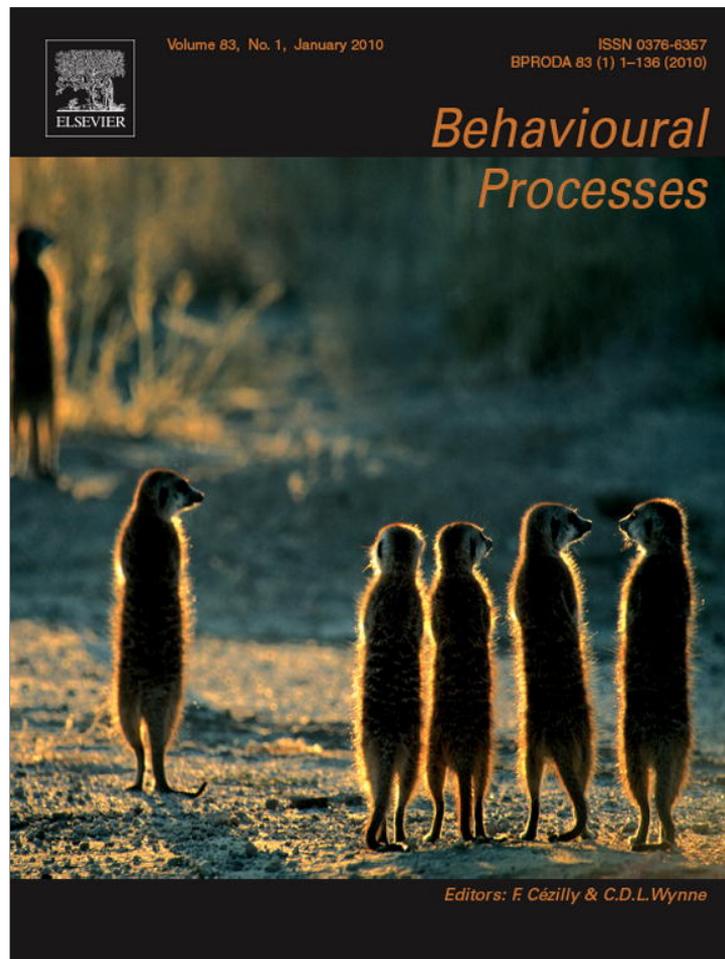


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Pigeons identify individual humans but show no sign of recognizing them in photographs

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ABSTRACT

Photographs, especially of humans, are widely used as stimuli in behavioural research with pigeons. Despite their abundant use, it is not clear to what extent pigeons perceive photographs as representing three-dimensional objects. To address this question, we trained 16 pigeons to identify individual, real-life humans. This discrimination depended primarily on visual cues from the heads of the persons. Subsequently, the pigeons were shown photographs of these individuals to test for transfer to a two-dimensional representation. Successful identification of a three-dimensional person did not facilitate learning of the corresponding photographs. These results demonstrate limitations of cross-recognition of complex objects and their photographs in pigeons.

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1. Introduction

Complex visual stimuli are widely used to investigate the principles of visuo-cognitive functions in pigeons (Huber, 2001; Jitsumori and Delius, 2001). Often, two-dimensional (2D) representations of three-dimensional (3D) natural objects are used, e.g., trees (Herrnstein et al., 1976), fish (Herrnstein and de Villiers, 1980), pigeons (Nakamura et al., 2006; Ryan and Lea, 1994; Watanabe and Ito, 1991), and people. Herrnstein and Loveland (1964) were the first to demonstrate that pigeons can readily classify photographs according to the presence or absence of people. People/no-people tasks have thereafter been used repeatedly in categorization studies with pigeons (Aust and Huber, 2001; Aust and Huber, 2002; Aust and Huber, 2003; Edwards and Honig, 1987; Siegel and Honig, 1970; Yamazaki et al., 2007). Other studies required classification of human photographs according to gender (Troje et al., 1999) or to the individual persons displayed (Herrnstein et al., 1976; Jitsumori and Makino, 2004).

Despite the extensive use of photographs, it has not been clarified sufficiently to what extent pigeons see a correspondence

between complex objects like humans and their pictorial representations (for reviews see Bovet and Vauclair, 2000; Delius et al., 1999). Herrnstein and Loveland (1964) initially suggested that the ease with which pigeons learned a people/no-people task indicated that they entered the experiment already possessing the “people” concept and applied this concept to the photographs. However, it is not self-evident that birds perceive photographs similarly to us. The last common ancestor of birds and mammals lived some 310 million years ago and the visual systems of both phyla have developed independently since then (Kumar and Hedges, 1998). Consequently, profound differences in visual functions have evolved, for example colour vision in pigeons is apparently pentachromatic in pigeons (for review see Delius et al., 1999). Pictorial representations are, however, designed according to the trichromatic vision of humans and therefore resemble reality to us humans, but probably much less so for birds (Delius et al., 1999).

Despite the evolutionary distant visual systems of birds, there are evidences for transfer between objects and their photographs in pigeons. Pigeons that were trained to classify 3D objects into “spherical” or “non-spherical” generalized the discrimination to photographs of these objects (Delius, 1992). Pigeons that were trained to classify objects or coloured photographs into grains (“food”) and other objects (“non-food”), discriminated correctly also novel instances and in addition transferred this discrimination to photographs or objects, respectively (Watanabe, 1993). In a follow-up study, Watanabe (1997) excluded the possibility that this transfer was due to object–picture confusion by demonstrating that pigeons could readily discriminate the objects from their pho-

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tographs. However, in this study the pigeons might have grouped the stimuli according to colour cues alone, i.e., without seeing a more abstract correspondence between the objects and their pictures, as pointed out by Spetch and Friedman (2006).

The particular role of colour for picture–object recognition by pigeons is controversial. Delius (1992) suggested that misrepresentations of colours disturb 2D information of depth, such as shading. However, a later study demonstrated that pigeons are able to use such cues for discrimination of coloured images (Cavoto and Cook, 2006). Further, chickens, which have at least tetrachromatic colour vision (Osorio et al., 1999), readily transfer a blue versus red discrimination from objects to photographs (Dawkins and Woodington, 1997). These studies indicate that trichromatic colour representation might be not as disturbing for visual perception of pigeons as suggested by Delius. Therefore, care has to be taken that successful 3D-to-2D transfer is not merely based on colours (or other spurious 2D cues), when object–picture correspondence is to be investigated.

To exclude this possibility, Cabe (1976) trained pigeons to discriminate two white painted objects. Subsequently, the pigeons were presented photographs, silhouettes, or drawings of these objects. The pigeons significantly responded more to the photographs and silhouettes corresponding to the objects that were previously rewarded, but failed to do the same with drawings. In a more comprehensive study, Spetch and Friedman (2006) replicated these results with two pairs of objects, which were indistinguishable by colour and were presented from different views. The pigeons transferred discrimination from objects to coloured photographs as well as from photographs to objects, suggesting that they saw correspondence between the two stimulus types. Notably, performances decreased remarkably during transfer, which might indicate that cross-recognition was not perfect.

However, it is questionable if the results generalize to stimuli as complex as photographs of humans. More complex and less constrained stimuli might offer discriminative 2D cues that are more obvious for the pigeon than the correspondence to a 3D object. For example, the design by Spetch and Friedman (2006) particularly encouraged the animals to process the global structure of the depicted objects, but pigeons are more likely to identify stimuli according to colour than to shape, if possible (Kirsch et al., 2008).

The strongest evidence up to now in favour of the view that pigeons cross-recognize humans and their pictures spontaneously, comes from an elegant study by Aust and Huber (2006). They trained pigeons on a people/no-people task with photographs in which one body part (either head or hands) was lacking. The pigeons generalized successfully to the unseen body parts. The authors suggested that the pigeons used a previously acquired representation of humans to identify the unseen body parts as being complementary to the training stimuli. However, due to the complexity of human photographs, it is extremely difficult to control the distinctive visual features. Pigeons have remarkable abilities to categorize pictures and to generalize to novel instances according to 2D cues alone, which is evidenced by categorization of abstract patterns (Cook and Smith, 2006; Makino and Jitsumori, 2007), alphabetic characters (Morgan et al., 1976) or shapes of objects without biological function to the pigeon, e.g., oak leaves (Cerella, 1979). Therefore, it cannot be excluded that the pigeons might have solved this task by applying a categorization based on 2D cues without employing an internal 3D representation.

The current study aimed to test 3D-to-2D transfer directly for a discrimination task involving human photographs. The objective of our study was to test if the identification of a 3D-person facilitates the discrimination of photographs depicting this person. To this end, pigeons were divided into two groups. Each group was fed by, and thus exposed to a different person. We first tested if the pigeons reliably discriminate their feeder from other persons

in their real-life 3D environment by employing a discriminative Pavlovian conditioning procedure. We then proceeded to test the pigeons in a Skinner box with coloured photographs of the known person as well as of novel ones. Transfer of the previously learned 3D-person to the pictorial representation should facilitate discrimination of the respective photographs.

2. Materials and methods

2.1. 3D discrimination

2.1.1. Subjects

16 naïve pigeons (*Columba livia*) were kept at 80% of their free-feeding weight. The animals were divided into two groups of eight pigeons. Each group was housed in a separate room, each pigeon in an individual cage. Water and grit were freely available. The experiments were conducted in accordance with the specifications of the German law for the prevention of cruelty to animals and hence, the European Communities Council Directive of 24 November 1986.

2.1.2. Training

Throughout the whole experiment (3D and 2D discrimination), each group was fed exclusively by one specific person (“feeder”). The two feeders (G1 and G2) also constituted the go-persons for 2D discrimination. Both feeders were male to decrease variability, and they wore a lab coat, which cloaked most of their clothing to prevent discrimination based on clothing items. Each feeder entered the housing room of the respective pigeon group during the feeding sessions only, and never entered the other housing room. The pigeons were fed twice a day to increase their exposure to the feeder: first they were given a little amount of food (mixed grain) at a random time; in the evening, they received an additional amount of food that depended on their weight. Weighing and handling of the birds was accomplished by a third person. Every day several other persons, mostly wearing lab coats, entered the same rooms to handle or feed other pigeons housed there. The feeding sessions can be regarded as discriminative Pavlovian conditioning with each feeder being the conditional stimulus for his group.

2.1.3. Testing

To test the discrimination abilities of the pigeons, their behaviour was recorded for further analysis. A video camera (DCR-TRV725E, Sony Corporation, Tokyo, Japan) and an additional light source (60 W) were positioned in the housing room by a third person. After waiting at least 15 min, either the feeder or a control person entered the room. The order of those entries was randomized. Each entering person was holding a filled feeding cup and was instructed to stand in front of the cages at a distance of 2–2.5 m for approximately 1 min. After a further waiting period of at least 15 min, the second person (control or feeder, respectively) entered the room. In these testing trials, the pigeons were not fed. To avoid the camera or the light becoming conditional stimuli, we recorded the pigeons' behaviour only three times. The first session took place 1-day before starting the critical Skinner box experiment (2D discrimination); the other two were at the final stages of the experiment.

2.1.4. Mask test

At the end of the study, further recordings were carried out to test which information was critical for 3D discrimination. We applied a Halloween mask and a hood to occlude visual cues from the persons' heads. The experiment was carried out within 1-day, waiting at least 15 min between the entries of the respective persons. First, the feeder entered the room to serve as a positive control, holding the mask in front of his abdomen. Second, a control person entered with head masked to serve as a negative control. Third,

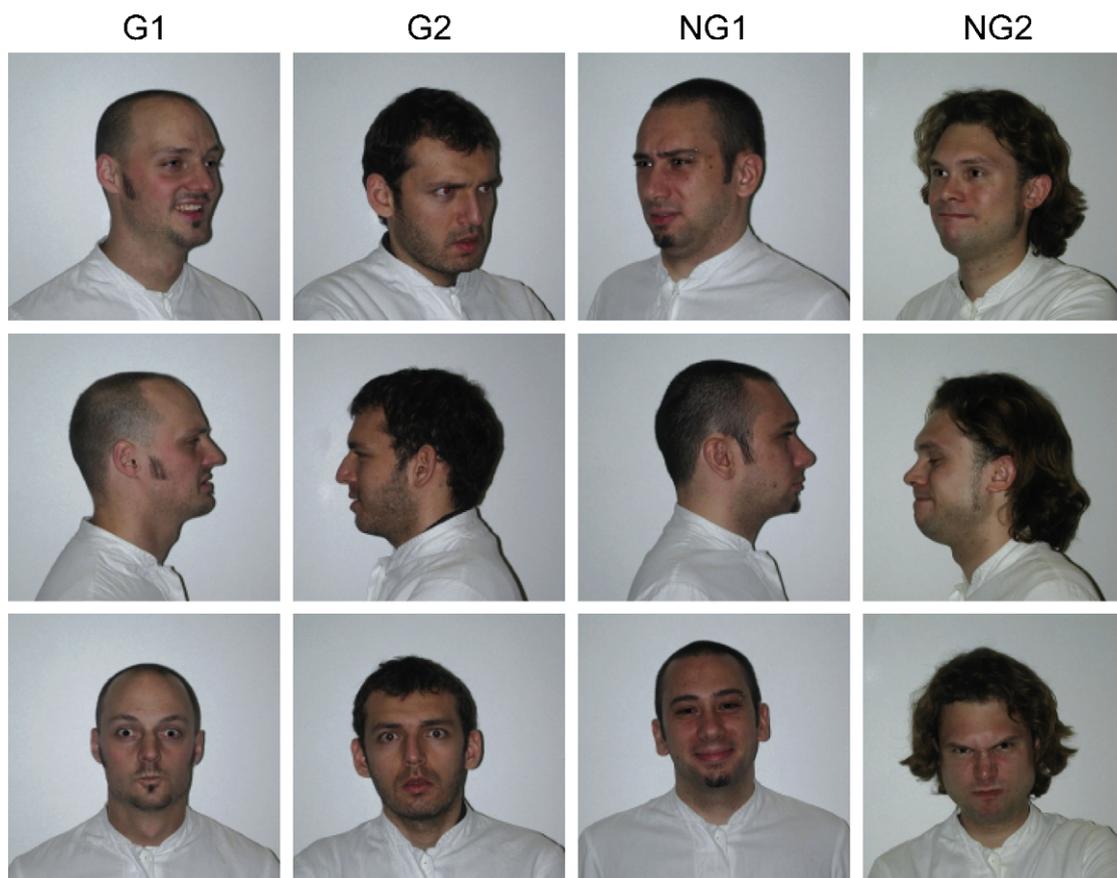


Fig. 1. Examples of the stimuli used in the 2D discrimination. Photos of four persons were assigned as go (G1 and G2) or nogo (NG1 and NG2). Different perspectives and facial expressions were used. The pigeons had previous 3D experience with either G1 or G2. Stimuli are depicted at original resolution.

the feeder entered with head masked. Fourth, the feeder entered to serve as a second positive control, again holding the mask in front of his abdomen.

2.1.5. Analysis of the videos

All video manipulations were carried out using Adobe Premiere Pro 1.5 (Adobe Systems Inc., San Jose, CA, USA). From each recording, a 10 s clip was created, starting 20 s after the entry of the respective person. The clips were further manipulated rendering only one pigeon visible at any given time. A film was then created with one clip for each pigeon in every recording in random order. The activity of every pigeon in the film was subjectively rated by six observers who were blind against all aspects of the study. They were instructed to rate the behaviour of each pigeon using a scale from 1 to 10 with 1 being not active and 10 being maximally active. The means of the six scorings were then used for statistics.

2.2. 2D discrimination

2.2.1. Apparatus

We used an operant conditioning chamber with a size of 28 cm × 32 cm × 28 cm (W × D × H). A pecking key (5 cm × 5 cm) was positioned at the front wall at a height of 18 cm. A food hopper was positioned below the pecking key. Stimuli were presented on a TFT monitor (Belinea 101536, Belinea, Wittmund, Germany), 2.5 cm behind the pecking key. The size of the stimuli was 180 × 180 pixels (4.8 cm × 4.8 cm). The chamber was illuminated by a house light (2 W). The hardware was controlled using the Biopsychology-Toolbox (Rose et al., 2008). All programs were written in Matlab (The MathWorks Inc., Natick, USA).

2.2.2. Stimuli

The stimulus pool included photographs of four different persons, the two feeders from the 3D discrimination (G1 and G2), and two novel ones (NG1 and NG2), all wearing a lab coat. 36 photographs of each person were taken with a digital camera (Coolpix 990, Nikon Corporation, Tokyo, Japan). To achieve perceptual variability, different perspectives were used (frontal, left and right half-profile, and left and right profile). Further, the persons were instructed to express different emotions (e.g., angry, happy, sad). These photographic conditions were balanced across the four persons. Examples are depicted in Fig. 1. The whole stimulus pool is available at <http://www.bio.psy.rub.de/biopsytoolbox/stimuluspool/3D-to-2D>. The contingencies of the photographs were the same for all pigeons, irrespective of if they were fed by G1 (G1-group) or G2 (G2-group). Responding to photographs of the two feeders from the 3D discrimination, G1 and G2 (go), was reinforced. Responding to photographs of the two novel persons, NG1 and NG2 (nogo), was punished with delay. Note that each pigeon had previous experience with only one of the displayed persons, either G1 or G2.

2.2.3. Procedure

The pigeons were trained to peck the illuminated pecking key with a standard autoshaping procedure, followed by a fixed ratio 2 schedule. Thereafter, the subjects were transferred to a fixed interval (FI) schedule with FI 3 s, and were then progressively trained in FI 5 s, FI 10 s, variable interval (VI) 15 s, and VI 20 s reinforcement schedules until they continuously responded to the key in each schedule. All sessions consisted of 48 trials. The pigeons were then transferred to a standard go/nogo procedure (e.g., Aust and

Huber, 2001; Vaughan and Greene, 1984). Each stimulus was presented for a fixed time of 10 s, and an additional VI 5 s. In go trials, the VI was followed by a time window of 2 s. If at least two pecks occurred during this time window, the pigeons were rewarded. If pecks occurred during the VI of a nogo trial, the stimulus presentation was prolonged until no further peck occurred within 8 s. Stimuli were presented in a pseudo-randomized order with no more than three positive or three negative stimuli in succession. In each session (48 trials), 12 photographs of each person were displayed, with four photographs of each perspective (frontal, half-profile, profile), if applicable balanced for left and right view. The stimuli were pseudo-randomly drawn from the stimulus pool, such that a particular stimulus was presented once per three sessions.

2.2.4. Analysis

Only responses within the first 10 s of stimulus presentation were used for analysis. Learning success was measured using standardized response rates (srr). This value is obtained by dividing the responses in a trial by the mean responses per trial of that session (see Huber et al., 2000). In the first sessions, in which photographs were presented, many pigeons omitted most trials and pecked only a few times, a behaviour that can cause extreme srr-values. Thus, only sessions in which the pigeons responded at least in half of the trials were included in the analysis. All pigeons were trained until they had 20 such sessions. Throughout the experiment, two pigeons from the G1-group did not show the required pecking behaviour, i.e. did not respond to the photographs in at least half of the trials per session, and were excluded from further analysis. Reported means are accompanied with 95% confidence intervals, which were adjusted for within-subject comparisons according to Cousineau (2005).

3. Results

3.1. 3D discrimination

To assess the pigeons' discrimination of 3D-persons, the spontaneous activity of each pigeon in the presence of the different persons was rated independently by six observers who were blind to all aspects of the experiment. Agreement between observers was high (Kendall's $W=0.92$, chi-square (158) = 873.42, $p < 0.001$, $N=6$). The pigeons' ability to discriminate their feeder (G1 or G2) from a non-feeding control person was tested three times, each time involving a different control person (Fig. 2). The activity of both pigeon groups was rated higher for the feeder than for the control persons in all three tests (two-tailed sign test, $N=8$, $p < 0.05$ for each group in each of the three tests). An exemplary video is presented in the supplementary material (video 1).

We further performed the mask test, in which we compared the pigeons' activity in the presence of different persons whose heads were either visible or occluded, to delineate the critical features for the 3D discrimination. Fig. 3 depicts the activity scorings for this test. A Friedman's test showed a significant effect for the different entries (Kendall's $W=0.86$; chi-square (3) = 18.13, $p < 0.001$, $N=7$ for G1-group; Kendall's $W=0.84$, chi-square (3) = 20.09, $p < 0.001$, $N=8$ for G2-group). One pigeon of the G1-group had to be excluded from the analysis in the control condition because the control person occluded it for the camera. The single conditions were then compared with a Bonferroni-corrected two-tailed sign test (for all Bonferroni-corrections in this manuscript, we report the adjusted p -values). In both groups, the pigeons responded significantly higher to the feeder in the head-visible condition than in the head-masked condition (sign test, $p=0.048$, $N=8$, for all comparisons). An exemplary video is presented in the supplementary

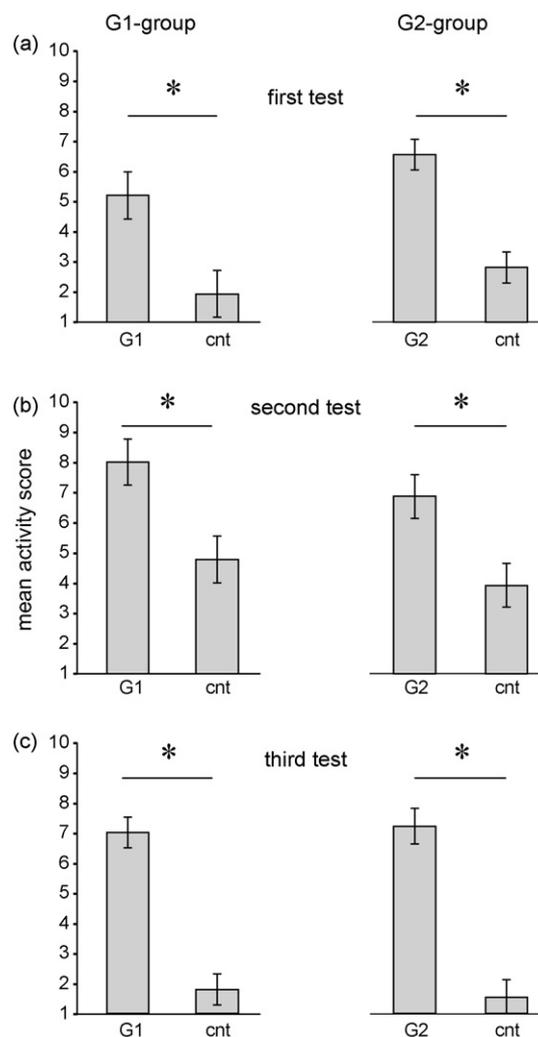


Fig. 2. Mean activity scores of pigeons in response to entry of the feeder or a control person. G1 and G2 were the feeders of G1-group and G2-group, respectively. The first test (a) was carried out before the 2D training, the second (b) and the third (c) tests were carried out at the final stages of the experiment. G1: G1 entered, G2: G2 entered, cnt: control person entered. Error bars indicate 95% confidence intervals, adjusted for within-subject comparisons. Asterisks indicate $p < 0.05$ (sign test, $N=8$).

material (video 2). In contrast, there was no statistical difference between the feeders and the control persons in the head-masked condition ($p=0.687$ for G1-group, $p=0.727$ for G2-group).

3.2. 2D discrimination

To test whether successful 3D discrimination of an individual human facilitates 2D discrimination of photographs depicting that person, a go/nogo experiment was carried out in the Skinner box. Positive stimuli (go) were photographs of the two feeders G1 and G2 (note that each pigeon had previous experience with only one of these individuals), negative stimuli (nogo) were photographs of NG1 and NG2, which were unfamiliar to all pigeons. Fig. 4 depicts the mean standardized response rates (srr) across learning for each of the four persons that served as stimuli separately. Means for each session were taken across pigeons and are accompanied with 95% confidence intervals. Overlap of the confidence intervals of no more than half the average indicates significance at approximately the 5% level (Cumming and Finch, 2005; note that confidence intervals were adjusted for within-subject comparisons). According to this criterion, the mean srr scores for NG2 separated from the scores

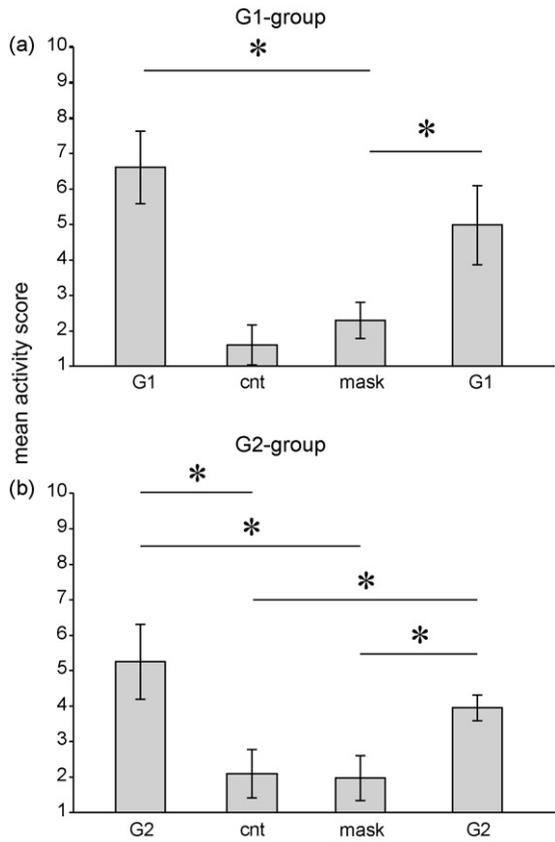


Fig. 3. Mean activity scores of pigeons in response to entry of different persons with head visible or masked. G1 and G2 were the feeders of G1-group and G2-group, respectively. G1: G1 entered, G2: G2 entered; cnt: control person entered with head masked; mask: the respective feeding person (G1 or G2) entered with head masked. In (a) one pigeon was excluded for the control condition, see text. Error bars indicate 95% confidence intervals, adjusted for within-subject comparisons. Asterisks indicate $p < 0.05$ (sign test, $N = 8$).

for the other stimuli from session 6 on, indicating that the pigeons first learned to discriminate photographs of this person. The mean srr scores for the other nogo-person (NG1) separated from those for the go stimuli from session 16 on. The learning curves for the familiar and the unfamiliar persons did not show any systematic differences in progression, but instead intersected with each other repeatedly throughout the 20 sessions. After 20 sessions, the mean srr scores and 95% confidence bounds were 1.31 (1.13, 1.45) for the familiar go-person, 1.38 (1.19, 1.58) for the unfamiliar go-person, 0.87 (0.73, 1.01) for NG1, and 0.44 (0.32, 0.55) for NG2.

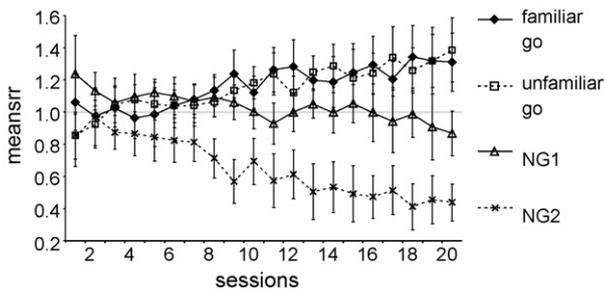


Fig. 4. Learning curves for 2D discrimination of photographs depicting familiar and unfamiliar persons. The mean standardized response rates (srr) for each stimulus-type are plotted against sessions. Average response rate over all stimuli is indicated by grey line. Error bars indicate 95% confidence intervals, adjusted for within-subject comparisons. $N = 14$.

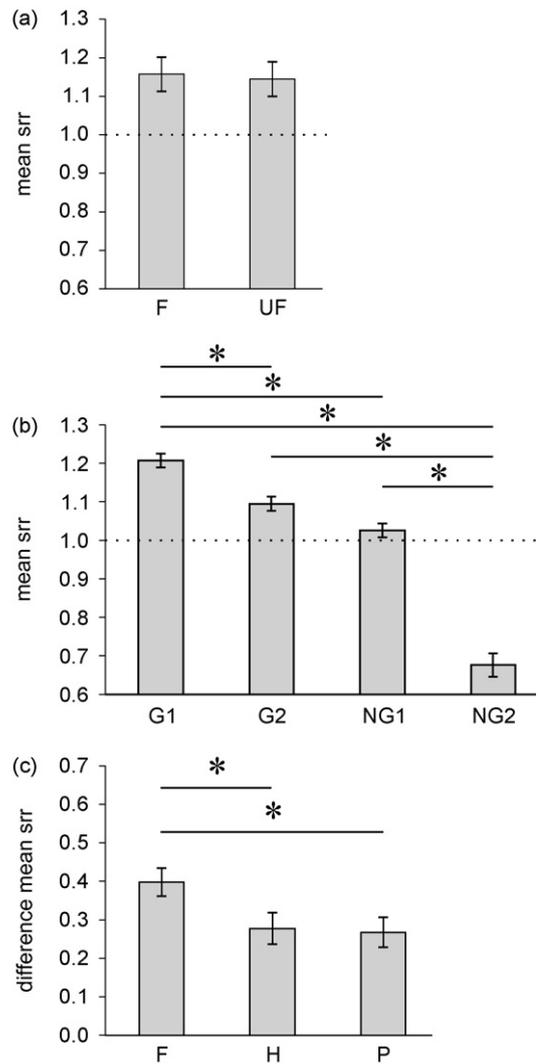


Fig. 5. Mean standardized response rates (srr) for different subsets of the stimuli. (a) F: familiar person; UF: unfamiliar person. For representational purposes the mean srr scores of the two groups were pooled according to familiarity (b) G1 and G2: go stimuli, NG1 and NG2: nogo stimuli. (c) The differences of the mean srr scores for go and nogo of the same perspective. F: frontal view; H: half-profile; P: profile. Average response rate over all stimuli is indicated by dashed line. Error bars indicate 95% confidence intervals, adjusted for within-subject comparisons. Asterisks indicate $p < 0.05$ (pairwise comparisons, $N = 14$).

For statistical analysis, performances (mean srr scores) with different subsets of stimuli across all 20 sessions were compared. A 2×2 mixed-design ANOVA with the between-subject factor group (G1-group versus G2-group) and the within-subject factor familiarity (familiar go versus unfamiliar go) did not identify a main effect of familiarity ($F(1,12) = 1.17, p = 0.300$), indicating that previous experience with a 3D-person did not facilitate discrimination of the corresponding photographs (Fig. 5a). No effect was found for the factor group ($F(1,12) = 0.050, p = 0.827$). However, our analysis revealed a significant interaction between group and familiarity ($F(1,12) = 18.34, p = 0.001$). Thus, irrespective of group and training conditions, the pigeons' performances were affected by the persons depicted in the photographs. Bonferroni-corrected, two-tailed paired t -tests revealed that photographs of G1 were discriminated better than photographs of G2. Remarkably, this preference was significant for the G2-group ($t(7) = 3.00; p = 0.040$) whereas it was only a trend for the G1-group ($t(5) = 2.93; p = 0.066$). To further see the effect of stimulus-type on performances we pooled the mean srr scores according to the person

depicted in the photographs (G1, G2, NG1, and NG2) using repeated measures ANOVA. The stimulus-type clearly affected the discrimination ($F(1,832,23.819) = 27.99$, $p < 0.001$, Greenhouse-Geisser corrected; Fig. 5b). Bonferroni-corrected pairwise comparisons of the estimated marginal means showed once more that photographs depicting G1 were discriminated better, i.e., had higher srr scores, than those depicting G2 ($p = 0.007$). In addition, G1's photographs had higher srr scores than photographs of NG1 ($p = 0.019$) and of NG2 ($p < 0.001$), and G2's photographs had higher scores than photographs of NG2 ($p = 0.001$). This shows that in general the pigeons acquired the discrimination. Finally, photographs of NG2 were discriminated better as negative stimuli, i.e., had lower srr scores, than photos of NG1 ($p = 0.001$).

To test whether the three different perspectives of the photographs had an effect on discrimination performance, the differences of the mean srr scores for go and nogo stimuli of the same view were calculated (Fig. 5c). An ANOVA with repeated measures on these differences revealed a main effect for perspective ($F(2,26) = 10.76$; $p < 0.001$). Post-hoc Bonferroni-corrected pairwise comparisons of the estimated marginal means revealed that frontal view stimuli were discriminated better, i.e., showed bigger differences between srr scores for go and nogo, than half-profile ($p = 0.006$) and profile stimuli ($p = 0.002$).

4. Discussion

In this study, we successfully used the pigeons' behaviour in their home cages to demonstrate that pigeons can discriminate life-size, three-dimensional, individual humans. This is in agreement with a recent report of recognition of individual humans by mocking birds under nest-defence conditions (Levey et al., 2009). Occlusion of the test person's heads further revealed that this discrimination was primarily based on head-related features rather than other cues such as absolute size, motion, uncloaked parts of the clothing or cues from other modalities, e.g., smell. However, although significant 3D discrimination was established, there was no evidence for transfer of the 3D discrimination to photographs of the corresponding persons. Pigeons needed as much training with photographs of the familiar, feeding person (familiar go) as with photographs of an unfamiliar person (unfamiliar go), in order to discriminate them from photographs of two further unfamiliar persons (nogo).

This negative finding is supported by several observations. First, as the 3D discrimination was primarily based on the head, and heads were depicted in all photographs, the lack of transfer cannot be attributed to the lack of the distinctive body parts in the 2D stimuli. Second, the similar learning curves for the stimuli depicting the familiar and the unfamiliar person could not be due to a ceiling effect because mean performance was still increasing at the final training session. Third, G1 and G2 probably did not look identical for the pigeons: photographs of G1 were easier to distinguish from the nogo stimuli than photographs of G2, irrespective of their assignment as familiar (feeder) or unfamiliar go-person. Therefore it appears unlikely that the pigeons spontaneously recognized their feeder on the photographs but consistently confused G1 with G2 because of a particular similarity of the two persons.

Moreover, we found a similar difference for discrimination performance for the two nogo-persons (NG2 was easier to discriminate than NG1), for which no 3D information was available. These results underline the importance of 2D cues without 3D correspondence for the pigeons' discrimination strategy. Correspondence of the photographs to the depicted persons seems to have played a considerably smaller role for discrimination than 2D differences between the stimuli, for which no representational insight is required.

The effects of the perspectives of the photographs on performance can be explained by their relative frequencies. Since

half-profile and profile photographs were further divided into left and right views, our stimulus set could be regarded as being composed of five rather than three different views. Accordingly, frontal-view stimuli were presented twice as often as stimuli of the other views, which might have facilitated learning for this stimulus subset. In summary, our results suggest that the pigeons did not see sufficient correspondences between the photographs of the individuals and their 3D counterparts to transfer their real-life discrimination ability to pictorial representations.

In contrast to the present results, previous studies demonstrated that pigeons can use previously learned 3D information during the discrimination of 2D stimuli. One obvious discrepancy between the present study and successful demonstrations of direct 3D-to-2D transfer is the way the stimuli were presented. Pigeons have limited capabilities to perform size invariant discriminations (Peissig et al., 2006) and stimulus distance has a pronounced effect for visual discrimination in chickens (Dawkins and Woodington, 1997). The 2D stimuli used in the present study were much smaller than the 3D humans and were presented at a different distance. The differences in size were not pronounced in terms of visual angles. The vertical size of a human head varied from approximately 5–35° when a person crossed the room to feed the pigeons and was approximately 18° in the Skinner box, assuming that pigeons decide whether to respond at a distance of 8 cm (Goodale, 1983). However, to form a perception of the often important real size of an object, viewing animals use information about distance in addition to the size of its image on the retina (Boring, 1946). Thus, the marked differences in absolute stimulus size might have hampered transfer.

Further, because of the different distances in which stimuli were presented, the pigeons probably processed the two stimulus types in different visual pathways. The 3D humans in our study were likely inspected with the thalamofugal visual system, which is specialized for lateral and distant viewing (Budzynski and Bingman, 2004; Hahmann and Güntürkün, 1993). Discrimination in a Skinner box, however, mainly depends on the tectofugal visual system, which is specialized for frontal viewing of close objects (Güntürkün and Hahmann, 1999). Transfer of information between these systems is limited, although easier from lateral to frontal viewing than vice versa (Mallin and Delius, 1983; Ortega et al., 2008; Remy and Emmerton, 1991). In successful demonstrations of direct 3D-to-2D transfer in pigeons, both objects and pictures had a similar size and were presented at a similar distance (Cabe, 1976; Delius, 1992; Spetch and Friedman, 2006; Watanabe, 1993). Thus, they were most likely processed by the same system, i.e., the tectofugal pathway, which might have facilitated transfer. In contrast, pigeons fail to recognize familiar places on photographs, a task which requires generalization across different sizes and viewing distances (Dawkins et al., 1996). For future studies we suggest counteracting the problems that arise from differences in stimulus size and distance by presenting life size photographs that are presented at the same distance as the 3D counterparts. This can be achieved for example by using transparent pecking keys through which the pigeons observe stimuli projected at a distance (Von Fersen and Lea, 1990).

However, despite these obstacles, pigeons apparently use a 3D concept to complement incomplete photographs in a people/no-people categorization task (Aust and Huber, 2006), contrasting with the negative finding of our study. One obvious difference between Aust and Huber's study and the present one is the type of discrimination required. Whereas in the present study the identification of particular persons was required, in Aust and Huber's study the pigeons classified photographs according to presence or absence of people. The former task is an instance of a classification at a subordinate level, whereas the latter one is classification at an ordinate level (Rosch et al., 1976).

Ordinate classes are defined as the level of abstraction for which cue validity is maximized, i.e., their instances have the highest possible number of co-occurring class defining attributes and least attributes shared with members of other classes. Examples for ordinate classes are “chairs”, “cars”, or “people”. In subordinate classes, such as “kitchen chairs” or photographs of one person as compared to those of another person, many attributes overlap between classes, and a smaller set of attributes is class defining (Rosch et al., 1976). Results from pigeons and primates apparently only partly matched Rosch's predictions (Lazareva et al., 2004; Roberts and Mazmanian, 1988; Vonk and MacDonald, 2002). However, a careful look suggests that the animals' performances can be explained by the different overlap of visual attributes within and between the classes (Vonk and MacDonald, 2002; Vonk and MacDonald, 2004). Thus, the number of overlapping attributes seems to be important for the classification abilities of animals. When comparing people/no-people categorization with discrimination of particular people, as employed in the present study, it is reasonable to assume that there are more class defining visual features in the former than in the latter, e.g., “skin colour” would define “people” but not “G1”. Information is reduced in the pictorial representation, e.g., no 3D cues are available, limited resolution and reduced size of the depicted object blur small details, and colours probably are misrepresented for the pigeons' visual system. Accordingly, the information available might allow pigeons to identify a photograph as depicting a human (e.g., by configurational cues or presence of skin colour) but not to identify a human individual if 3D discrimination is based on small details (e.g., shape of the eyes), specific colours (e.g., differences in hair colour), or other cues that are misrepresented. More research is needed to clarify the influence of classification level on object–picture correspondence.

Interestingly, during the revision process of the present manuscript, a publication appeared, in which the complementary information procedure test was performed with pigeons, which were raised without seeing human heads (Aust and Huber, 2009). The authors found further indication that pigeons see correspondence between humans and their photographs in pigeons, namely that pigeons, which have never seen 3D human heads, were impaired in generalizing 2D people/no-people categorization from headless figures to heads. However, some of the results were contrasting with the assumption of representational insight, e.g., that the same pigeons did not prefer 2D hands over 2D heads when both were presented simultaneously. Thus, further studies are needed to clarify the amount of representational insight used by pigeons when discriminating photographs. At this point, we want to bring to mind that even in humans instantaneous recognition of depicted scenes requires experience with pictorial representations (Deregowski et al., 1972; Miller, 1973). Therefore, the full capability of pigeons for picture–object recognition might become evident only after explicit pre-training, e.g., by training pigeons to use 2D cues of depth (Cavoto and Cook, 2006) prior to testing transfer of discrimination from objects to pictures or vice versa.

In conclusion, the present study demonstrates limitations of cross-recognition of humans and their pictures by pigeons. Unless future studies can clarify the remaining questions, researchers are advised to exert caution when interpreting results from studies involving pictorial stimuli.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.beproc.2009.10.006.

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