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Peck tracking: a method for localizing critical features within complex pictures for pigeons

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Abstract The pigeon is a standard animal in comparative psychology and is frequently used to investigate visuo-cognitive functions. Nonetheless, the strategies that pigeons use to discriminate complex visual stimuli remain a difficult area of study. In search of a reliable method to identify features that control the discrimination behaviour, pecking location was tracked using touch screen technology in a people-absent/people-present discrimination task. The correct stimuli contained human figures anywhere on the picture, but the birds were not required to peck on that part. However, the stimuli were designed in a way that only the human figures contained distinguishing information. All pigeons focused their pecks on a subarea of the distinctive human figures, namely the heads. Removal of the heads significantly impaired performance, while removal of other distinctive parts did not. Thus, peck tracking reveals the location within a complex visual stimulus that controls discrimination behaviour, and might be a valuable tool to reveal the strategies pigeons apply in visual discrimination tasks.

Introduction

The pigeon (*Columba livia*) is a widely used animal in comparative psychology. Due to their excellent visual abilities, pigeons are particularly studied in the field of visuocognitive research. These studies have significantly advanced our knowledge in topics such as visual categorization (Huber 2001), part/whole processing (Cook 2001) and cerebral asymmetries (Manns and Güntürkün 2009).

One crucial step towards understanding the mechanisms of visual processing is to identify the cognitive strategies that are used to solve a given task. The applied strategy is most likely influenced by the demands of the task, the learning history, and also the perceptual aptitudes of an animal. For example in a task that requires categorizing human faces by gender, humans are more sensitive to manipulations of shape, whereas pigeons are more sensitive to manipulations of texture (Troje et al. 1999). The reliable identification of the cues used by an animal in a certain task is a prerequisite to pinpoint its discrimination strategies. The identification of discrimination-relevant cues, however, is a demanding problem in comparative psychology and different approaches have been used to accomplish this.

In one line of research, stimuli are maximally reduced in their complexity to gain absolute control over the used stimulus dimension (for critical review see Cook 1993). The obvious drawback of this strategy is the departure from

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testing conditions that resemble reality. This can even curtail the discovery of specific cognitive abilities of a species. For example, the amazing categorization abilities of pigeons were not discovered until photographs from everyday scenes were introduced as stimuli (Herrnstein and Loveland 1964).

In another line of research, effort is put into the identification of critical features in complex stimuli such as photographs, which probably resemble natural conditions more accurately. The most common approach is to manipulate single features or stimulus dimensions and to test the impact on performance (e.g. Aust and Huber 2002, 2003; Brown and Dooling 1993). However, the identification of relevant features by manipulating them has some major drawbacks. First, it introduces a bias by the preselection of candidate cues. It might well be that an animal uses a cue that is not explicitly manipulated by the experimenter and is therefore not appropriately assessed. Also, if for experimental reasons the test stimuli cannot be presented as catch trials without feedback, the animals are encouraged to acquire new strategies using the residual information, which limits the conclusiveness of the results. For example, Brown and Dooling (1993) found for budgerigars that some stimulus characteristics that are not used for discrimination when they are varied together with others are used when they are varied alone. Moreover, manipulating many stimulus dimensions and testing each of them in a single experiment is a time consuming work that was referred to by Cook (1993) as "almost Sisyphean".

An improved version of stimulus manipulation is the bubbles method (Gosselin and Schyns 2001). Here, randomly distributed windows reveal only part of the image. Each stimulus location is then analysed for how often it contributed to a successful discrimination. This method offers many advantages, especially the comparability between species (Gibson et al. 2005, 2007). Unfortunately, the problem of possibly changing strategies during the testing phase remains unsolved. The bubbles method even seems to be especially sensitive for this effect. The test stimuli cannot be presented as catch trials without feedback, because the salient window mask would likely cause rapid extinction learning. In addition, each window location has to be presented several times to be statistically accessible. This leads to extended use of reinforced test trials, which facilitates relearning due to residual information.

Another widely used approach is post hoc assessment of diagnostic features (e.g. Brown and Dooling 1992; Huber et al. 2000; Lea and Ryan 1983; Lubow 1974). However, for complex stimuli, it is likely that the exact features the pigeons use are elusive to a merely subjective examination by a species as distantly related as the human.

Sophisticated statistical tools, such as multidimensional scaling or principal component analysis, bring with them the fundamental problem of interpretation of the extracted stimulus dimensions. Only few of them usually are as straightforward as "colour" or "shape". It might also be that a calculated dimension matches the subjective dimension used by an animal only partly (Gibson et al. 2005).

For primates, the visual features attended to normally are indicated by gaze location (for review see Awh et al. 2006) and thus can be inferred by eye tracking methods (Yarbus 1967). Rehder and Hoffman (2005) successfully employed eye tracking to demonstrate that attentional shifts towards distinctive stimulus dimensions precede increases in performance during category learning. Compared to the approaches mentioned above, this method offers three advantages: (1) The locus of attention and its changes can be observed over the whole course of acquisition, thus providing information about cognitive processes during learning. (2) No additional testing phase is required, which excludes changes of strategy due to altered informational content of the testing stimuli, and saves experimental time. (3) There is no need to predefine candidate regions, which in other approaches might bias the results. In contrast, the critical stimulus locations are directly deduced from the behaviour of the subject.

Despite these advantages, tracking the sensory input directly does not seem achievable in pigeons at present. Eye tracking would be technically challenging. Saccades are typically embedded in head thrusts (Wohlschläger et al. 1993), are sometimes asymmetric or even occur in one eye only (Bloch et al. 1984), and are accompanied by oscillatory eye movements that likely serve ocular perfusion (Pettigrew et al. 1990; Yang et al. 2008). Overcoming these problems, e.g. by referring to head position rather than eye position, as has been done in other bird species (Kjaersgaard et al. 2008; Ohayon et al. 2008), would still not solve a more general problem: In contrast to mammals and some other birds (e.g. owls and peafowls), pigeons have two distinct retinal areas that are specialized for acute vision (for review see Güntürkün 2000). They can use information from both of those areas within one task (Ortega et al. 2008), so that the processed information cannot be inferred reliably from its retinal position.

A more feasible indicator of the critical visual cues might be the pecking location. Jenkins and Sainsbury (1970) trained pigeons to discriminate simple stimuli that differed only with respect to the presence or absence of a single feature. Using carbon paper and divided pecking keys, they found that pecking was concentrated at the diagnostic feature. It appeared more pronounced in late than in early sessions, indicating that the cue only became attractive for pecking after it had been learned to be

meaningful. Other studies confirmed this effect for visually simple stimuli (Bermejo and Zeigler 1998; Goodale 1983; Jenkins and Sainsbury 1970; Wasserman and Anderson 1974; Watanabe 1976; Wills et al., in press). Up to now, only one publication has reported pecking location for a discrimination of complex stimuli. Allan (1993) noted that in a people-absent/people-present task pigeons tended to peck more on the parts of the photographs that depicted a human. Thus, pecking at the features that control discrimination behaviour apparently generalizes to complex stimuli. If this proves to be a strong and reliable effect, pecking location could be a highly valuable tool to localize critical features in complex stimuli, yet neglected for decades.

The aim of the present study was to test if pecking location can be used to localize the features that control discrimination behaviour within complex stimuli. To link with a frequently used stimulus type and for comparability with a previous report (Allan 1993), we employed a people-absent/people-present task with pigeons which already had successfully participated in such a study (Yamazaki et al. 2007). To nevertheless create a highly controlled situation, we designed the stimuli in a way that rendered all parts of the stimuli but the humans ambiguous. We chose to apply touch screen technology in order to combine exact examination of pecking location with exact numerical analysis. We first aimed to see whether pigeons would peck on the humans rather than on ambiguous stimulus parts, i.e. if the pecks would focus reliably on the stimulus parts which control discrimination behaviour. Subsequently, we tested whether more densely pecked locations within the human figures had gained more control over behaviour than others by selectively removing them.

Methods

Animals

Six pigeons (*C. livia*) were used in the present study. They were maintained at approximately 80% of their free feeding weight. Water and grit were freely available. The animals had previous experience with a similar people-absent/people-present discrimination task, in which they significantly generalized to unfamiliar instances of the "human" category (Yamazaki et al. 2007). The present study started 1 year after these experiments.

Apparatus

The experiment used an operant conditioning chamber measuring 33.5 × 34 × 31.5 cm. On the front panel, a Pocket PC with an analogue resistive touch screen (screen size 5.35 × 7.13 cm, Axim X30, Dell Inc., Round Rock, TX, USA) was mounted in a height of 7.5 cm. Pecking data were transferred to a PC via an IO-warrior interface (FBI Science GMBH, Essen, Germany). The PC was also used for controlling the experiment and saving the data, using OLCUS software (FBI Science GMBH). A food hopper was mounted below the touch screen. The chamber was illuminated by a house light (2 W).

Stimuli

In the preceding study (Yamazaki et al. 2007), the animals had learned to categorize human versus non-human pictures and had been able to generalize to novel pictures in transfer tests. However, in such tasks, pigeons also make use of item-specific cues that are not category relevant (Aust and Huber 2001, 2003). In single cases, those might not only be cues from the human figures but also prominent background features. In order to test systematically if pecking location indicates which part of a complex stimulus controls a pigeon's classification behaviour, we designed stimuli in which the distinctive areas were known. Those were photo collages in which only the human figure could be used for discrimination; all other parts were non-diagnostic. Pecking anywhere on the correct stimulus, however, was reinforced.

For designing the stimuli, we took photographs from the internet (http://www.gettyimages.com; http://www.lophoto.com). Pictures with humans (S+) consisted of a background with one or two human figures (whole body or upper part of body) pasted on it. In addition, the photo of a complex, non-living object was also pasted on the same picture. This allows us to exclude the possibility that enhanced pecking on the humans could be assigned to mere foreground appearance or visual salience that could have been introduced by the pasting procedure. Pictures without humans (S−) consisted of the same background with two non-living objects pasted on it. Three picture sets were designed, each with different humans and objects. We used three different background photos, one for each set. All sets consisted of ten S+ and ten S−. Two S+ from set III were later excluded from analysis because the human figures had been unintentionally taken from familiar photos. However, exclusion of these stimuli did not affect any of the presented results. In sets I and II, one of the objects of each S− appeared also on an S+; the second one was unique for a given S−. Thus, these sets were composed of stimuli that differed in a symmetrical way (Jenkins and Sainsbury 1970). Theoretically, these sets could be discriminated by recognizing objects on S− (feature negative discrimination). To exclude this possibility, stimuli in set III differed in an asymmetrical way, thus, both of the objects on each S− appeared also on an S+. In addition, in this set, the

non-living objects and the humans had the same size within a given S+ to exclude that enhanced pecking on the humans could be assigned to size cues. Figure 1 depicts some examples.

This stimulus design ensured that only the human figures could be used to identify a particular S+. Both the background and the non-living foreground object appeared also in S− and thus were ambiguous. Human figures and non-living objects were balanced for appearance on either side or centre of the stimulus. The size of the figures varied between stimuli. The size of the presented stimuli was 128 × 128 pixels (2.84 × 2.84 cm). Two stimuli were presented above one another with a distance of 0.71 cm. For retraining before the experiment, stimuli from the familiar pool of Yamazaki et al. (2007) were resized and assigned to stimulus sets containing ten S+ and ten S− each.

In a second experiment, we tested the role of the heads of the human figures for discrimination. For each pigeon, we selected 10 stimuli, each showing pronounced responses to the head region during training. In each stimulus, we removed one-third of the human figure. In five of the stimuli, the removed part included the heads; in five others it only included parts of the remaining bodies. The two groups of stimuli were balanced as far as possible for performance and for belonging to one of the familiar training sets for each pigeon. To obtain a homogeneous stimulus set, the modified human figures were pasted on a new background together with the corresponding non-

Fig. 1 Representative stimuli for experiment 1 (set III). The non-human objects and the backgrounds appeared on S+ and S−, only the human figures were distinctive

human object that also belonged to them in the original set (see Fig. 5). Negative stimuli were constructed from the resulting non-human objects.

Pretraining

The pigeons were trained to peck on the touch screen with an autoshaping procedure. After an intertrial interval of 20 s, a white circle with a diameter of 2.23 cm was presented for 10 s which was followed by a reward. Rewards consisted of 3 s access to food in all used protocols. A peck on the stimulus caused immediate access to food. As soon as the pigeons responded in more than 80% of the trials, they were transferred to a fixed ratio 1 (FR1) schedule, in which food reward only occurred after a response. When responding in 80% of the trials, they were transferred to FR3 and thereafter to FR6, with three or six pecks required to get a reward, respectively. In the FR schedules, the stimulus was presented for 6 s or until the required pecks occurred, the intertrial interval was 20 s. When the pigeons succeeded in more than 80% of the trials in the FR6 schedule, they were transferred to the first retraining set. Pigeons that did not start pecking on the retraining stimuli were manually shaped to additional photographs from the familiar pool. Stimulus sequences and positions were randomized. Six pecks on S+ were followed by reward. A single peck on S− was followed by 3 s of darkness (house light off) for negative feedback. In case of responding to S−, the stimulus pair was presented again but not counted for analysis. When the pigeons performed reliably above 80% in two of the retraining sets, they were transferred to the first experimental set.

Training

The schedule in the experimental set was as in retraining. When the pigeons succeeded in at least 80% of the trials in three consecutive sessions or 90% in two consecutive sessions, they were transferred to the next training set. To assure the accumulation of sufficient data for each training set (I–III), the pigeons performed at least 11 sessions, even if they reached criterion before. The number of sessions performed by each pigeon is indicated in Table 1. If criterion was reached before the 11th session, the respective session including the three criterion sessions is given in parentheses. The pigeons are sorted by the mean number of sessions required to reach criterion in all tables and figures. The order of the sets was the same for all pigeons.

When the pigeons had completed set III, they were transferred to the set with manipulated stimuli (parts of human figures removed). As before, pecking six times on a stimulus containing a human figure was rewarded, irrespective of how the figure was manipulated. In this

Table 1 Number of sessions performed for each pigeon and each set

	P1	P2	P3	P4	P5	P6
Set I	11 (4)	11 (6)	13	11	13	11 (8)
Set II	26	21	14	38	40	61
Set III	11 (3)	11 (10)	17	11 (7)	11 (10)	13
Mean number of sessions to reach criterion	11	12.3	14.7	18.7	21	27.3

Values in parentheses represent sessions to criterion

experiment, each pigeon performed ten sessions, independent from its performance. All sessions consisted of 50 trials.

Analysis

Only pecks that were performed in correct trials were used for analysis of pecking location. In order to test the amount of pecking on a region of interest for statistical significance, we performed a Chi-square test for goodness of fit. Effect sizes were determined by calculating Cohen's w (Cohen 1992). Small, medium and large effect sizes were defined as $w > 0.1$, $w > 0.3$, and $w > 0.5$, respectively. α was set to 0.05. The null hypothesis of a uniform distribution of pecks was rejected when $p < 0.05$ and Cohen's $w > 0.1$. The latter criterion was necessary since we were not interested in trivial deviations from the uniform distribution, which might be detected due to the large number of data points available for each Chi-square test. Thus, the term 'significant' is used for results that meet both criteria.

To obtain a more intuitive measure, we calculated the ratio between the observed probability to peck a region of interest and the expected probability to peck the same region, given a uniform distribution:

$$p(\text{observed})/p(\text{expected}) = (\text{pecks on ROI/all pecks})/$$
$$(\text{size of ROI/size of stimulus}),$$
$$(1)$$

where ROI is the region of interest. Unbiased pecking on the stimulus results in a probability ratio of 1 for any region of interest. A value of 2 would indicate that twice as many pecks were performed on the region of interest as expected, given any total number of pecks on the stimulus.

The regions of interest investigated in this study were the whole human figures, the objects, the heads of the humans, and the rest of the bodies. If two human figures were present on a stimulus, the region of interest comprised the relevant areas of both figures, e.g. both heads. For the analysis of sets of trials, e.g. a whole session, the region of interest comprised the relevant areas of all stimuli involved and size of stimulus was the cumulative size of all stimuli involved.

Results

Visual inspection of the pecking patterns revealed that the pigeons pecked predominantly at the distinctive parts of the stimuli. Figure 2 shows representative pecking patterns for pigeon P1. The pecks apparently were directed towards the human figures. Within the human figures, pecking was focused on the heads. Therefore, we calculated the probability ratios not only for pecking on the human figures and on the non-human objects but also for pecking on the heads of the human figures and on the rest of the bodies. In Fig. 3, the probability ratios resulting from all performed trials combined are depicted for each pigeon. All pigeons pecked more on the human figures than expected given a uniform distribution, resulting in a probability ratio higher than one (Fig. 3). This was significant for five out of six pigeons (Table 2). In contrast, five out of six pigeons pecked less on the non-distinctive objects than expected, resulting in a probability ratio below one (Fig. 3). This was significant for two of the pigeons (Table 2). Pecking on the heads was significant for all six pigeons (Table 2). Four out of six pigeons pecked significantly above chance level also on the rest of the bodies, whereas one pigeon pecked on the bodies significantly below chance level (Table 2). Since the exact values of the probability ratios directly depend on the size of the regions of interest, the options for a direct comparison between those ratios for regions of different size are limited. However, heads and bodies are subareas of the same human figures. Reduction of the size of the region of interest caused an increase in the probability ratios when it was reduced to the heads while it caused a decrease when it was reduced to the bodies. This was found for all pigeons (Fig. 3) and clearly confirms the observation that pecks were focused particularly on the heads within the human figures.

In order to test if improvements in performance during training were paralleled by changes in the amount of focusing on the distinctive areas of the stimuli, we calculated the probability ratios for human figures for each session separately. The probability ratios correlated positively with performance for three out of six pigeons (Fig. 4a). The probability ratios for non-distinctive objects correlated negatively with performance for five out of six pigeons
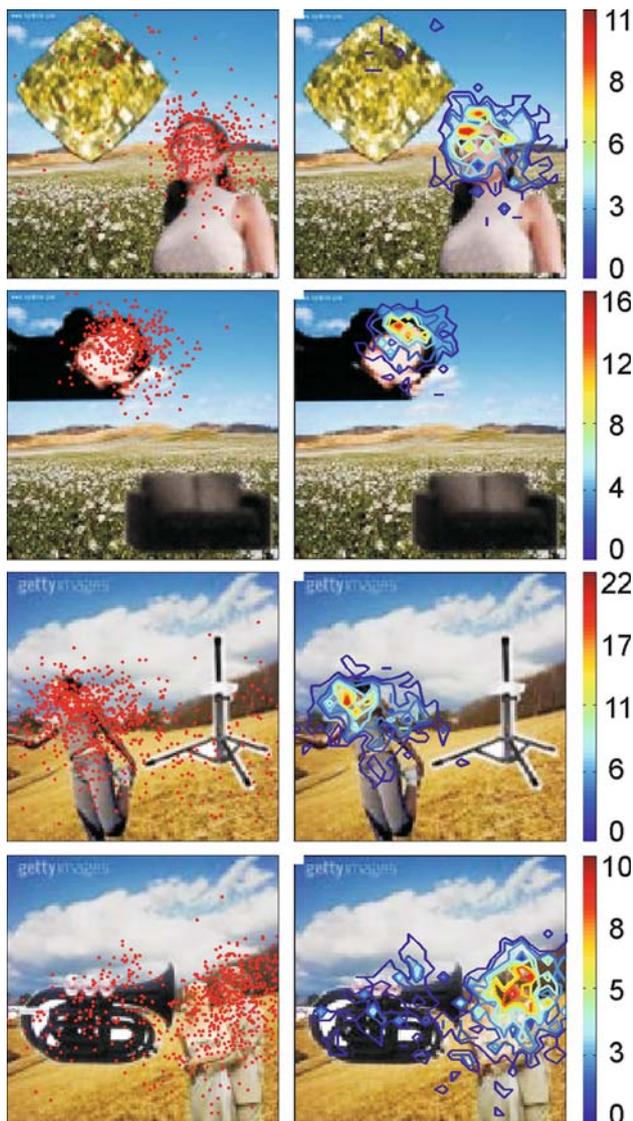
Fig. 2 Representative pecking patterns of pigeon P1. *Left column* Single location plots. Each pecked locus is indicated by a *red dot*. *Right column* Contour plots of same examples. These plots visualize also repeated pecking at the same locus. Colour codes the number of pecks, see *bars* on the *right*. Bin size is indicated by *white square* on *top left* of each picture. The probability ratios for pecking on the humans are from *top row* to *bottom row*: 1.76, 2.98, 4.06, and 2.94

(Fig. 4b). Thus, the more the pigeons learned to discriminate the stimuli, the less they pecked on the non-distinctive objects and, by trend, the more they pecked on the distinctive human figures. It should be noted that for all pigeons the probability ratios for human figures were above chance level even in the first session (geometric mean 1.87).

Manipulations of the human figures revealed that removal of the pecked-at regions—the human heads—had a significant impact on discrimination performance while removal of other distinctive subareas had not. Mean performances of all ten sessions with manipulated stimuli
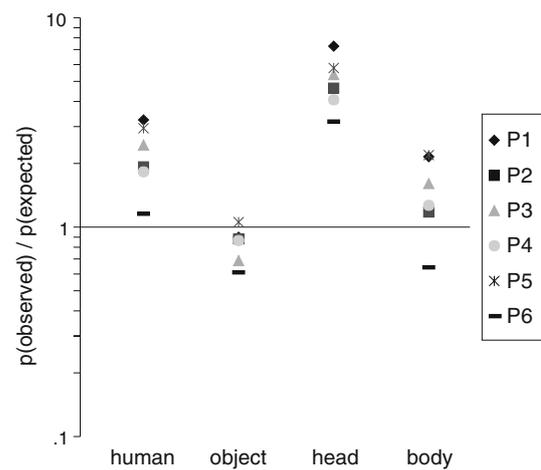

Fig. 3 Probability ratios for the different regions of interest for each pigeon. Probability ratios were calculated across all trials. Chance level = 1. For *N*, see Table 2. The scale is logarithmic in order to display the values above and below chance in a comparable way

Table 2 Chi-square tests for the observed pecking patterns during training for different regions of interest

	N	Human			Object		
		χ^2	p	w	χ^2	p	w
P1	10,056	**10,311.00**	**<0.001**	**1.01** (+)	15.53	<0.001	0.04
P2	8,928	**1,601.30**	**<0.001**	**0.42** (+)	21.91	<0.001	0.05
P3	8,946	**4,081.40**	**<0.001**	**0.68** (+)	**135.17**	**<0.001**	**0.12** (−)
P4	12,600	**1,806.20**	**<0.001**	**0.38** (+)	33.21	<0.001	0.05
P5	12,366	**9,459.50**	**<0.001**	**0.88** (+)	4.87	0.027	0.02
P6	17,688	91.30	<0.001	0.07	**397.48**	**<0.001**	**0.15** (−)
	N	Head			Body		
		χ^2	p	w	χ^2	p	w
P1	10,056	**16,453.00**	**<0.001**	**1.28** (+)	**2,020.10**	**<0.001**	**0.45** (+)
P2	8,928	**4,712.30**	**<0.001**	**0.73** (+)	45.27	<0.001	0.07
P3	8,946	**7,602.10**	**<0.001**	**0.92** (+)	**481.44**	**<0.001**	**0.23** (+)
P4	12,600	**4,634.40**	**<0.001**	**0.61** (+)	**141.75**	**<0.001**	**0.11** (+)
P5	12,366	**11,262.00**	**<0.001**	**0.95** (+)	**2,686.00**	**<0.001**	**0.47** (+)
P6	17,688	**3,060.50**	**<0.001**	**0.42** (+)	**325.35**	**<0.001**	**0.14** (−)

Bold values represent significant deviations from the uniform distribution, with more (+) or less (−) pecks on the region of interest than expected, $df = 1$

were subjected to a 2×2 analysis of variance (ANOVA) with repeated measures, with "manipulation" (before, after) and "stimulus group" ("head", "no head") as within-subject factors. The ANOVA revealed main effects for "manipulation" ($F_{1,5} = 47.385$, $p = 0.001$) and for "stimulus group" ($F_{1,5} = 42.545$, $p = 0.001$). The interaction between both was also significant ($F_{1,5} = 33.492$, $p = 0.002$). Bonferroni-corrected (adjusted $\alpha = 0.0083$) pairwise comparisons of the estimated marginal means
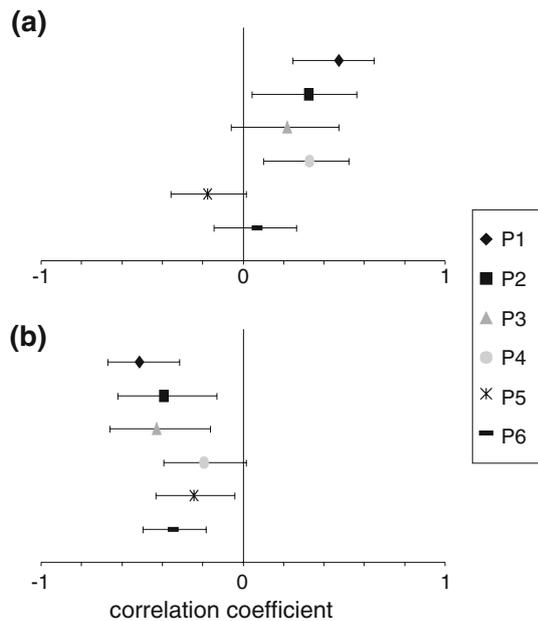
Fig. 4 Spearman's rank correlation coefficients for correlation of performance with probability ratios over sessions for each pigeon. *Bars* indicate confidence intervals of 95% that were obtained by bootstrapping (10,000 iterations). Failure to overlap with zero indicates significance at a level of 0.05. The regions of interest for the probability ratios are human figures (**a**) and non-distinctive objects (**b**)

revealed that performance was only affected when the heads of the humans were removed. In this condition, performance was lower than before manipulation (pairwise comparisons, $p < 0.001$) or with manipulated stimuli with intact heads (pairwise comparisons, $p < 0.001$) (Fig. 5). The mean performances across the ten test sessions are reported in Table 3 for each pigeon separately.

All pigeons discriminated manipulated stimuli with intact heads significantly above chance level (50% correct) from the first session on (binomial test, $p < 0.05$, mean across pigeons $79 \pm 1.73\%$ SEM). In contrast, performance for stimuli without heads was significant for only three pigeons (P2, P4 and P6) in the first session (binomial test, $p < 0.05$, mean across all pigeons $61 \pm 5.67\%$ SEM). These were the pigeons which had the lowest effect sizes (Cohen's w) for pecking on the heads during training (Table 2). All pigeons pecked on the human figures significantly for stimuli with intact heads (Table 3). For stimuli without heads, only four out of six pigeons pecked on the human figures significantly, whereas one pigeon pecked on the humans significantly below chance level (Table 3).

Discussion

The stimuli in this study were designed to maximize the probability that discrimination behaviour would be under

control of defined areas within the stimuli, the human figures. All pigeons significantly focused their pecks on a subarea of the human figures, namely the heads. By removing the heads and other body parts, we verified that the heads indeed contained the most critical information for the pigeons. Thus, not only we were able to demonstrate that pigeons direct their responses towards predefined distinctive regions of complex stimuli, but also we could further gain information about the relative importance of certain subareas. These findings confirm and extend previous reports about the correlation between pecking location and distinctive features (Bermejo and Zeigler 1998; Goodale 1983; Jenkins 1973; Jenkins and Sainsbury 1970; Wasserman and Anderson 1974; Watanabe 1976; Wills et al., in press) particularly that it generalizes to complex stimuli (Allan 1993). Most importantly, our findings demonstrate that this effect is strong enough to identify the features that control discriminative behaviour in case they are not known.

The directed response to the critical region depends on its subjective value for the discrimination the pigeon is actually performing. This is evidenced by the dependency of the pecking patterns on performance over the learning course. The more reliably the pigeons identified the distinguishing features, the more they focused their responses on them and the less they pecked at other parts of the positive stimuli. This effect was pronounced for pecking on non-distinctive objects, which correlated negatively with performance for five pigeons. It was less pronounced for pecking on the distinctive human figures, which correlated positively with performance for only three pigeons. This is probably due to a ceiling effect. The pigeons had previously learned to categorize human photographs (Yamazaki et al. 2007) and had been retrained using stimuli from this study. Therefore, the pigeons were presumably associating photographs of humans with reward already in the first training session of the present study. This is reflected by the high probability ratios for human figures from the first session on. Further increase of focusing during learning probably caused only small changes of the probability ratios for human figures. Overall, the shift of pecks towards the distinguishing stimulus parts over learning presented here is in line with the results from studies that used simple stimuli (Jenkins and Sainsbury 1970; Wasserman and Anderson 1974). The confirmation of this effect also for complex stimuli implies that peck tracking can be used to infer the change of strategies or their refinement over a learning course when complex stimuli are used, e.g. during categorization learning.

The robust finding that discrimination behaviour was more under control of the heads than of the rest of the bodies deserves further attention. It was not initially intended by the stimulus design but is interpretable. In our

Fig. 5 Effect of removal of stimulus parts on mean performance for all pigeons. Performance values are the means of all performed sessions in the respective condition. *Error bars* indicate standard deviations. Removal of the heads impaired performance, removal of other parts of the figures did not. Pairwise comparisons of estimated marginal means, *$p < 0.0083$ (Bonferroni adjusted significance level of 0.05)
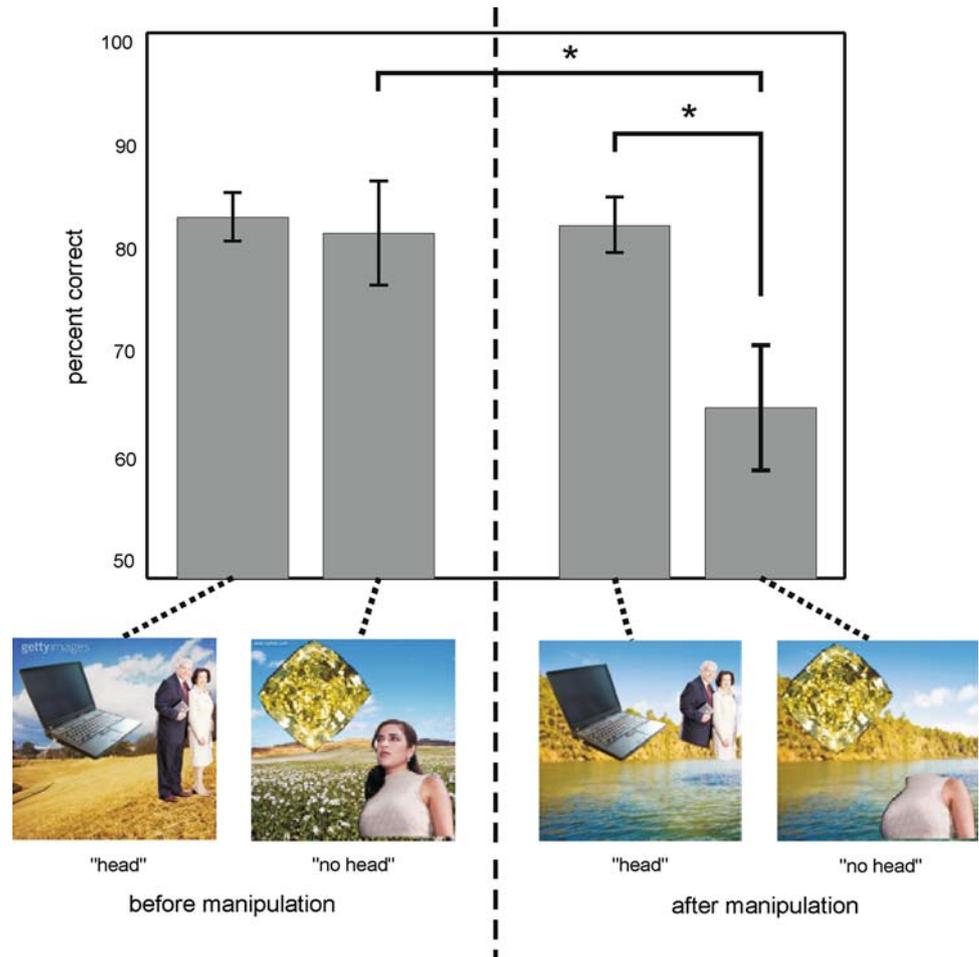

Table 3 Performances for the manipulation test and Chi-square tests for the observed pecking patterns for the manipulated human figures

	Heads intact					Heads removed				
	Percent correct	N	χ^2	p	w	Percent correct	N	χ^2	p	w
P1	82.43	1,482	**349.18**	**<0.001**	**0.54** (+)	68.40	1,188	3.87	0.049	0.06
P2	83.94	1,566	**23.61**	**<0.001**	**0.15** (+)	74.75	1,422	**21.66**	**<0.001**	**0.15** (−)
P3	82.55	1,332	**2,689.40**	**<0.001**	**1.55** (+)	63.51	1,068	**211.52**	**<0.001**	**0.48** (+)
P4	85.84	1,218	**680.49**	**<0.001**	**0.75** (+)	61.38	864	**154.01**	**<0.001**	**0.42** (+)
P5	78.83	1,356	**328.07**	**<0.001**	**0.54** (+)	58.02	1,302	**132.75**	**<0.001**	**0.36** (+)
P6	79.98	978	**370.18**	**<0.001**	**0.62** (+)	66.10	786	**76.36**	**<0.001**	**0.31** (+)

Bold values represent significant deviations from the uniform distribution, with more (+) or less (−) pecks on the region of interest than expected, $df = 1$

experimental design, we did not aim to differentiate between categorization and rote learning since we focused on a methodological question. However, the ease with which pigeons generalize to novel instances in people-absent/people-present tasks (e.g. Aust and Huber 2001) and the previous experience of our pigeons with such a categorization task (Yamazaki et al. 2007) make it likely that they applied a categorization strategy. Categorization of photographs can be based on merely perceptual similarities

or on representational insight (Aust and Huber 2006; Herrnstein 1990). In both cases, the human faces are likely to be the most prominent features in our stimuli. In case of representational insight (i.e. the pigeons use their knowledge of what a human is to identify humans on the photographs), the faces likely were the most obvious "human" parts in many of our stimuli, for the rest of the body was often truncated. In case of a merely perceptual categorization, the faces are likely to be the basis of this category

because they represent a constant pattern that appears in all stimuli used with a relatively small variability as compared to the bodies. However, we cannot exclude the possibility that the pigeons based their discrimination merely on rote learning. In this case, the heads would have been more salient than the bodies (e.g. due to their complexity) and thus preferentially used for discrimination.

Pigeons are capable of using several stimulus aspects simultaneously in discrimination tasks (Jitsumori 1996; Makino and Jitsumori 2007; Von Fersen and Lea 1990). In the present study, the heads were not the only features controlling the discrimination behaviour; to a lesser extent control was also exerted by other parts of the bodies. This was reflected by significant pecking on the bodies for four pigeons and significant discrimination of the stimuli with heads removed from the first session on by three of the pigeons. However, the spatial proximity of the apparently very salient heads and the bodies might have facilitated pecking on the bodies. It should be subjected to further studies what the pecking pattern will be like if there are several, spatially distinct features that all control the pigeon's behaviour.

The fact that the pecks were directed less clearly towards the distinctive area of the stimuli when the heads were removed likely reflects the overall low performance for those stimuli. Given the high rate of incorrect responses, we can assume that a substantial proportion of the correct trials result from correct guessing rather than from control by the distinctive features. Therefore, these responses are proposed to have occurred at random locations on the stimulus, which leads to overall smaller probability ratios and smaller effect sizes in the Chi-square tests.

The above conclusions mainly result from the comparison of the pecking patterns with the location of the features that control behaviour. The location of these features was ascertained by the stimulus design. For sets I and II, however, there was an additional possibility of performing a feature negative discrimination, which was excluded only for set III. The number of sessions required to reach criterion was not higher for set III than for the other sets (see Table 1). Thus, feature negative discrimination did not seem to play an important role for discrimination. This supports our initial assumption that the pigeon's behaviour was under the control of features present in the human figures.

However, although feature positive discrimination is learned more readily in most tasks and across species (for review see Hearst 1984), in some conditions, feature negative discrimination can be the dominant strategy (Haggbloom 1983; Reberg and Memmott 1979). Therefore, we stress that peck tracking as presented here only reveals the distinctive positive features, not the negative ones.

Interestingly, previous studies reported that false responses to S− were directed away from the feature in feature negative discrimination tasks (Jenkins 1973; Jenkins and Sainsbury 1970; Wasserman and Anderson 1974). If this effect is indeed due to pecking away from the negative feature rather than pecking towards the ambiguous stimulus parts (which were the most reward predicting parts of S− in those stimuli), then it might be used to gain information about the negative features. This would require an experimental design that involves considerable pecking on S−, such as a Go/Nogo task. This option deserves further investigation, but was not within the scope of this study.

The possibility of identifying the features that control discrimination behaviour during any phase of training allows for experimental designs similar to eye tracking studies in humans. However, the behavioural mechanisms that underlie both techniques are certainly different. Eye tracking, or more generally "gaze-tracking", examines the sensory input which is naturally correlated with attended features. In contrast, the mechanisms of a strong correlation of the response location with critical features are less obvious.

Pecking on the distinctive features could be due to an energy efficiency strategy. In a Skinner box, the decision to peck is made shortly before the peck itself and at close range from the stimulus (Goodale 1983). It would be rather puzzling if the pigeon would not peck on the spot that the decision is based on but instead waste time and energy by reorienting before it responds. A more cognitive explanation is offered by the simultaneous discrimination theory (Jenkins and Sainsbury 1969, 1970). This theory assumes that a pigeon perceives a stimulus as a simultaneous presentation of distinct features, rather than in a holistic way. Accordingly, reward will be associated only with the feature pecked and not with the whole stimulus (also see Jenkins 1973).

Although the present results confirm a large overlap of pecked locations and the features that control behaviour, we want to stress that this coherence is not exclusive. In a matching-to-sample task that biased pigeons to process one dimension or location of the sample preferentially and neglect other dimensions or locations, pecks shifted towards the biased attribute in the majority of trials (Brown et al. 1984). Thus, the outcome was in line with the findings of the present study. However, the biased matching behaviour was also detectable in remaining trials, in which the pigeons pecked on other locations. Therefore, we must assume that factors in addition to directed attention influence the pecking location. One possible factor is stimulus position. In the present study, pigeon P6 discriminated stimuli with removed heads significantly from the first session on, indicating that not only the heads but also the bodies were controlling discrimination behaviour.

Nevertheless, for this pigeon pecking on the bodies was significantly below chance level during training. Inspection of the pecking patterns revealed that the animal pecked predominantly slightly above the heads of the human figures. By occasional observation in the Skinner box, we found that this pigeon tended to stand on the food hopper, rather than in front of it or next to it. The elevated position might have shifted the pecking locations upwards and by that means might have caused the low probability ratio for the human bodies for this pigeon. As it sometimes is desirable to present stimuli at various locations on the screen (e.g. Huber et al. 2005), the effect of stimulus position on pecking location certainly deserves further investigation.

A further factor that might influence pecking location is viewing condition. Occlusion of one eye is a valuable tool for the investigation of cerebral asymmetries in pigeons. This technique has revealed that the cerebral hemispheres contribute differently to categorization processes (Yamazaki et al. 2007). Monocular viewing, however, has on its own impact on the pecking location, shifting it towards the open eye (Beale and Corballis 1967, 1968). It would be desirable to test whether in monocular viewing conditions the pecking location resembles the locus of attention as reliably as in binocular conditions, in order to clarify the feasibility of peck tracking for the investigation of cerebral asymmetries.

In summary, we conclude that pecking location can be used to identify the feature within a complex stimulus that controls discrimination behaviour of pigeons. Thus, peck tracking provides a tool to gain insight into the cognitive strategies that pigeons use to solve visual tasks. It shares some major methodological advances with eye tracking. (1) Peck tracking enables the experimenter to investigate the relevant stimulus locations over the whole course of acquisition, which facilitates the investigation of learning processes. (2) No additional testing phase is required, which not only saves experimental time but also further prevents the animals from changing their strategies due to altered informational content of test stimuli as in feature manipulation methods. (3) There is no need to define candidate features a priori. Peck tracking assesses the critical stimulus locations without biasing the available feature space and without restricting the behaviour of the animals in any way. Cook (1993) anticipated that some of the most interesting results involving complex stimuli might require reinterpretation as soon as it is possible to reliably decompose the discriminative features. We believe that the results presented here can significantly contribute to this process.

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