradshaw & Dawkins, 1993; D'Eath & Stone, 1999). Studies on social recognition in chickens clearly indicate that this species discriminates between different flockmates when live conspecifics served as stimuli (Abeyesinghe, McLeman, Owaen, McMahon, & Wathes, 2009). Moreover, there is strong evidence that visual cues are used for social discrimination in this species (D'Eath & Stone, 1999). However, research investigating the influence of prior social contact with conspecifics that afterwards were presented as images in an experimental setup does not support these assumptions. Bradshaw and Dawkins (1993) tested hens in a visual discrimination task including photographs of familiar and unfamiliar conspecifics. The authors reported that the subjects did not react differently to novel views of known birds than to those of unfamiliar animals. Moreover, the authors did not find any differences regarding the learning speed depending on the degree of familiarity of the individuals used as stimuli. Although it was shown that hens discriminated between familiar and unfamiliar conspecifics when live birds were used, scientists failed in their attempt to train them to discriminate video images of familiar individuals and strangers (D'Eath & Dawkins, 1995). This was also the case when the subjects were tested on photographs of the same individuals (Dawkins, 1996). Following these results it was concluded that hens do not associate slides of hens with real conspecifics.

In contrast to the research carried out with hens, there is strong evidence that other species might be able to perceive a correspondence between photographs of a conspecific and the real animal. Dasser (1987) presented longtailed macaques (*Macaca fascicularis*) with photographs of the face region of either unfamiliar conspecifics or group members of the subjects. In a two choice task the subjects were trained to discriminate between the pictured individuals and were afterwards tested in a transfer test. The test pictures showed novel views of the face as well as other body parts. The macaques successfully transferred the learned discriminative behaviour only to those test pictures showing individuals of the subjects' group. Boysen & Berntson (1989) used another methodological approach, namely heart-rate measures, to examine the recognition of individuals that were shown as photographs was examined in chimpanzees (*Pan troglodytes*). A chimpanzee was tested on photographs showing either an unfamiliar conspecific, a group member to which the subject had a positive relationship or an aggressive familiar individual. The subject responded differently to the photographs depending on the identity of the individual shown. The heart-rate change was interpreted as reflecting the nature of the social relationship as well as the familiarity between the subject and stimulus chimpanzees.

Evidence of an animal's capability to associate pictures of conspecifics with their experience with real animals is not only present in primates. In a visual discrimination task, it has been demonstrated that sheep (*Ovis orientalis aries*) are able to use previous experience when those conspecifics are presented as pictorial stimuli (Kendrick et al., 1996). The subjects learned to distinguish between photographs of different faces of other sheep significantly faster when the depicted individuals were of the same breed as the subjects. Moreover, the animals' performance was influenced by social experience with the pictured individuals. The inclusion of pictures of socially familiar conspecifics made it easier to distinguish between photographs of different individuals resulting in significantly faster learning.

In visual discrimination tasks with pigeons, researchers have focussed on the role of previous experience with places rather than social stimuli. This is due to the great interest in the importance of visual cues in a pigeon's orientation and homing behaviour. Positive evidence for familiarity effects on the discrimination of photographs of landscapes comes from Wilkie, Willson, and Kardal (1989). By using an operant discrimination procedure, two groups of pigeons were trained to distinguish between photographs, which were taken from two different locations, including pictures of the vicinity of the loft from which the experimental group were trained to home. The control group consisted of birds without homing experience. The authors reported that the visually experienced pigeons acquired the task significantly faster than the control birds and showed better transfer to new views of the location. In a later experiment pigeons were trained and tested with photographs of so called home slides and not-home slides (Kendrick, 1992, cited by Cole & Honig, 1994). One group of subjects were kept in a compartment that allowed them to see the location, which was one of the two pictured locations used as stimuli in the discrimination task. The "visitor group" was exposed to an irrelevant place that was not shown in the task. Therefore, half of the stimuli were highly familiar to pigeons of the "home group", while to the others both stimulus classes showed unknown locations. The groups did not differ in their initial acquisition of the discrimination. However, the "home group" performed significantly better than the "visitor group" when they were tested in a transfer test involving new views of both locations. Again the findings of this study indicate that the experience with a real stimulus influences the pigeons' response to photographs representing this stimulus. A contrasting finding was shown by Dawkins, Guilford, Braithwaite, and Krebs (1995). In this study one group of pigeons was allowed to visit the location of which photographs were presented as stimuli in an operant setup. The control group was familiarized to an irrelevant place. The authors did not find an effect of outdoor experience on acquisition or transfer to novel stimuli.

In a slightly different kind of test, Cole and Honig (1994) trained two groups of pigeons to discriminate between photographs of two ends of a room. Pictures of one side of the room were associated with food while pictures of the other end of the room served as negative stimuli. After the pigeons learned the task they were allowed to search for food in the real room. For the "congruent transfer group" the food was placed at the end of the room that served as positive stimulus category during training. For subjects of the "incongruent transfer group" food was hidden at the other end of the room shown in negative pictures. Pigeons of the "congruent transfer group" acquired the learning criterion faster than birds of the "incongruent transfer group". When pigeons were tested the other way round, i.e. from the real room to photographs, no difference between groups occurred. This study is of great interest because it clearly shows that pigeons are able to recognise the similarity between real items and the pictured items and further that they can use this perceived correspondence to solve a spatial discrimination task.

In contrast to the research on landscape discrimination the overall issue of familiarity effects on pigeon's performance in visual discrimination tasks was addressed by Watanabe (1997) in an experiment on viewpoint invariance. Two groups of pigeons were trained to peck the screen when either a familiar object or an object the subjects had never seen in real life was presented as a still image. The author reported that subjects trained on pictures of the familiar object showed generalization to new views of the stimulus while the other group failed in this test. In a later experiment the pigeons were familiarized with the real objects by placing them in the home cages of the subjects (Watanabe, 1999, cited by Watanabe, 2000). After this exposure phase the pigeons were trained to discriminate video images of the objects. Watanabe reported a facilitative effect of real life experience with the pictured objects on the acquisition of the discrimination task. In a view point invariance test the subjects also responded more often to new views when the stimulus was familiar than when the picture showed an unknown object.

Although the findings in terms of familiarity are conflicting, there is evidence that experience with objects shown in pictures does have an impact on the performance of pigeons in visual discrimination tasks to some degree. Whether this influence is caused by the species' understanding of the representational content of pictures or not is a question that so far remains unresolved (but see Aust & Huber, 2006). Although the underlying mechanism of the reported inference between the reality and the pictured version is still unknown, it has been successfully shown that pigeons are able to recognize at least some correspondence between the three-dimensional environment and the two-dimensional representation and, further, that they can use this perceived similarity for solving discrimination tasks. The pre-experience with real items, that afterwards are shown as pictures, results in a better performance in respect to task acquisition and transfer of the discriminative behaviour to novel pictures.

Taken together, pigeons are known for their proficiency at sorting images into different classes according to their content (e.g., Herrnstein & Loveland 1964). Furthermore, it has been demonstrated that this species is able to discriminate between, and generalise to, novel photographs of unfamiliar conspecifics (Nakamura et al., 2003). This provides evidence for the pigeon's capacity to use static visual cues for discrimination; however, this task does not require individual recognition. The features on which visual discrimination may be based are various. Troje and colleagues, for example, reported that pigeons relied on colour, intensity gradients and local shading when they had to discriminate between photographs of male and female human faces (Troje et al., 1999). However, the question of whether real life experience with the pictured items is also relevant to sort photographs into different classes remains controversial. This issue has mainly been addressed by research focussing on the discrimination and recognition of familiar landscapes in homing pigeons (e.g., Wilkie et al., 1989; Dawkins et al., 1995). Although the results are mixed it was suggested that real life experience may play a role in visual discrimination tasks. Combining these findings with the importance of the ability to distinguish between known conspecifics and strangers in the wild it seems reasonable to address this question from a different point of view, by using photographs of conspecifics as stimuli. Pigeons are known as social birds that form loosely structured groups (Vogel, 1997). The monogamous, long-lasting pair-bonds that are formed by adults represent the basic units of the social system. Within a breeding colony a clear dominance hierarchy exists. Males of a group compete for optimal breeding sites whereby dominant individuals occupy preferred places and show pronounced territorial behaviour. Taking into account that this species lives socially, the recognition of familiar and unfamiliar conspecifics should provide pigeons with a great biological advantage. This capacity could be important in social interactions allowing the individual to respond differently and appropriately to social partners. Since this ability is crucially important in nature, this set of experiments examined whether pigeons can use their social experience in a visual discrimination task which asked subjects to categorise photographs of flockmates and strangers on the basis of familiarity (Experiment 1).

In further experiments (Experiments 2 and 3) the overall objective was to evaluate the information a stimulus has to contain to be classified as familiar by pigeons.

3 EXPERIMENT 1

Experiment 1 was carried out in order to examine whether pigeons are capable of using social experience to classify photographs of with conspecifics in a visual discrimination task. In a first step two groups of pigeons were trained to discriminate between two sets of photographs of conspecifics. While half of the stimuli showed flockmates of the experimental group, all the birds pictured in the stimuli were unfamiliar to the pigeons belonging to the control group. In the case that familiarity facilitates the discrimination of pictured conspecifics, the experimental group was expected to show faster acquisition than the control group. However, for the training it was assumed that both groups would learn to discriminate the photographs, since pigeons possess an excellent picture memory (Vaughan & Greene, 1984; Cook, Levison, Gillet, & Blaisdell, 2005; Fagot & Cook, 2006) and successfully managed to do a similar discrimination task involving images of unfamiliar conspecifics in previous researches (Nakamura et al., 2003; Nakamura et al., 2006).

After the discrimination training the subjects were asked to categorize novel views of the stimulus birds in a first generalization test (Test 1). It was hypothesised that both groups would to be able to generalize their learned discrimination to new pictures of the stimulus pigeons, since Nakamura et al. (2003) demonstrated the pigeon's ability to master this task when the stimulus birds shown to the subjects were strangers. If the experimental group, however, was able to use the previous experience of the depicted individuals, their performance would be expected to be superior to that of the control subjects.

In a second test, the birds were presented with pictures showing unknown individuals and flockmates of the experimental group that were not presented during training (Familiarity Test). Solving this transfer test is highly demanding. To categorise a photographed object on the basis of familiarity an animal is required to use its experience gained in nature and to apply it to the two-dimensional representations of the stimulus. Moreover, it has to judge the subject pictured on the photograph as being familiar and the other as being novel. The categorization of visual stimuli as a function of their perceptual similarity is well known in pigeons. Perceptual classes are characterized by some common features shared by the stimuli. Since there are no consistent perceptual similarities across known objects on which transfer to novel stimuli can be based, the categorization in terms of familiarity is highly abstract.

Abstract categorization requires a subject to respond to visual stimuli according to their relations rather than to rely on the visual features common in different items. A prominent example for abstract categorization is the judgement of whether items are the same or different. Same-Different discrimination tasks have been used in a number of studies (e.g., Wasserman, Hugart, & Kirkpatrick-Steger, 1995; Young & Wasserman, 1997; Young, Wasserman, & Garner, 1997; for reviews, see Katz, Wright, & Bodily, 2007; Zentall, Wassermann, Lazareva, Thompson, & Rattermann, 2008). Researchers often tested pigeons on multi-item discrimination tasks including more than two items in which subject had to decide whether the shown items are the same or different. Having a closer look at the mechanisms involved in solving such a task, research revealed that pigeons make use of entropy in the classification of complex visual arrays which is a perceptual and not abstract mechanism (Young & Wasserman, 2001). However, more recent research indicates that pigeons do have the cognitive capability to fully learn a Same-Different abstract-concept by using a two-item same and different paradigm (Katz & Wright, 2006). This ability has suggested to represent a qualitative similarity in being able to learn an abstract task among primates and birds (Wright & Katz, 2007; Katz, Wright, & Bachevalier, 2002; Wright, Rivera, Katz, & Bachevalier, 2003).

A task demanding discrimination in terms of familiarity can not be solved by a strategy based on global perceptual features such as entropy or oddity but depends only on the experience of a subject with a particular stimulus. Research concerning recognition memory in pigeons has demonstrated that pigeons easily acquire a task requiring them to respond to pictures on the basis of familiarity or novelty of the stimulus displayed (Macphail & Reilly, 1989). The necessity to transfer the real-life experience to photographs in an experimental setup and to further base the discrimination on it makes the present transfer test much more demanding. Therefore, it was hypothesised that it will be difficult for a pigeon to master this task. Since solving Test 2 (Familiarity Test) is only possible by using the real experience with the pictured conspecifics, it is expected that the control group will not transfer to the new stimuli. In contrast, if pigeons were able to discriminate photographs of conspecifics on the basis of the familiarity with the pictured birds, the subjects of the experimental group should show transfer to the novel examples of the stimulus classes.

3.1 METHODS

3.1.1 Subjects

Two groups of adult homing pigeons (*Columba livia*) were used in this experiment. They were assigned to either the control group (n=6) or the experimental group (n=6) according to their real-life experience. The experimental subjects were kept in an outdoor aviary (2m x 2m x 2m) in a flock of eleven pigeons of mixed sex and breed. Before participating in the experiment they had shared their aviary for at least two years. As the pigeons were in daily visual, auditory and olfactory, as well as in social contact with their conspecifics, group members were highly familiar to each other. The control subjects were housed in a group of 13 pigeons in an aviary (3m x 1.1m x 3m) that is located at the other side of the aviary complex from the experimental group (see Figure 1). As with the experimental subjects the control subjects had been kept together for several years and were highly familiar to each other. The large distance between the home aviaries of both subject groups led to no direct visual contact between members of the control and experimental group. In addition, it was ensured that the control birds had never been kept together with the experimental pigeons to exclude the possibility of social interaction in the past. Thus, the housing conditions led to a high degree of familiarity between birds within a subject group but did not allow any kind of interaction between pigeons of the experimental and the control group. The positioning of the aviaries of the subject groups is schematically presented in Figure 1. Both groups of subjects had already experience visual discrimination tasks before the onset of the experiment. However, none of them had participated in experiments that required the discrimination of conspecifics. Food was mainly provided during the experimental sessions in addition to some supplementary feeding after training or testing. Water and grit were freely available in the aviary at any time.

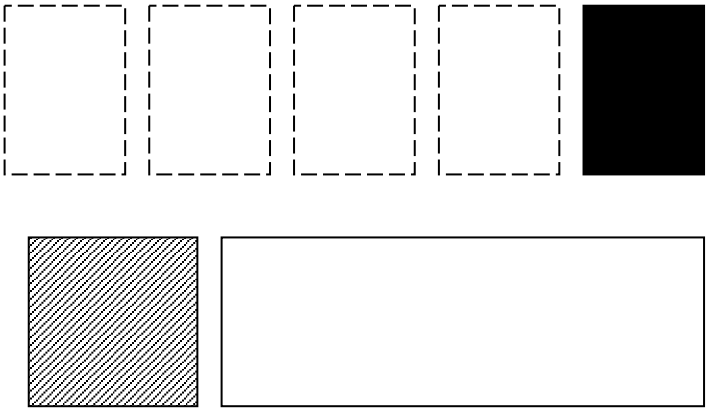

Figure 1. Housing conditions of the subject groups. The black box represents the aviary of the control group. The aviary of the experimental group is represented by the striped box. Birds living in this aviary served as experimental and stimulus pigeons. The aviaries of other pigeons are represented by the dotted boxes. The white box stands for an aviary compartment that is visually separated from the other aviaries. Birds living in this aviary were used as entirely unfamiliar stimulus birds.

3.1.2 Apparatus

The pigeons were trained and tested in a 51 x 40 x 43 cm experimental chamber (“Skinner-box”). The frontal wall of the chamber was constituted by a 15.0″ XGA Color TFT-LCD monitor (resolution = 1024 x 768 pixels) mounted behind an infrared touchframe (CarrollTouch by Elo). Food reward was administered by means of a special feeder, the ^{3}grain lifter^2. It consisted of an electric motor that lifted a piston with a depression on top up through a food reservoir. Thereby, grain was accumulated in the depression. The piston was then lifted through a hole in the bottom of the testing chamber and the grain became accessible to the pigeon directly below the touchscreen. The Skinner box was connected to a PC equipped with a digital input-output board and a software package (^{3}CognitionLab^2, Steurer, M.) that controlled all events in the operant chamber during experimental sessions.

3.1.3 Stimuli

Colour photographs of homing pigeons were used as stimuli. The six subjects of the experimental group were used as stimulus birds. As we could not present the experimental subject with photographs of itself a seventh stimulus pigeon, one bird housed in the same aviary under the same conditions was included in the stimulus set. The second set of images was taken of six individuals that were reared in a visually separated compartment (see Figure 1). Because of the special housing conditions none of the subjects had ever had any chance to see or to interact with these pigeons. Thus, the stimulus pigeons provided two categories of photographs: firstly, pictures that showed conspecifics with which neither individuals of the control group, nor pigeons of the experimental group had had any kind of visual or social experience. The second stimulus class depicted pigeons that were highly familiar to the subjects of the experimental group but unknown to the subjects of the control group.

The stimuli consisted of twelve photographs of each of the thirteen birds. Views included at least eight different perspectives. The pictures showed the pigeons from the front, from behind, the left side and the right side. Furthermore, they were photographed from angles in between the frontal view and the right and left side, respectively, and the back view and the right and left side, respectively. The remaining four pictures showed variation of these eight perspectives. Therefore, a total of 156 photographs were used. These included 84 photographs of individuals familiar to members of the experimental group and 72 photographs of unknown pigeons. The birds were photographed under natural light conditions. To take the pictures the stimulus pigeons were placed alone or in pairs in an empty aviary compartment, where they were allowed to move about freely. The compartment contained two perches on which the pigeons were sitting most of the time. All pictures were taken with the same camera and on two different days. To control for light level differences individuals of both groups were photographed alternately and on both days. Afterwards the stimuli were modified in a similar manner to the stimuli used by Nakamura et al. (2006). All stimuli pictured an entire bird, on half of the photographs the individual was shown sitting on a perch. The natural background was removed and replaced by a uniform green background by using photograph manipulation software Photoshop 4.0. This was done in order to eliminate possible additional information that could have been present in the pictures and on which visual discrimination could have been based. Images were presented as 269 x 269 pixel bitmaps with a resolution of 180 dpi resulting in a size of 3,8 x 3,8 cm. Examples of the stimuli are shown in Figure 2.

Figure 2. Examples of the stimulus sets. The left picture of each stimulus pair shows a flockmate of the experimental group while the right picture represents an unfamiliar conspecific taken from the corresponding perspective.

3.1.4 Procedure

The stimulus pool of photographs was divided into two classes. These classes were (1) photographs of subjects of the experimental group and (2) photographs of the entirely unknown pigeons. To exclude the possibility that the pigeons' behaviour toward stimuli were an artefact of the reinforcement contingency the pigeons of each group were arbitrarily assigned to the two different possible reinforcement conditions. Three pigeons of the experimental groups and three control birds were assigned to the subgroup "Unfamiliar positive" while the remaining birds of both groups were assigned to the subgroup "Familiar positive” for counterbalancing. For the latter, photographs of birds of the experimental group were reinforced. In contrast, the entirely unknown pigeons served as positive stimulus class for subjects of the group “Unfamiliar positive”. One bird of both the experimental and the control group, were trained and tested on the identical set of stimuli to control for differences in regard to the difficulty of the presented stimuli. The subjects and the groups they belonged to are listed in Table 1 below.

Table 1. Subjects and Assignment to Groups

Experimental Group		Control Group	
Subjects	Positive Stimuli	Subjects	Positive Stimuli
Agnes	Unfamiliar	Arthur	Unfamiliar
Fred	Unfamiliar	Birgit	Unfamiliar
George	Unfamiliar	Ferdinand	Unfamiliar
Heinz	Familiar	Heidrun	Familiar
Judith	Familiar	Meggie	Familiar
Vanessa	Familiar	Trisha	Familiar

Note. Experimental birds and control birds listed in one row received the same training and tests including the identical set of stimuli.

The experiment was conducted using a forced two choice procedure. Therefore a trial consisted of the simultaneous presentation of one positive and one negative picture. The pictures appeared on a black background in fixed positions that were to the left and to the right of the center of the screen. The position of a particular stimulus varied randomly from trial to trial. The subject had to select one of the two shown stimuli by pecking that stimulus. In training trials subjects received computer feedback after their choice. Whenever the subject chose the positive picture the grain feeder opened for 3 sec and additionally, an auditory signal occurred. After choosing the negative picture the screen became red for 3 sec. This was combined with another acoustic signal followed by a correction trial, whereby the same trial was repeated. In this case choosing correctly led to food access, while a further wrong decision was again followed by a correction trial. Between the presentation of two successive trials a black screen was shown. This intertrial interval (ITI) was set at 6 seconds.

Depending on the phase of the experiment, the procedure was modified and adjusted accordingly as described below.

3.1.4.1 Pretraining

Before being exposed to the discrimination training, the subjects were accustomed to the apparatus and the procedure. This was necessary because the pigeons were used to another procedure (Go/no-go procedure) and they had not participated in any experiments for a long time before the onset of the present study. Using a standard autoshaping procedure the subjects were trained to peck at a small coloured square placed in the middle of the touch screen. The period of stimulus presentation was followed by access to grain. As soon as the pigeons started pecking, food access was made contingent on the subjects' response. Once the pigeon was pecking reliably the two-choice procedure was introduced. The same "positive stimulus" used for autoshaping was now presented simultaneously with a new "negative stimulus". Only pecking towards the positive stimulus was rewarded. After subjects reliably chose the positive picture, they were trained on a more advanced variation of this two choice task involving several new positive and negative pictures. After having learned to respond appropriately to the two sets of stimuli, the subjects started the discrimination training.

3.1.4.2 Discrimination Training

For the discrimination training pictures of four individuals of the experimental group and four out of the entirely unknown pigeons served as stimuli for each subject. Only ten out of the twelve photographs of each of the eight pigeons were used as training stimuli. Therefore, a training session consisted of 40 trials, each trial included a picture of one entirely unknown pigeons as well as of one experimental bird. The pictured individuals as well as the shown views of the stimulus pigeons differed across subjects. However, as previously mentioned one individual of the experimental group and of the control group were trained on the same set of stimuli. For pigeons of the experimental group photographs of themselves were excluded. Presentation of stimuli varied randomly. Subjects received one to two training sessions per day and at least twenty sessions in total. The criterion of mastery was set at ≥ 30 correct first choices (which equalled 75%) in four out of five consecutive sessions, and at least 28 correct first choices (which equalled 70%) in the remaining one. The maximum number of training session was set at a hundred sessions. If a subject was not able to reach the criterion within this time it was excluded from the experiment.

3.1.4.3 Test 1: Generalization Test

Subjects that acquired the learning criterion within the given number of sessions were given a generalization test with novel photographs of the trained stimulus birds. This was done in order to investigate whether this learned categorical discrimination was restricted to the training stimuli. The remaining two views of each stimulus pigeon that were not included in training sessions served as the test stimuli. Test sessions consisted of 40 training trials and eight randomly intermixed test trials consisting of one novel picture of an entirely unknown pigeon and a novel image of an experimental subject. The birds were tested for three sessions showing the stimuli in different combinations. Thus, in total the generalization test consisted of 120 training trials as well as 24 test trials. Pecking towards test stimuli led to no feedback. This means that subjects received neither a reward for choosing the correct picture, nor a correction trial in the case of a wrong decision. Since test trials led to no differential reinforcement, learning have not been taken place during the tests. Subjects that failed in this generalization test were presented with the same set of test trials a second time. In this case the subject was retrained for ten training session before being re-tested. This was done to ensure that a lack of transfer was not due to insufficient training or irritation by the presence of unknown stimuli and the absence of feedback. After retraining the subjects, they were tested a second time on the same generalization test. Pigeons that did not pass the test this time were excluded from further testing. Those subjects that successfully transferred their learned discriminative behaviour to new views of stimulus pigeons received further training until they reached the criterion again. Afterwards they were tested in the second transfer test. The phase of inter-test training was conducted after each completed test.

3.1.4.4 Test 2: Familiarity Test

The second test was conducted to examine whether pigeons possess the ability to categorize conspecifics on the basis of social familiarity. This was done by testing subjects with photographs of two entirely unknown pigeons and two familiar birds that had never been shown in training before. All twelve views of each of the four birds were used as test stimuli. The test consisted of four consecutive sessions including 160 training trials and 24 test stimuli pairs in total. The test trials were interspersed with in 40 ordinary training trials at a rate of six per session. There was no differential reinforcement for pecks on the test stimuli. Subjects that failed in this test were excluded from further testing.

3.2 RESULTS

To examine whether the subjects differed in dependence of the subject group (Experimental Group vs. Control Group) and the subgroup they were assigned to (Unfamiliar positive vs. Familiar positive), a two-way variance analysis was conducted. Analysis revealed no influence of the factor "group" and "subgroup" on the subjects' performance in Experiment 1, nor an interaction effect between these factors (F's ≤ 4.2, p's ≥ .05). Therefore, the results from subgroup "Unfamiliar positive" and "Familiar positive" were aggregated as they were used for counterbalancing.

3.2.1 Discrimination Training

To reach criterion, the pigeons were required to score 75% correct or more in four out of five consecutive sessions and at least 70% correct performance in the remaining one. The learning curves for the experimental group are shown in Figure 3. All six pigeons of the experimental group learned to discriminate between the two stimulus sets and reached the learning criterion within the hundred training sessions. However, the variance among the pigeons was high. While the fastest bird, Fred, learned the task within 23 sessions, Agnes required 67 training sessions to successfully discriminate between the two sets of stimuli.

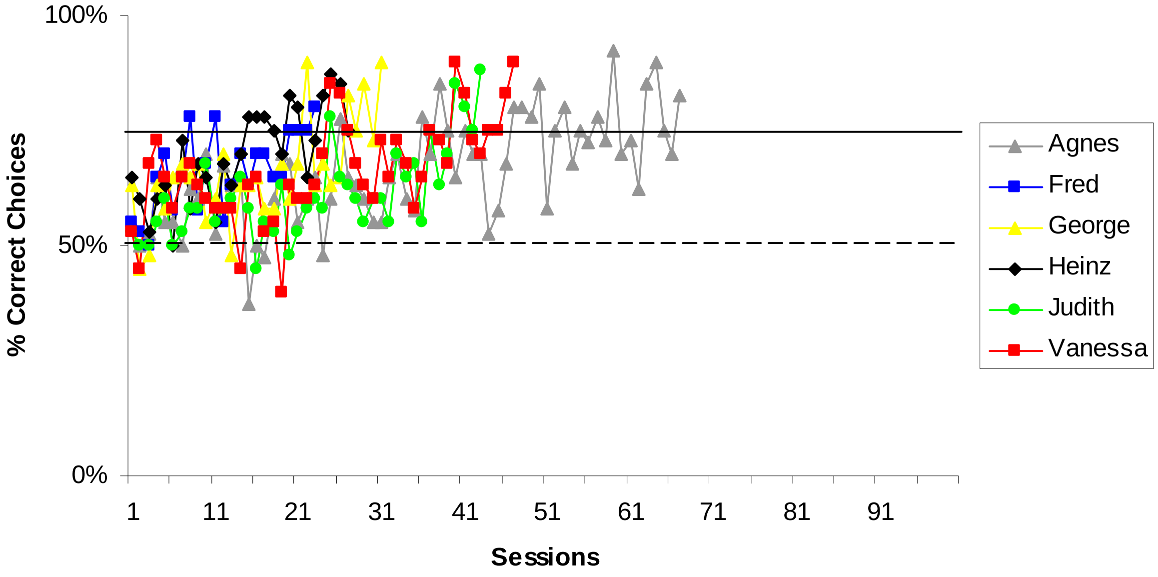

Figure 3. Percentage of correct first choices of the six pigeons of the Experimental Group in the training phase. The *dashed line* represents chance level (50%), the *solid line* represents 75% correct first choices. This was the learning criterion to be reached in four out of five consecutive sessions.

The learning curves of the control pigeons are shown in Figure 4. Four out of the six birds of the control group learned to discriminate the two classes of stimuli. Similarly to the experimental group, the learning speed varied noticeably among subjects. The number of training sessions needed to learn the task reached from 26 sessions for Trisha to 69 sessions for Ferdinand. Furthermore, two birds, Meggie and Arthur, failed to master the task within the given number of training sessions. Thus they were excluded from the experiment.

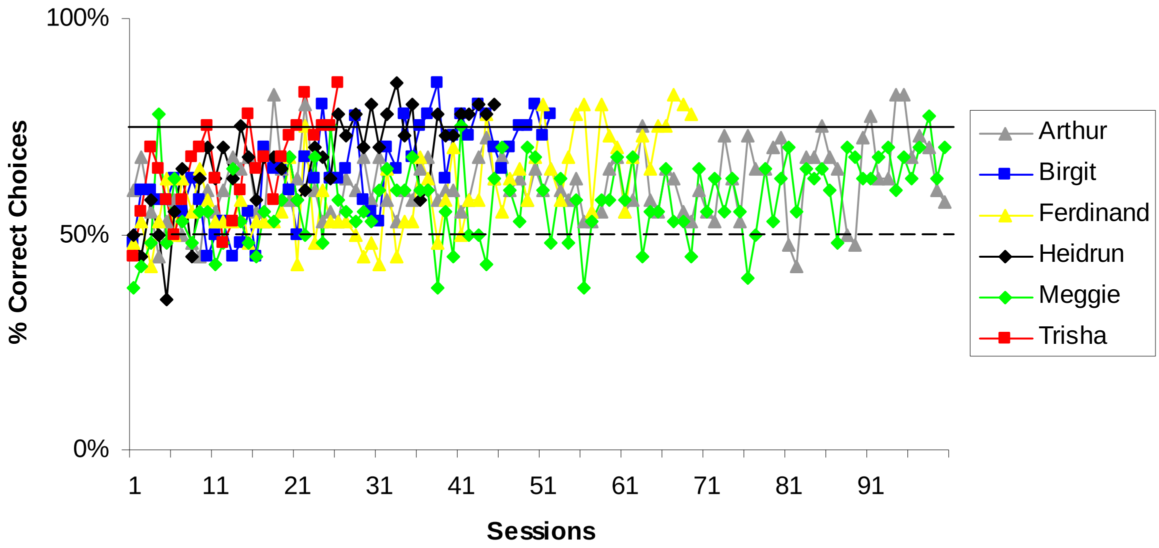

Figure 4. Percentage of correct first choices of the six pigeons of the Control Group in the training phase. The *dashed line* represents chance level (50%), the *solid line* represents 75% correct first choices. This was the learning criterion to be reached in four out of five consecutive sessions.

The results of the training phase of the experiment are summarized in Figure 5 showing the mean number (±SD) of the received training sessions for both groups. All six pigeons of the experimental group acquired the initial training task needing an average of 40 (±16) sessions to reach criterion. In contrast subjects of the control group required 65 (±28) training sessions. Task acquisition was characterized by large variations between subjects within each group, resulting in no significant difference between the groups regarding their learning speed (ANOVA $F_{(1,11)}=3.309$; $p=0.099$). However, there is a trend towards faster learning in the experimental group compared to the control group. Direct comparison between the learning speed of the control and experimental individuals that were trained on the same set of photographs revealed that in most of the pairings the subject of the experimental group learned the task remarkably faster than the control bird. Trisha was the only control pigeon that outperformed the corresponding experimental bird regarding the task acquisition (see Appendix, Table 2).

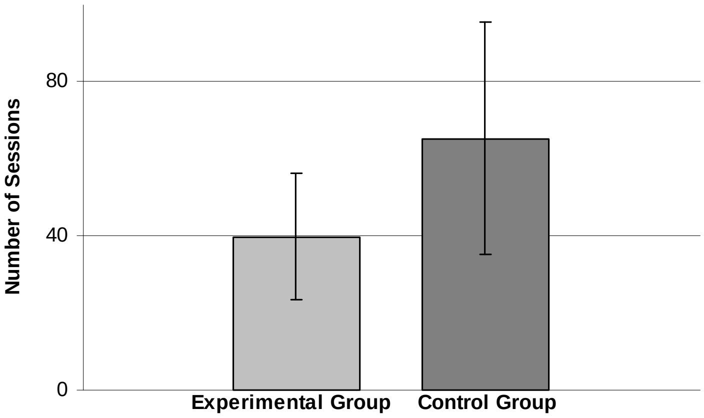

Figure 5. Mean number (±SD) of training sessions required for the Experimental and the Control Group to reach criterion.

3.2.2 Test 1: Generalization Test

The ten subjects that learned the discrimination between the two sets of stimuli were tested on novel photographs showing the stimulus birds from unknown views. The discrimination performance in this generalization test was assessed by means of one-tailed binomial test (chance probability = 0.5). The results of this test are illustrated separately for each experimental bird in Figure 6 as percentage of correct choices for the 24 test trials in comparison with performance on the 120 training stimuli presented in the test sessions. All six subjects of the experimental group performed significantly above chance level on the training stimuli presented in test sessions (Binomial test, $p < 0.0001$ for each subject). Two birds failed in their first attempt to generalize their learned discriminative behaviour to novel views of the stimulus birds. The subjects then received ten more training sessions and were afterwards tested a second time on the same task. Fred's performance on test trials increased remarkably from 14 positive choices in his first try to 21 correct responses in the second test resulting in a performance significantly above chance level. Although the number of correct choices also increased for Heinz from 15 to 16 correct choices, his performance remained under significance level. Thus, he was excluded from further testing. Because of a human error one bird, namely George, was tested on Test 2 before it achieved the criterion of 17 out of 24 correct choices in Test 1. This bird only responded correctly in 16 test trials. Therefore, for both, George and Heinz (Heinz's third test) that performed barely under significance level (16 instead of 17 correct choices) the test session during which they performed worst on training trials was repeated. George's performance on training as well as on test trials increased resulting in a significant performance of 75%. Heinz's performance on training trials strongly decreased resulting in a worse performance than during the original session. Thus, he was excluded from Test 2. Summarizing the results, five out of the six experimental subjects mastered the test by choosing new photographs of the stimulus pigeons of the positive class significantly more often then those of the negative class. For detailed information about the subjects' performance on test and training trials see Table 3 in the Appendix.

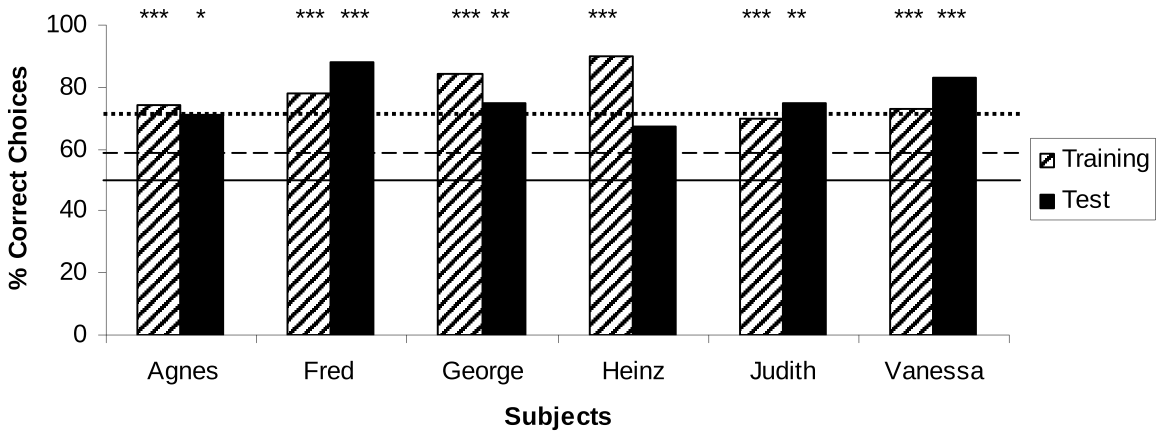

Figure 6. Percentage of correct choices in Test 1 of subjects of the Experimental Group. *Striped bars* depict the pigeons' performance on the training trials during the test sessions and *black bars* the performance on the 24 test trials. The *solid line* represents chance level (50%), the *dotted line* represents the one-sided significance level of 0.05 for the test trials. The *dashed line* represents the one-sided significance level of 0.05 for the training trials. Results of the Binomial test: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Figure 7 shows the percentage of correct choices on test as well as on training trials of Test 1 for each control bird. All four tested subjects performed significantly above chance level on the training stimuli (Binomial test, p < 0.001 for each subject). Two birds failed to master the task when they were tested for the first time. Within the 24 test trials, both birds correctly chose the positive stimulus only 14 times. After retraining, Heidrun responded correctly to 18 test trials and therefore performed significantly above chance level. In contrast, Ferdinand failed to master the test a second time choosing the positive stimulus 15 out of 24 times. Since his performance on test trials did not reach statistical significance, he was excluded from the experiment. Taken together, three subjects of the control group showed transfer to novel photographs of the stimulus birds. For detailed information about the subjects' performance on test and training trials see Table 4 in the Appendix.

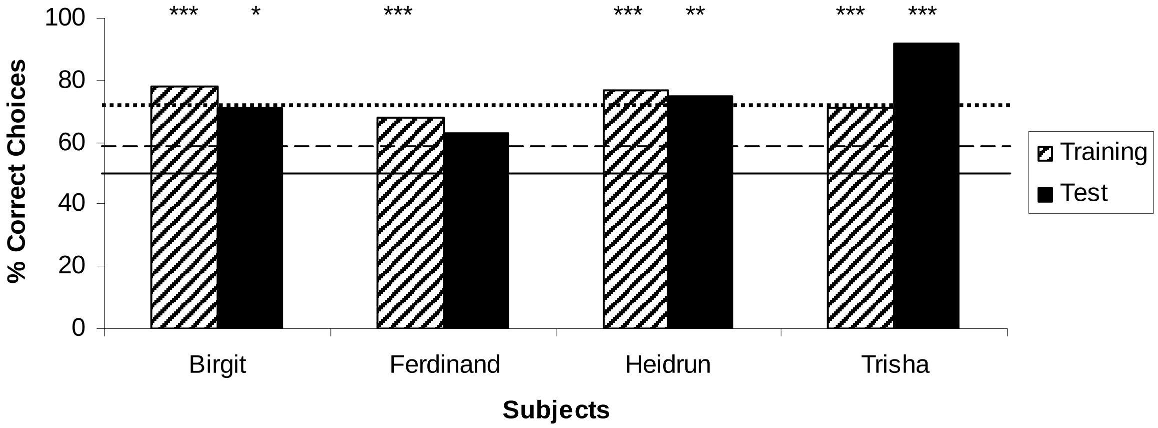

Figure 7. Percentage of correct choices in Test 1 of subjects of the Control Group. *Striped bars* depict the pigeons' performance on the training trials during the test sessions and *black bars* the performance on the 24 test trials. The *solid line* represents chance level (50%), the *dotted line* represents the one-sided significance level of 0.05 for the test trials. The *dashed line* represents the one-sided significance level of 0.05 for the training trials. Results of the Binomial test: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

The results show that most of the subjects that learned the discrimination transferred this discriminative behaviour to novel photographs showing other views of the stimulus birds.

3.2.3 Test 2: Familiarity Test

The five experimental birds and the three subjects of the control group that successfully solved the previous task were tested with pictures showing novel flockmates of the experimental group and entirely novel unknown pigeons. These pigeons were never previously used as stimulus pigeons. The discrimination performance in Test 2 was assessed by means of two-way binomial test (chance probability = 0.5). Figure 8 shows the performance of individuals of the experimental group as a percentage of correct choices during test trials in comparison with the performance on the intermixed training stimuli. The performance on training trials during the test sessions was highly significant for all five experimental birds (Binomial test, $p < 0.001$ for each subject). The response to test pictures varied between subjects. George, who was reinforced for pecking on the unfamiliar stimuli, selected pictures of new unknown pigeons significantly more often than photographs of novel flock mates. Judith, who was reinforced for pecking on pictures of familiar pigeons, preferentially pecked at photographs of flockmates both on training trials and test stimuli pairs. Both subjects chose test pictures of the newly introduced stimulus birds of the positive stimulus class significantly more often than pictured conspecifics of the negative category. The other three tested birds of the experimental group showed no preference for either class of stimuli. For detailed information about the subjects' responses to test and trainings trials of Test 2 see Table 5 in the Appendix.

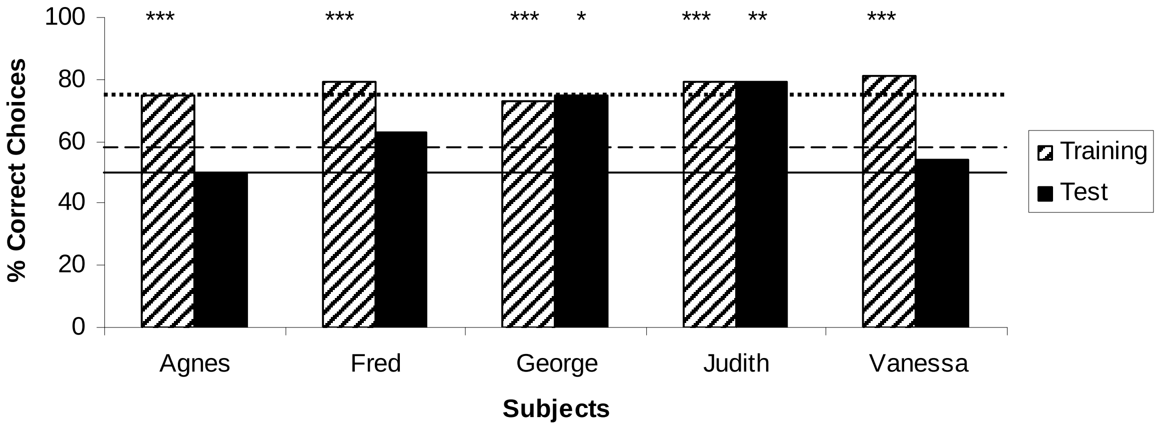

Figure 8. Percentage of correct choices in the Familiarity Test of subjects of the Experimental Group. *Striped bars* show the pigeons' performance on the training trials during the test sessions and *dark grey bars* the performance on the 24 test trials. The *solid line* represents chance level (50%), the *dotted line* represents the two-sided significance level of 0.05 for the test trials. The *dashed line* represents the two-sided significance level of 0.05 for the training trials. Results of the Binomial test: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

The performance of each of the subjects of the control group on training trials during the test was highly significant (Binomial test, $p < 0.0001$ for each subject). In contrast to the experimental group, none of the control birds showed a significant preference for either group of stimuli during test trials. The control birds' responses to training as well as to test trials during the Familiarity test are illustrated in Figure 9. For more detailed information about the subjects' performance on test and training trials see Table 6 in the Appendix.

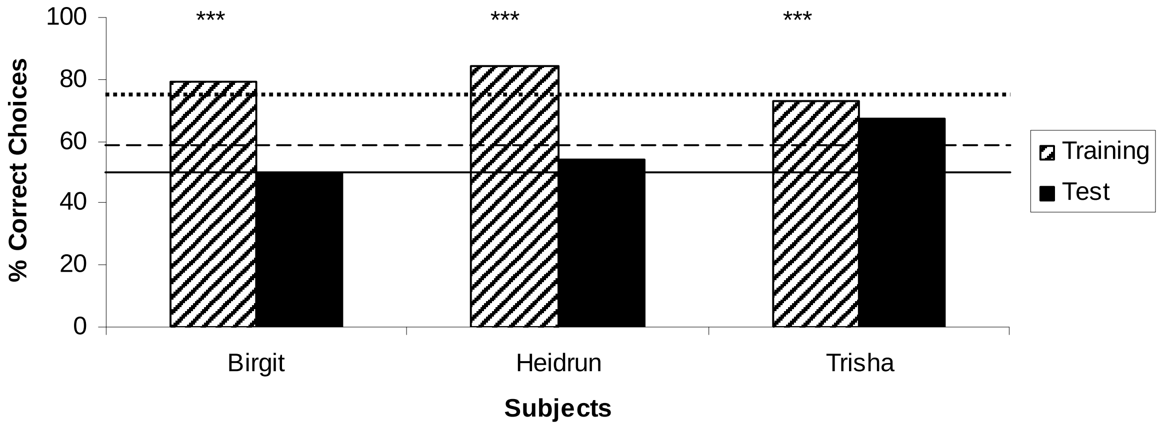

Figure 9. Percentage of correct choices in Familiarity Test of subjects of the Control Group. *Striped bars* show the pigeons' performance on the training trials during the test sessions and *dark grey bars* the performance on the 24 test trials. The *solid line* represents chance level (50%), the *dotted line* represents the two-sided significance level of 0.05 for the test trials. The *dashed line* represents the two-sided significance level of 0.05 for the training trials. Results of the Binomial test: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

In summary, the results show that two out of the five experimental birds transferred the learned discriminative behaviour to photographs showing novel instances of familiar and unfamiliar conspecifics whereas none of the control subjects were able to do this.

3.3 DISCUSSION

Pigeons were trained to discriminate between photographs showing two groups of pigeons. For the six birds of the experimental group one class of stimuli contained images of flockmates, while the others showed unfamiliar pigeons. In contrast, both sets of photographs pictured conspecifics that were unknown to the members of the control group. All individuals of the experimental group, but only four birds of the control group learned the discrimination task. Furthermore, there was a non significant tendency toward a faster acquisition of the task for birds of the experimental group. Test 1 revealed that most of the subjects could generalize to novel views of the training stimuli. In a second, critical test, the subjects were presented with photographs of pigeons that had not been used as training stimuli. Two were aviary-mates of the experimental group and two were unfamiliar. Two of the five experimental birds were able to classify these stimuli correctly whereas the control group could not.

When having a closer look at the results of the training phase, the learning curves reveal that most of the pigeons learned the association between the stimulus sets and the reinforcement contingency. During training, pecking toward an example of the class of training stimuli provided animals with a food reward, while choosing an image belonging to the other stimulus set led to no reinforcement. Therefore, at this phase of the experiment discrimination could be achieved without any knowledge about the pictured individuals, simply by memorizing each picture and its outcome. Pigeons are very good at rote learning and have a large memory capacity for visual stimuli as has been demonstrated in previous studies (e.g., Vaughan & Greene, 1984; Cook et al., 2005). Thus, it is not surprising that groups did not differ significantly concerning their learning speed. Nevertheless, familiarity with the pictured conspecifics may have facilitated the discrimination learning, resulting in slightly faster acquisition of the experimental group. Such a positive effect of real life experience on the acquisition of a visual categorization tasks has been reported in prior studies (e.g., Wilkie et al. 1989).

The extent to which the acquired knowledge could be transferred to novel images of the same stimulus birds was addressed by Test 1. Once again subjects did not require any kind of real life experience with the stimulus birds to solve the task, but prior exposure to them could have facilitated the discrimination of experimental birds on test trials. However, the pigeons' performance on test pictures showing new photographs of the stimulus birds did not differ between groups. Two pigeons of both groups failed the first generalization test, when they were tested on novel views of the stimulus birds. There are a number of possible reasons for the lack of transfer at this phase of the experiment. Insufficient training or irritation caused by the presentation of novel and unrewarded pictures, as well as simple rote learning may explain why subjects failed in this test. To rule out the first two possibilities, these subjects received ten more training sessions and were afterwards tested again. After this extra-training, all subjects' performance on test trials increased. Two of the four pigeons, one of each group, performed significantly above chance level when they were tested a second time. This suggests that the lack of transfer was caused by insufficient training, as these birds learned to focus on the similarities between the stimuli, after having experienced a larger number of training sessions. Thus, they finally managed to generalize the learned discriminative behaviour to novel items. Additionally, the familiarization to the test procedure by the repeated presentation of novel items possibly led to the subjects' improved performance. In contrast, the other two birds again failed to perform significantly above chance level on the test trials. This indicates that these subjects learned the discrimination task by rote instead of classifying the pictures of conspecifics on the basis of perceptual similarities, or regarding to familiarity in case of the experimental bird.

Nevertheless, most of the tested subjects showed transfer to unknown views of the pictured conspecifics. This result is in accordance with the findings of Nakamura et al. (2003), who demonstrated that pigeons are capable of distinguishing between static images of two groups of five unfamiliar conspecifics each and can transfer the learned discriminative behavior to photographs of the same pigeons taken from different perspectives. The result suggested that the pigeons' transfer of the learned discrimination between pictures of individual conspecifics to novel images was due to perception of the similarity of the training stimuli to the test pictures (Vaughan, 1988; Vaughan & Herrnstein, 1987). Although the findings contribute to the increasing evidence that static visual cues are involved in individual recognition in pigeons, the chosen methods did not allow clarification of the features on which the discrimination among individuals was based.

Interestingly, the findings do not indicate that the experimental birds had the advantage over the control group suggesting that the familiarity with the pictured flockmates did not enhance subjects' transfer. Moreover, this test gives no information about the question of whether the subjects perceived some correspondence between real conspecifics and their pictures or whether the subjects recognized the depicted birds as pigeons. In general, it is unclear what pigeons perceive when they are faced with pictorial images. The reasons for possible problems in understanding the representational state of pictures are numerous. On the one hand, photographs are always abstractions of the real objects and may lack information that normally supports the recognition of them in real life, as for example movements, olfactory and auditory cues. Furthermore, static visual cues not depicted in photographs, as for example UV light, may also influence reliable recognition of conspecifics. Photographs are adjusted to the visual system of humans. This differs in many aspects from that of a pigeon. For example, differences in colour vision of the two species may result in problems in terms of understanding photographs as representations of the real world in pigeons. In contrast to our trichromatic colour vision, pigeons have tetra- or possibly even pentachromatic vision (Husband & Shimizu, 2001). Thus, the colours contained in photographs are not sufficient to create all hues that pigeons can see. Moreover, the understanding of the representational state of pictures is an ability that arises through experience. Reports that adults of other cultures, who are not used to seeing pictures, had problems equating photographs with the objects they show indicate the importance of experience in connection to this ability (Miller, 1973, cited in Bovet & Vauclair, 2000). Daily exposure to pictures allows us to reliably infer the real objects that are represented. In nature, the information that is used for individual recognition in animals may therefore differ from the features contained in photographs. It is likely that behavioural patterns, olfactory and auditory, as well as particular visual features not contained in photographs contribute to the discrimination between conspecifics. However, it is likely that pigeons are able to use two-dimensional, visual cues in nature also when they see it on a photograph. The use of these can be assumed independently of the overall issue of picture-object recognition since the pigeons discriminated between pictures of conspecifics and transferred this learned discrimination to new pictures of the same stimulus birds and photographs always represent a degraded stimulus in comparison to the real item (Delius, Emmerton, Hörster, Jäger, & Ostheim, 2000). Since pigeons are able to use specific static visual cues for the discrimination of pictured conspecifics, it is reasonable to assume that this information of photographs can also be used in distinguishing real life conspecifics.

The second transfer test addressed whether pigeons can use their real experience with conspecifics as a feature on which the discrimination between pictures can be based. Thus, pictures of two novel flockmates of the experimental birds and two pigeons with which none of the subjects had any experience were shown as test stimuli. The subject pigeons had to categorize these new examples of the classes in terms of familiarity. Two birds of the experimental group performed significantly above chance level when they were tested on pictures showing novel unfamiliar and familiar pigeons.

The transfer of the discrimination in Test 1 indicates that perceptual features contained in both the training stimuli and the test pictures, provided the basis for the transfer since both subject groups solved the task. On the other hand, the pictures used for Familiarity Test obviously did not provide any common visual cues with the training exemplars as no bird of the control group could correctly classify the pictured conspecifics. The two sets of photographs were indeed only distinguishable through real life experience with the stimulus birds and did not contain any additional perceptual information on which the discrimination could have been based. Transfer based on the generalization from stimulus-feature learning can therefore be ruled out. This finding underlines previous reports of the pigeons’ capability to use real life experience in visual discrimination tasks (e.g., Aust & Huber, 2006; Wilkie et al., 1989; Watanabe, 1997).

However, the results do not clarify the underlying information that controlled the subjects' behavior. Firstly, it is possible that the transfer occurred on a purely perceptual basis. In this case, it could have been mediated by basic invariant features of the related stimuli, such as particular colours or shapes visible in the real animal and its pictured version, without the understanding of the pictures as representations of the real conspecifics. Furthermore, the successful pigeons might have solved the transfer test on a more abstract basis by perceiving the correspondence between the real pigeons and their photographs while being aware that the pictures represent real conspecifics and by forming a distinct category of flockmates and strangers, respectively, on the basis of familiarity.

Apart from the question of what the two successful subjects perceived in the photographs, the subjects' transfer of the discrimination between the flockmates and unfamiliar pigeons to novel instances of the stimulus classes was obviously mediated by learning an abstract relationship of familiarity. Pigeons are known for their ability to easily learn natural concepts which are based on perceptual similarities among items. In contrast to this categorization that is based on feature generalisation, pigeons have been shown to have difficulties in solving any task that requires the formation of an abstract concept. In fact there is only one study that convincingly shows abstract concept learning in pigeons (Katz & Wright, 2006). For learning an abstract concept a subject has to judge the relationship among the items on the basis of a rule independent of any perceptual similarities. The present study shows that two pigeons categorised the pictured conspecifics by judging them as familiar or unfamiliar. Taking into account that there is little evidence of the ability in pigeons to solve such an advanced and cognitively demanding task, as to form an abstract concept of familiarity, this finding is very impressive and of particular interest.

4 EXPERIMENT 2

In Experiment 1, two birds successfully classified novel photographs of conspecifics in terms of familiarity. This finding raises a number of questions regarding how the pigeons solved the task and what familiarity means to the birds. Experiment 2 examined the role of social contact between the subjects and the stimulus birds for the successful discrimination between photographs of conspecifics in terms of familiarity. To find out whether social interaction between target birds and subjects was crucial for solving the task, pictures of flockmates were replaced with photographs of only visually known birds in test trials. As stimuli photographs of pigeons that were housed in an aviary opposite the aviary of the experimental group were used. These housing conditions allowed permanent visual contact between the experimental subjects and the target birds. At the same time any kind of social interaction was prevented by the distance between the home enclosures. If purely visual experience with the stimulus birds is sufficient for classifying the conspecifics as familiar then the subjects were expected to respond in the same way to the novel stimuli as they did to pictures of flockmates. However, if social experience, meaning direct social interactions between subjects and target birds, affects the pigeons' rating of familiarity, then test trials of the newly introduced stimulus class should result in chance performance in this experiment.

4.1 METHODS

4.1.1 Subjects

The two successful experimental birds from the previous task served as subjects. As determined before the onset of the study one bird, Judith, belonged to the group "Familiar positive" and was reinforced for pecking pictures of familiar pigeons, whereas the other pigeon, George, was assigned to the group “Unfamiliar positive” and was reinforced for pecking pictures of unfamiliar pigeons.

4.1.2 Stimuli, Apparatus and Procedure

The apparatus as well as the set of training stimuli were the same as described in the Methods section of Experiment 1. The standard procedure used for Experiment 2 is explained in the Methods section of Experiment 1. Depending on the phase of the experiment, the procedure was modified and adjusted accordingly and a novel set of test stimuli were introduced as described below.

Before the onset of this experiment the subjects received ten normal training sessions as described for the discrimination training in Experiment 1. After this re-training, the subjects were tested in four successive test sessions in total, one test session per day. A test session included 40 training trials and six randomly intermixed test trials that were not differentially reinforced. The training stimuli were the same as in Experiment 1. Thus, training trials included the presentation of a flockmate and of an entirely novel pigeon. For test trials, a new stimulus class, namely pictures of semi-familiar pigeons was introduced. Two pigeons that were housed in the compartment that is located opposite the home enclosure of the experimental group were used as stimulus birds for this test. The minimum distance between the experimental subjects and the semi-familiar stimulus birds was one meter and the maximum distance was five meter. These individuals were defined as semi-familiar conspecifics, because the positioning of their enclosure allowed daily visual contact between the stimulus birds and subjects of the experimental group. This, however, did not offer the possibility of direct, social interaction such as competition or courtship behavior. Photographs of two new unfamiliar birds served as the other test stimuli. Twelve photographs of each of the four birds showing them from different perspectives were taken. The same camera was used for photographing these birds as for the first sets of stimuli. Moreover the conditions under which the pictures were taken as well as the views of the pigeon were equal. All modifications made to these pictures were the same as those on the training stimuli. Examples of the stimuli are shown in Figure 10.

Test trials consisted of the simultaneous presentation of a picture of an unknown individual and one of the semi-familiar stimulus birds. As the pigeons were assigned to different reinforcement conditions, for Judith photographs of the visually known pigeons served as the positive stimulus class. In contrast, the pictures of unfamiliar conspecifics represented the positive stimuli for George.

Figure 10. Examples of the test stimuli. The left picture of each stimulus pair shows a semi-familiar pigeon while the right picture represents an unfamiliar conspecific taken from the corresponding perspective.

4.2 RESULTS

Figure 11 shows the performance of the subjects as the percentage of correct choices on training and test trials. Both birds showed a highly significant performance on training trials (Binomial test, $p \leq 0.0001$ for each subject). George chose the positive stimuli in 125 out of the 160 training trials, and thus he performed at 78% correct. Judith performed 74% correct, responding appropriately to 118 training stimuli pairs. On test trials, however, their performance dropped below significance level for correct choices. Judith chose the pictures of the visually familiar conspecifics in 16 out of the 24 test stimuli pairs which equals a correct performance of 67% on test trials (p = 0.152). George chose the positive stimulus class only eight times, resulting in a correct performance of 33% (p = 0.152). Although the subjects were assigned to different subgroups and thus the positive category differed for subjects, both birds showed a non significant tendency to chose pictures of semi-familiar conspecifics over photographs of strangers.

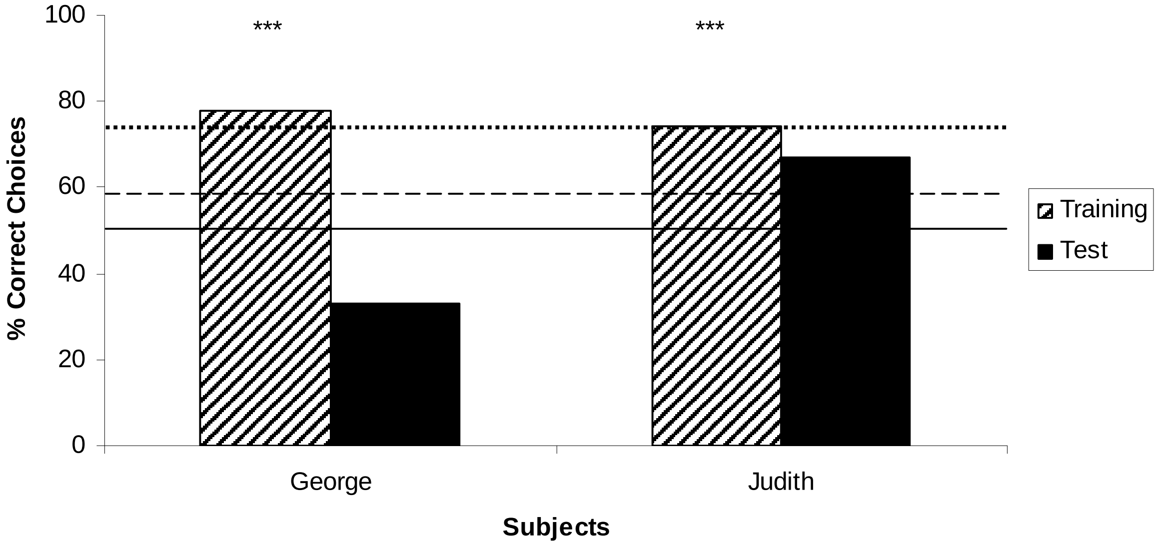

Figure 11. Percentage of correct choices of the two Experimental subjects. *Striped bars* depict the pigeons' performance on the training trials during the test sessions and *dark grey bars* the performance on the test trials. The *solid line* represents chance level (50%), the *dotted line* represents the two-sided significance level of 0.05 for the test trials. The *dashed line* represents the two-sided significance level of 0.05 for the training trials. Results of the Binomial test: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

4.3 DISCUSSION

When presented with photographs of semi-familiar pigeons, the subjects lost the ability to categorize novel images of conspecifics on the basis of familiarity. There are several possibilities to explain the lack of transfer when subjects were tested with images of pigeons that I defined as semi-familiar conspecifics. One explanation for the lack of transfer might be that familiarity is influenced by the biological relevance of the stimulus or social experience with it. It is easily conceivable that visual experience itself is not sufficient for categorizing conspecifics as familiar. The subjects are used to the presence of a large number of other pigeons that do not influence their lives. Kept in separated enclosures of a big outdoor aviary the conspecifcs are meaningless in terms of any biological aspects, such as mating success or competition. Thus, it is possible that pigeons over time learned to ignore those birds and therefore do not respond to their appearance and behaviour any longer. It is likely that social experience, or biological relevance rather than visual experience with another pigeon may be necessary for it to be categorized as familiar.

Another factor that might have influenced the subjects' performance is the distance between the aviaries of the experimental birds and the stimulus pigeons. Visual familiarity between subjects and stimulus birds was assumed because the positions of the aviaries principally allow visual contact between groups. However, the semi-familiar stimulus group is housed in an aviary opposite to, but distant from, the home enclosure of the experimental subjects. Thus, the distance between the compartments may be too large to develop a high degree of familiarity with individual conspecifics of the other group. Since it has been reported that individual recognition seems to be difficult at larger distances in chicken, the distance between two individuals may be a crucial factor for social recognition in some species (Dawkins, 1996; D'Eath and Stone; 1999). The reason for these difficulties in recognizing individuals are tiny features, such as certain plumage patterns that are not visible at large distances. To ensure visual familiarity it would therefore be necessary to determine the distance in which pigeons are recognized by others.

Finally, it should be mentioned that both subjects responded in a similar way to the new photographs although the subjects belonged to different subgroups of the experimental group. For Judith familiar conspecifics were assigned to the positive stimulus class, while flockmates served as negative stimuli for George. The fact that both subjects showed a non significant trend for pecking towards pictures of the semi-familiar pigeons suggests that these test stimuli contained attractant features that were not related to the principle requirements of the task.

The inability to classify the stimuli used in this experiment does not exclude the possibility that pigeons discriminate between strangers and visually familiar conspecifics in nature. The result only indicates that the pictures of visually known birds were not treated in the same manner as those of flock-mates. Further studies are needed to reveal the circumstances under which a conspecific is classified as familiar.

5 EXPERIMENT 3

Experiment 1 revealed the pigeon's capacity to classify slides of flockmates and unknown pigeons in terms of familiarity with the pictured individual. This ability, however, was absent when the target pigeon was visually known but socially unknown (Experiment 2). The results raised the question whether the pigeons formed a general category of highly familiar items rather than a specific category of familiar conspecifics. To find out whether discrimination on the basis of familiarity was restricted to conspecifics or could be extended to any other highly familiar items two new sets of photographs showing familiar and unknown objects were introduced in Experiment 3.

5.1 METHODS

5.1.1 Subjects

The subjects used in this experiment were the same as in the previous one, as they were shown to correctly respond to newly introduced exemplars of unfamiliar and familiar conspecifics (Experiment 1).

5.1.2 Stimuli, Apparatus and Procedure

The apparatus as well as the set of training stimuli were the same as described in the Methods section of Experiment 1. The standard procedure used for Experiment 3 is explained in the Methods section of Experiment 1. Depending on the phase of the experiment, the procedure was modified and adjusted accordingly and a novel set of test stimuli were introduced as described below.

Before the onset of the experiment the subjects received ten normal training sessions, identical to those described for the discrimination training of Experiment 1. After this re-training the subjects were tested in four successive test sessions, one test session per day. A test session consisted of 40 training trials and six intermixed test trials. The training stimuli were the same set of stimuli as in Experiment 1. Pictures of four objects served as test stimuli. The test stimuli consisted of photographs of the food trough and the water dispenser that are placed in the aviary daily. As these objects are visible to the subjects, and provide them with food and water, they are highly familiar but also of great importance to the birds. Secondly, pictures of a yellow Wellington boot and an orange plastic spade were taken. These items had never been seen by the pigeons and therefore, they were employed as unknown objects. Just as with the stimulus birds, the objects were photographed from twelve different perspectives. The pictures were taken and modified in the same way as described in the Methods section of Experiment 1. Examples of the test stimuli are shown in Figure 12. Test trials, thus, consisted of the presentation of one picture of a familiar object in combination with a photograph of an unknown object. There was no differential reinforcement of the test trials.

Figure 12. Examples of test stimuli. The left stimulus pairs represent different views of unfamiliar objects. The stimuli on the right side show familiar objects.

5.2 RESULTS

The pigeons' discriminative behaviour during the transfer test including training and test trials are shown in Figure 13. Judith performed significantly above chance level on training trials as well as on test trials. She responded correctly to 116 out of the 160 training trials which equals a correct performance of 73% ($p \leq 0.0001$). Judith chose pictures of the food trough and the water dispenser on 19 out of 24 test trials resulting in a correct performance of 79% ($p \leq 0.007$). George performed 77% correct on training trials which is highly above chance level ($p \leq 0.0001$). In contrast, he showed no significant preference for either group of test pictures. By choosing the positive test pictures in only ten out of the 24 trials, which equals 42% of correct choices, the bird performed slightly below chance level on test trials ($p \leq 0.541$).

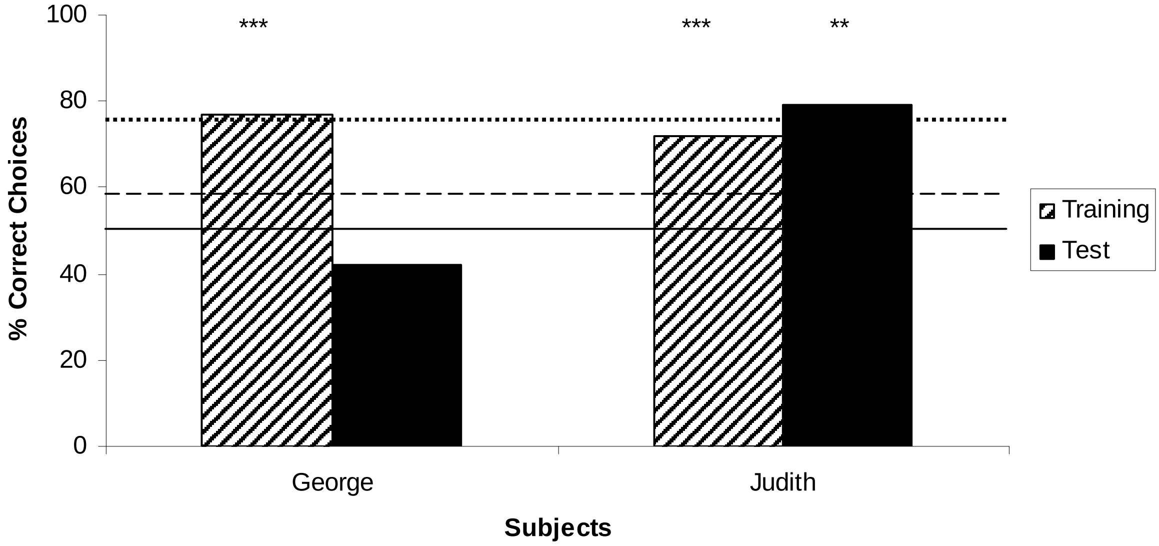

Figure 13. Percentage of correct choices of the two tested Experimental subjects. *Striped bars* depict the pigeons' performance on the training trials during the test sessions and *dark grey bars* the performance on the test trials. The *solid line* represents chance level (50%), the *dotted line* represents the two-sided significance level of 0.05 for the test trials. The *dashed line* represents the two-sided significance level of 0.05 for the training trials. Results of the Binomial test: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

5.3 DISCUSSION

Experiment 3 revealed that one of the birds had a significant preference for pictures showing familiar objects compared to unfamiliar objects. While the subjects had never had any kind of experience with the objects representing the category "Unfamiliar positive", the use of images of the food trough and the water dispenser ensured a high degree of contact and visual familiarity. Moreover, as these items provide the birds with food and water, they are of great biological relevance to them. Thus, it is likely that the daily observation as well as the interaction with the target objects led to a more general understanding of the concept of familiarity, allowing Judith to transfer the learned discrimination of conspecifics to familiar objects.

In contrast to the transfer to familiar objects in the present experiment, neither of the subjects successfully classified pictures of semi-familiar conspecifics and strangers in terms of their experience with the real pigeons in Experiment 2. The difference between the stimuli regarding the subject pigeons' experience with the real items and also their importance to the subjects may have caused the difference in performance seen on test trials in Experiment 2 and Experiment 3.

6 GENERAL DISCUSSION

Abstract concept formation goes beyond categorization on the basis of perceptual similarities. It rather includes the judgement of a relationship between items on the basis of a rule. If an animal is able to apply this rule to novel items it is considered to show abstract concept learning (Katz et al., 2007; Young & Wasserman, 2001). Two subjects in this set of experiments responded to novel instances of familiar and unfamiliar conspecifics in the same way as they did to training pictures. It can thus be concluded that these pigeons learned an abstract concept of familiarity. This result adds to the evidence of the pigeons' capability of abstract concept learning (Katz & Wright, 2006).

Overall, the results of the current study revealed different levels of category formation in pigeons. Two subjects successfully learned the discrimination task during the training phase but failed to generalize the learned discriminative behaviour to novel views of the stimulus birds in Experiment 1. Following this lack of transfer the birds showed categorization by rote learning. To achieve this level an animal needs to discriminate and memorize an arbitrary list of stimuli. The classification criteria, in this case, are dependent upon contingency rules (Zayan & Vauclair, 1998). As already mentioned, pigeons are known for their proficient capacity to learning a large number of stimuli and to successfully sort them into arbitrary categories as well as for memorizing large amounts of information (e.g., Vaughan & Green, 1984). Although two individuals learned the discrimination of the stimulus sets by rote, all the other subjects showed a higher level of categorization, namely the formation of open-ended categories. This was indicated by the generalization of their learned discriminative behaviour to novel pictures of the same stimulus birds. Contrary to rote categorization, which depends on memorizing each stimulus, the perceptual similarity between instances of a particular class forms the basis for open-ended categorization. Previous experiments demonstrated the pigeon's ability to distinguish photographs of individual pigeons, despite very similar appearance among the stimulus birds, and to accurately transfer this discrimination to novel views of the same conspecifics (e.g., Watanabe & Ito, 1991; Nakamura et al., 2003). The present findings contribute to the increasing evidence that the morphological properties that are unique for each individual present a polymorphous set of features that represent a single natural category for a subject. Finally, two subjects even formed an abstract concept of familiarity which goes beyond the formation of perceptual categories.

But what did familiarity exactly mean to the subjects? With respect to this question, the results allow different possible interpretations. Firstly, the findings show that pigeons possess the ability to distinguish between pictures of conspecifics they know and of strangers (Experiment 1, Test 2). The subject may have solved the task by understanding the representational state of the pictures and by forming a distinct class of flockmates and strangers, respectively. In the case of one subject the classification in terms of familiarity was restricted to photographs of pigeons. However, the test pictures showing objects were introduced without any pre-training of this new type of stimuli. This abrupt introduction of a novel stimulus type possibly led to the breakdown of the subject's performance resulting in the lack of transfer. In contrast, another subject extended this discriminative behaviour to photographs of objects. The subject may have solved this transfer task by possessing a broader understanding of familiarity not restricted to conspecifics (Experiment 3). The inclusion of different stimulus classes such as objects, conspecifics, and individuals of other species for training as well as testing could provide more information on whether the concept of familiarity can be extended to any other items.

Since none of the subjects successfully classified visually familiar (semi-familiar) birds and strangers in terms of familiarity it is reasonable to assume that stimuli are only classified as familiar if the subject has the chance to spend lots of time to observe them closely or interact with them everyday. Being in physical contact or close visual contact with something may be the key for the categorization in terms of familiarity. The importance of the temporal connection between the exposure to a stimulus in reality and to its pictured version with regard to the development of a correspondence between a stimulus and its two-dimensional representation has already been suggested by other researchers. Wilkie et al. (1989) reported that homing pigeons with real life experience with one of two depicted locations learned to discriminate between the two sets of photographs faster than pigeons without any experience with the shown places. Homing pigeons also performed significantly better during the initial transfer tests including novel images of both landscapes. However, the difference was only present for the initial transfer tests. Homing pigeons were normally released for outdoor flights whereby they were allowed to visit the real environment shown as familiar stimuli during the experiment. It was stated that these flights were stopped because of a sudden change in weather. Interestingly, this was the time when the performance of homers and non-homing pigeons converged. The authors concluded that the continual exposure to the real environment may have affected the discriminative behaviour of the birds. In a similar discrimination task Kendrick (1992) used pictures of the surroundings of the subjects' home enclosure as familiar stimuli. Being highly experienced with this location as well as permanently exposed to it these birds outperformed the control individuals, which had no experience either of the depicted locations. Other experiments about the discrimination and recognition of landscapes that did not find such a familiarity effect differed considerably in terms of the pigeons' experience with the depicted place. Dawkins et al. (1996), for example, placed two groups of pigeons in cages at six viewpoints of two locations. Both groups had no prior experience with the places. The pigeons were then trained on a visual discrimination task including photographs of the location visited by only one group of subjects. This simple pre-exposure to the landscape did not result in faster acquisition or better transfer to novel slides of the location.

In the present study pigeons of the experimental group were housed with the conspecifics that were the familiar stimulus class for the entire experiment. The pigeons had been housed together for at least two years before the onset of the study. Therefore they were in permanent contact with each other, which provided a high degree of visual familiarity. Within the group, most of the pigeons have formed long lasting pairbonds with each other and socially interacted with their flockmates in a variety of contexts such as competition over females or food. Thus, the housing condition did not only lead to visual familiarity among subjects but also provided a high degree of social familiarity. Subjects were only kept separate during the experimental sessions and were released in their aviary immediately afterwards. The subjects, thus, were able to see and interact with the real birds before and immediately after the experimental session during which the conspecifics were presented as photographs. This continuous experience with the real conspecifics might have influenced the subjects' performance resulting in a transfer to novel examples of the categories.

Furthermore, it is conceivable that the biological relevance of a familiar stimulus and/or the attention paid to it influenced the positive transfer in the present experiments. Studies examining the effect of brain lesions on the pigeon's ability to visually distinguish between items found some dissociation between food and artificial pattern discrimination as well as between conspecifics and species discrimination (Watanabe, 1996). The results indicate that ecologically and behaviourally important stimuli are processed in a different manner than visual information without any relevance to the pigeon's life. The recognition of an animal in terms of familiarity is crucially important as it allows an individual to respond differently and appropriately to social partners and other conspecifics. The subjects of the experiment interacted with others in a variety of social contexts involving pair-bond formation and competition. Moreover, the food trough and the water dispenser that were used as stimuli in the object task offered a biologically important class of stimuli since they provide the subjects with food and water. In contrast, the semi-familiar conspecifics are irrelevant in terms of biological importance to the subjects. Since the pigeons are housed in different aviaries in a large outdoor complex they are used to a large number of conspecifics being around them. The birds are always exposed to them but these conspecifics do not influence their life in anyway because the housing conditions make social interactions impossible. This may lead to a decrease in attention that is paid to the conspecifics outside their own aviary and thus lead to the absence of the ability to classify them as familiar. However, the visual familiarity between the groups was assumed by the experimenter and not behaviourally tested. Thus, both, the role of purely visual experience with the stimuli and the role of their biological relevance to a subject in this categorization task needs to be further investigated. To more closely investigate this aspect it would be reasonable to test the subjects on photographs of birds housed directly next to the subjects' home enclosure only separated by wire mesh ensuring visual familiarity.

The present study clearly demonstrates that the real-life experience with the individuals used as stimuli influenced the pigeons' behaviour. The mechanisms underlying this effect are still not clear. In many studies focussing on the ability of animals to link a visual stimulus to reality it has been argued that the visually perceived features of the particular object facilitate the response to the related picture. As a consequence, the basis of the interference of real items and their pictured versions may be explained by priming. Priming effects have been studied in a variety of species including pigeons (e.g., Blough, 1991). Although little research has focussed on how priming is linked to picture perception, perceptual priming has been shown in an experiment that required pigeons to categorize pictures of an occluded object after they were exposed to the unfragmented version of the same stimulus. The experience with an image resulted in a facilitated categorization of the same but degraded stimulus (Brodback, 1997). Priming is often a possible explanation for an animal's response to a degraded stimulus dependent of whether it has been exposed to the stimulus in reality or not. It has recently been shown that cats and dogs show a preference for photographs of familiar conspecific faces when they were required to choose between a photograph of conspecifics that live in the subjects' group and that of an unknown individual (Lomber, Hall, & Cornwell, submitted). Priming may be the underlying mechanism for this preference for familiar conspecific faces. However, priming cannot explain the findings of the present study. If a priming effect had caused the pigeons' behaviour, it would be present at the onset of the experiment. This would have caused an enhanced response to pictures of the familiar conspecifics from the very first training session. In contrast the findings revealed stepwise learning in the subjects' learning curves. Since the birds did not reveal an enhanced response to photographs of the known conspecifics from the very beginning but learned the discrimination task over time, priming can be ruled out as underlying mechanism of the transfer. Moreover, the different behaviour of George depending on the stimulus type contradicts the priming hypothesis. This subject correctly classified novel instances of flockmates and unknown conspecifics but failed the same task carried out with familiar and unfamiliar objects as stimuli. If priming had caused the transfer, no difference in performance would be expected no matter which kind of stimuli are used, so long as the experience with them is the same.

Therefore, the birds obviously perceived some correspondence between the real items and their pictures. But did the pigeons solve the tasks because they saw birds and objects, respectively, in the photographs? Or was the observed transfer rather mediated by simple 2D features visible in the real items and their images? The use of pictorial stimuli is always linked to the question what the subject exactly perceives when observing them. This is due to the fact that picture perception, in general, depends on the physical properties of the image. Moreover, it is strongly influenced by the characteristics of the perceiver in terms of the functional properties of the visual system as well as the experience with pictures. Since photographs are geared to the human visual system that differs in many aspects from that of a pigeon, it is likely that pigeons see photographs in a totally different manner to what we do (Fagot, Martin-

Malivel, & Dépy, 2000; Bovet & Vauclair, 2000). These aspects lead to some difficulties in answering the question of how the photographs were perceived in respect of their representational state of real items in the present study.

The findings do not necessarily indicate that the subjects perceived the photographs in an equivalence mode, i.e. a kind of association between reality and the picture, while being aware that the photograph is not the same as the reality. The simple visual features present in the related stimuli could have mediated the transfer from reality to the picture (Experiment 1, Familiarity Test; Experiment 3). In general, it is very hard to tell whether the basis of the transfer from reality to pictures or vice versa is perceptive or rather abstract, because the real items and their images usually have some perceptual similarities in common.

On the one hand, it has been concluded that perceiving the equivalence between photographs and their two-dimensional representation may be severely limited in pigeons (Delius et al., 2000). As a consequence, the basis of the influence of the real stimulus and its pictured version may be due to the familiarity with basic invariant features of each individual, such as a certain pattern or colour that allowed the subjects to respond correctly to the related stimuli. On the other hand, evidence for the pigeon's ability to recognize the representational content of pictures was provided by Aust & Huber (2006). After the authors trained pigeons on photographs showing humans missing a particular body part, the subjects showed a significantly stronger response to stimuli picturing the previously missing part in a subsequent transfer test. According to this result the experimental subjects of the present study may have regarded the photographs as representations of the real flockmates, strange pigeons, and objects, respectively. This approach would allow an interpretation of the behaviour shown by George, the one subject that did not respond correctly to novel familiar and unfamiliar items when objects served as stimuli but did so when conspecifics were presented. This pigeon may have formed a specific concept of flockmates and strangers rather than a general concept of familiarity. Since both tasks could have been solved by the use of common visual traits shared by the real items and their pictorial versions, this mechanism makes it difficult to explain why this pigeon showed a different behaviour in dependence of the stimulus type.

The present study underlines previous findings that this species perceive some correspondence between real items and their pictorial versions. Furthermore, it provides strong evidence for the pigeons' ability to form an abstract concept of familiarity, defined as prior real life experience with depicted conspecifics, in an operant setup. As the current study revealed this capability for the first time, it raises a number of questions. On the one hand, the present results justify further consideration of the question of how this species perceives pictorial information. Linked to this issue, it would be of great interest to clarify the role of experience with both, pictorial information itself and the pictured items. The use of conspecifics as stimuli that represent a highly familiar stimulus class as well as the high degree of previous experience with pictorial information of the subjects suggest the importance of the stimulus choice. Therefore, it might be crucially important to investigate the role of the stimulus type in tasks requiring picture-object recognition.

Taking into account that conspecific recognition plays a crucial role in animals' social life it can be assumed that conspecifics represent a stimulus class that differs in various aspects from any other object class. In humans, non-human primates and other mammals the faces of their own species seem to represent a special stimulus class compared to objects or individuals of other species. This is indicated by the occurrence of phenomena as the "inversion effect" or the "other race effect" when faces serve as visual stimuli. The expertise in discriminating and recognizing conspecifics, neural specializations for their recognition, as well as differences in respect to the stimulus processing are discussed for the exceptional position of facial information of conspecifics (e.g., Diamond & Carey, 1986; Kendrick et al., 1996; Phelps & Roberts, 1994; Yin, 1969). Following, research focussing on possible differences depending on the stimulus type could contribute to a better understanding of how pigeons achieve the correspondence between pictures and reality and if this species possesses a specialization for visually based recognition of conspecifics similar to the one present in other animals. In order to investigate the latter issue pigeons should be tested on a categorization task requiring the discrimination of pictured conspecifics of a different breed on the basis of familiarity.

Finally, similar discrimination tasks using stimuli of other modalities, such as auditory or olfactory signals, would provide more detailed information about the extent of the familiarity concept in this species. Moreover, this approach would lead to a more general understanding not only of the information transfer between modalities but also of the information used by pigeons to distinguish between flockmates and strangers.

Due to the numerous questions raised by the present work it represents a starting point for further research that is needed to increase our knowledge about a number of issues such as abstract concept formation in non-human animals and picture-object recognition, as well as furthering our knowledge about the mechanisms involved in species or individual recognition.

In summary, the present study shows that pigeons are not only able to discriminate photographs of familiar and unfamiliar conspecifics but can even generalize this learned discriminative behavior to novel views of the training stimuli. Moreover, two out of five experimental subjects correctly classified pictures of novel stimulus birds that were not shown in training purely on the basis of familiarity whereas the control group could not. One bird even transferred the learned concept to a newly introduced stimulus type, namely objects. Thus, the results provide evidence for three aspects of visual cognition. They suggest that pigeons (i) recognize some correspondence between computer stimuli and real items, (ii) possess the ability to form an abstract concept of familiarity, and (iii) are able to distinguish between social partners and strangers in nature.

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APPENDIX

Supporting Information

Table 2. Learning Speed in the Discrimination Training

Experimental Group		Control Group	
Subjects	Sessions	Subjects	Sessions
Agnes	67	Arthur	100[a]
Fred	23	Birgit	52
George	31	Ferdinand	69
Heinz	27	Heidrun	45
Judith	43	Meggie	100[a]
Vanessa	47	Trisha	26

Note. Data presented are the number of training sessions before meeting the learning criterion. The learning criterion was set at 75% correct choices in four out of five consecutive sessions, and at least 70% correct choices in the remaining training session. The training involved the same set of stimuli for the experimental bird and the control subject listed in a line.

[a] Subjects failed to reach the criterion within the determined maximum number of sessions.

Table 3. The Experimental Group's Performance in Test 1 (Experiment 1)

		Experimental Group	
Subject	Subgroup	Test 1	
		Test trials	Training trials
Agnes	Unfamiliar	17 (0.032)	89 (≤0.0001)
Fred	Unfamiliar	21 (0.0001)	93 (≤0.0001)
George	Unfamiliar	18 (0.011)	101 (≤0.0001)
Heinz	Familiar	16 (0.076)	108 (≤0.0001)
Judith	Familiar	18 (0.011)	84 (≤0.0001)
Vanessa	Familiar	20 (0.0008)	88 (≤0.0001)

Note. Listed are the number of correct choices out of the 24 test trials and the 120 training trials for each experimental subject. *P*-values (one-sided binomial test) are given in parenthesis.

Table 4. The Control Group's Performance in Test 1 (Experiment 1)

		Control Group	
Subject	Subgroup	Test 1	
		Test trials	Training trials
Birgit	Unfamiliar	17 (0.032)	94 (≤0.0001)
Ferdinand	Unfamiliar	15 (0.154)	81 (≤0.0001)
Heidrun	Familiar	18 (0.011)	92 (≤0.0001)
Trisha	Familiar	22 (≤0.0001)	85 (≤0.0001)

Note. Listed are the number of correct choices out of the 24 test trials and the 120 training trials for each control subject. *P*-values (one-sided binomial test) are given in parenthesis.

Table 5. The Experimental Group's Performance in Test 2 (Experiment 1)

Subject	Subgroup	**Experimental Group** Test 2 Test trials	 Training trials
Agnes	Unfamiliar	12 (1.000)	126 (≤0.0001)
Fred	Unfamiliar	15 (0.307)	117 (≤0.0001)
George	Unfamiliar	18 (0.023)	127 (≤0.0001)
Judith	Familiar	19 (0.007)	131 (≤0.0001)
Vanessa	Familiar	13 (0.839)	130 (≤0.0001)

Note. Listed are the number of correct choices out of the 24 test trials and the 160 training trials for each experimental subject. *P*-values (two-sided binomial test) are given in parenthesis.

Table 6. The Control Group's Performance in Test 2 (Experiment 1)

Subject	Subgroup	**Control Group** Test 2 Test trials	 Training trials
Birgit	Unfamiliar	12 (1.000)	126 (≤0.0001)
Heidrun	Familiar	13 (0.839)	135 (≤0.0001)
Trisha	Familiar	16 (0.152)	116 (≤0.0001)

Note. Listed are the number of correct choices out of the 24 test trials and the 160 training trials for each control subject. *P*-values (two-sided binomial test) are given in parenthesis.

Zusammenfassung

Kategorisierung stellt einen fundamentalen Aspekt der Informationsverarbeitung dar, weshalb sie zu einem zentralen Thema der Kognitionsforschung wurde. Tauben sind für ihre Befähigung, Bilder an Hand ihres Inhaltes in verschiedene Klassen einzuordnen, bekannt (Herrnstein & Loveland, 1964). Zudem konnte gezeigt werden, dass diese Spezies zwischen Fotographien von verschiedenen Artgenossen unterscheiden und überdies hinaus dieses diskriminative Verhalten auch auf neue Bilder derselben Tiere generalisieren können (Nakamura, Croft, & Westbrook, 2003). Dieses Forschungsergebnis deutet auf die Verwendung statischer, visueller Merkmale zur Diskriminierung hin, obgleich eine derartige Aufgabe keine Erkennung des Individuums erfordert.

Generell betrachtet sind die Merkmale, die der visuellen Diskriminierung unterliegen können, vielfältig. Ob auch die in der Realität gesammelte Erfahrung mit einem Objekt genutzt werden kann, um dessen zweidimensionale Abbildungen erfolgreich in Klassen einzuordnen, ist hierbei eine Frage, die noch nicht vollständig geklärt ist. Forschungsarbeiten, die diese Fragestellung streiften, untersuchten meist die Fähigkeiten von Brieftauben zur visuellen Diskriminierung und des Erkennens vertrauter geographischer Örtlichkeiten (Cole & Honig, 1994; Wilkie, Willson, & Kardal, 1989). Die aus diesen Studien gewonnenen Ergebnisse sind kontrovers und erlauben keine eindeutige Schlussfolgerung.

In der vorliegenden Arbeit beleuchtete ich die Frage von einem anderen Blickwinkel, indem ich Fotographien von Artgenossen als Stimuli verwendete. Der Unterscheidung zwischen bekannten und unbekannten Artgenossen könnte eine besondere Bedeutung im sozialen Leben der Taube zukommen. Diese Fähigkeit würde zu einem biologischen Vorteil führen, indem sie Individuen ermöglicht, adäquat auf soziale Partner zu reagieren. Da diese Befähigung eine wesentliche Rolle in der Natur spielt, untersuchte ich, ob Tauben Bilder von Artgenossen an Hand ihrer Bekanntheit mit denselben kategorisieren können (Experiment 1).

Unter Verwendung einer two-choice touch screen procedure wurden zwei Gruppen von je sechs Tauben Fotographien verschiedener Artgenossen präsentiert. Die Hälfte der verwendeten Stimuli zeigte Tauben, mit denen die Tiere der Experimentalgruppe in einer Voliere untergebracht waren. Die andere Hälfte der Stimuli zeigte unbekannte Artgenossen, mit denen keines der Versuchstiere zuvor in Kontakt stand. Die Kontrollgruppe hingegen hatte keinerlei Erfahrung mit allen abgebildeten Tauben. Der Großteil der Tauben lernte zwischen den beiden Stimulussets zu unterscheiden. Die Testergebnisse zeigten weiters, dass die meisten Tiere die erlernte Diskriminierung auf neue Ansichten der Trainingsstimuli generalisierten. In einem zweiten, entscheidenden Test wurden Fotographien von Individuen, die nicht als Trainingsstimuli verwendet worden waren, gezeigt. Zwei dieser Tauben waren gemeinsam mit der Experimentalgruppe in einer Voliere untergebracht, die übrigen beiden Tiere waren unbekannte Artgenossen. Zwei der fünf Tauben der Experimentalgruppe - jedoch kein Kontrolltier - klassifizierten die Bilder erfolgreich.

Ziel zweier Folgeexperimente war es, herauszufinden, welche Art der Erfahrung mit einem Stimulus erforderlich ist, um dessen zweidimensionale Repräsentation als bekannt klassifizieren zu können. In Experiment 2 ersetzte ich die Bilder der bekannten Artgenossen durch Fotographien visuell bekannter Tauben („Semi-bekannte Artgenossen“), die jedoch nicht gemeinsam mit Tieren der Experimentalgruppe gehalten wurden, wodurch die Möglichkeit zur sozialen Interaktion zwischen Stimulustauben und Versuchstieren limitiert war. Bilder von Artgenossen wurden in Experiment 3 durch Fotographien ersetzt, die vertraute Objekte wie beispielsweise den Futtertrog, bzw. fremde, noch nie zuvor gesehene Gegenstände zeigten. Während keines der Versuchstiere das erlernte diskriminative Verhalten auf die "semi-bekannten" Stimulustauben übertragen konnte, kategorisierte eine Taube die gezeigten Objekte an Hand ihrer Bekanntheit.

Die Ergebnisse liefern demzufolge Hinweise auf drei Aspekte visueller Kognition: Sie deuten darauf hin, dass Tauben (i) eine Übereinstimmung zwischen Fotographien und den repräsentierten Einheiten wahrnehmen, (ii) die Fähigkeit zur Bildung eines abstraktes Konzept des Bekannten besitzen, und (iii) zwischen sozialen Partnern und fremden Artgenossen unterscheiden können.

Summary

Categorization is a fundamental aspect of information processing and thus a central issue in cognitive science. Pigeons are known for their proficient ability to sort images into different classes according to their content (e.g., Herrnstein & Loveland, 1964). Furthermore, it has been demonstrated that this species is able to discriminate between, and generalise to, novel photographs of unfamiliar conspecifics (Nakamura, Croft, & Westbrook, 2003). This provides evidence for the pigeon's capacity to use static visual cues for discrimination; however, this task does not require individual recognition. The features on which visual discrimination may be based are various. Troje and his colleagues, for example, reported that pigeons relied on colour, intensity gradients and local shading when they had to categorically discriminate between photographs of male and female human faces (Troje, Huber, Loidolt, Aust, & Fieder, 1999).

A small amount of research has examined whether previous real life experience with pictured items can be accessed when sorting them into different classes was the question addressed by research focussing on the discrimination and recognition of familiar landscapes in homing pigeons (e.g., Cole & Honig, 1994; Wilkie, Willson, & Kardal, 1989). The results are mixed, thus I examined the question from a different point of view. The recognition of familiar conspecifics should provide pigeons with a biological advantage allowing them to respond differently and appropriately to social partners. As this ability is crucially important in nature, this experiment examined whether pigeons were able to categorize pictures of conspecifics on the basis of social familiarity (Experiment 1).

I used a two-choice touch screen procedure, and presented two groups of birds with photographs of conspecifics. For the experimental group half of the pictures were of familiar pigeons with whom they shared an aviary, the other half were of unfamiliar pigeons who they had never seen. The control group were unfamiliar to both sets of birds. The pigeons mastered the task, and tests revealed that most could generalize to novel views of the training stimuli. A second, critical, test presented photographs of pigeons that had not been used as training stimuli. Two were aviary-mates of the experimental group and two were unfamiliar. Two of the five experimental birds were able to classify these stimuli correctly whereas the control group could not.

In Experiments 2 and 3 the overall objective was to evaluate the pigeonns' category of familiarity by assessing the information a stimulus has to contain to be classified as familiar by pigeons. I replaced the photographs of flockmates by pictures of visually known but socially unfamiliar conspecifics in Experiment 2. Photographs of familiar and unfamiliar objects were used as test stimuli in Experiment 3. While neither of the tested subjects successfully transferred the learned discriminative behavior to the "semi-familiar" stimulus birds, one subject categorized the depicted objects in terms of familiarity.

The results provide evidence for three aspects of visual cognition. They suggest that pigeons (i) perceive a correspondence between computer stimuli and the real entities, (ii) possess the ability to form an abstract concept of famili-

arity, and (iii) are able to distinguish between social partners and strangers in nature.

List of Figures

Declaration
I assure that I wrote this Master's thesis independently, using only the indicated sources and aids. Places and passages inferred from other factories literally or according to the sense are marked under specification of sources as are pictures, tables and figures.

Erklärung
Ich erkläre, dass ich diese Masterarbeit selbstständig verfasst, und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe. Alle Stellen dieser Arbeit, die im Sinne oder Wortlaut anderen Werken entnommen wurden, sind unter Angabe der Quelle kenntlich gemacht. Selbiges gilt für alle Fotos und Darstellungen.

Wien, July 18th 2009

Hanna Lisa Specht

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Publications

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Specht, H. L., Wilkinson, A. & Huber, L. (2009) Familiarity in the Pigeon (*Columba livia*): Does a pigeon know who he knows? Opening Conference on comparative Social Cognition (COMPCOG), Budapest, Hungary

Publication

Wilkinson, A., Specht, H., & Huber, L. (in preparation) Familiarity in the Pigeon (*Columba livia*): Does a pigeon know who he knows?