

1	
2	Labelling and Family Resemblance in the
3	discrimination of polymorphous categories
4	by pigeons
5	
6	Elizabeth Nicholls, Catriona M. E. Ryan,
7	Catherine M. L. Bryant, Stephen E. G. Lea
8	
9 10 11 12 13 14 15 16 17 18 19	University of Exeter School of Psychology Washington Singer Laboratories Perry Road Exeter EX4 4QG Email: s.e.g.lea@exeter.ac.uk Tel: +44 1392 264612 Fax: +44 1392 264623
20	Animal Cognition MS AC-09-0161, Accepted for publication subject to revision
21	This draft last saved 1 July 2010 by SEGL
22	
23	

24 Abstract

25

26 Two experiments examined whether pigeons discriminate polymorphous categories 27 on the basis of a single highly predictive feature or overall similarity. In the first 28 experiment, pigeons were trained to discriminate between categories of photographs 29 of complex real objects. Within these pictures, single features had been manipulated 30 to produce a highly salient texture cue. Either the picture or the texture provided a 31 reliable cue for discrimination during training, but in probe tests, the picture and texture cues were put into conflict. Some pigeons showed a significant tendency to 32 33 discriminate on the basis of the picture cue (overall similarity or family resemblance), 34 whereas others appeared to rely on the manipulated texture cue. The second 35 experiment used artificial polymorphous categories in which one dimension of the 36 stimulus provided a completely reliable cue to category membership, whereas three 37 other dimensions provided cues that were individually unreliable but collectively 38 provided a completely reliable basis for discrimination. Most pigeons came under 39 the control of the reliable cue rather than the unreliable cues. A minority, however, 40 came under the control of single dimensions from the unreliable set. We conclude 41 that cue salience can be more important than cue reliability in determining what 42 features will control behaviour when multiple cues are available.

43 Key words: Pigeon, Category discrimination, Feature learning, Family
44 resemblance, Labelling, Salience

46 General Introduction

47

48 The ability to categorise natural objects is expected to be widespread across the 49 animal kingdom, since it permits a reduction in the amount of information an animal 50 must acquire about its environment in order to respond adaptively (Makino and 51 Jitsumori 2007). Since the pioneering experiments of Herrnstein and Loveland (1964) 52 birds have been shown to be capable of discriminating a wide range of categories, 53 with category members varying from simple artificially constructed stimuli (e.g. Lea 54 and Harrison 1978) to photographs of complex natural-language categories such as 55 trees (Herrnstein et al. 1976; for a review see Huber 2001).

56

57 A typical categorisation experiment involves pigeons learning to associate one 58 stimulus set or category with a food reward, when there is no single feature that is 59 necessary or sufficient for category membership. However it is not clear what pigeons 60 learn to associate with the food reward. It could be that the pigeon has elaborated a 61 concept corresponding to the category. Typically however it is assumed that 62 successful category discrimination does not necessarily imply that pigeons have a 63 concept corresponding to the experimenter-defined category (despite the terminology 64 of early experiments e.g. Herrnstein et al. 1976), or in the case of natural photographs, 65 the ability to generalise from images to the corresponding real objects (Bovet and 66 Vauclair 2000). But if pigeons are not using concepts to categorize complex stimuli, 67 how might they be doing it? There are two well studied possibilities. It could be that 68 they learn how to respond to one or more specific exemplars, with other stimuli being 69 categorised by a process of generalisation. Alternatively, it may be that they learn to 70 respond to a collectivity of features that are between them good enough predictors of

category membership, even if none of them is individually necessary or sufficient.
These possibilities are usually referred to respectively as exemplar learning and
learning by family resemblance or overall similarity.

74

It is often useful to compare the cognitive abilities of non-human animals and human infants, because in both cases subjects have to complete tasks without the elaborate language competence that facilitates so many cognitive performances in adult humans. The present experiment draws on two results that have been established in the field of infant categorization, in order to pose questions about categorization in pigeons.

81

82 Both phenomena involve the use of single, highly predictive features within sets of 83 multidimensional stimuli. However, they are to some extent contradictory. On the 84 one hand, under conditions where adults and older children typically categorise items 85 according to a single stimulus dimension, infants have been found to group items 86 according to overall similarity or family resemblance across numerous stimulus 87 dimensions (Smith and Kemler 1977; Smith 1981). On the other hand, the provision 88 of a verbal label which is invariantly associated with the members of one category has 89 been found to facilitate children's category acquisition (Waxman and Markow, 1995), 90 even among infants too young to have functional speech (e.g. Balaban and Waxman, 91 1997); so in contrast to the control by family resemblance seen in spontaneous categorization, the presence of a single reliable feature is found to facilitate category 92 93 acquisition.

95 The first of these findings, the tendency of younger children to categorize on the basis 96 of overall similarity, has supported a general arguments that such categorization must 97 require simpler cognitive mechanisms than using a single stimulus dimension (e.g. 98 Ashby et al. 1998; Pothos 2005). Unidimensional discrimination is assumed to 99 require the ability to verbalise a rule, something that a pre-verbal infant cannot do. In 100 accordance with this assumption, Couchman et al. (2010) found that, when they used 101 stimulus sets of a kind introduced by Kemler Nelson (1984), which can be 102 discriminated either on the basis of a single dimension or on a family resemblance 103 across three other dimensions, human participants categorised them unidimensionally 104 whereas two rhesus monkey subjects categorized them mainly by family resemblance.

105

106 However, it is not the case that non-human animals always categorize complex stimuli 107 by overall similarity rather than unidimensionally, or that unidimensional categorization implies more complex cognitive processing (e.g. Lea and Wills 2008; 108 109 Wills et al. 2009). Although it is certainly possible for pigeons to use multiple 110 stimulus dimensions in making complex discriminations (e.g. Blough 1972; 111 Herbranson et al. 1999; Kirkpatrick-Steger and Wasserman 1996; Soto and 112 Wasserman 2010; von Fersen and Lea 1990), this is not necessarily what they do most 113 easily or spontaneously. Rather than categorizing in terms of overall similarity, which 114 would involve all available features, birds in categorization experiments with complex 115 stimuli often come under the control of just one or two features (e.g. Lea et al. 1993, 116 2006); and it would be absurd to suppose that pigeons can verbalise rules (cf. Lea and 117 Wills, 2008). Furthermore, the fact that infant categorization proceeds more easily in 118 the presence of a verbal label - which is really nothing but a single highly valid stimulus dimension (Plunkett et al., 2008) – suggests that discriminating a single
dimension may be a cognitively simpler task than discriminating overall similarity.

121

122 The aim of the present study is to explore whether, under conditions where both 123 strategies would be equally effective, pigeons would solve categorization tasks by 124 using a single highly predictive feature, or by using the overall similarity across a 125 group of features of more modest individual predictiveness. However, previous results 126 have shown that when pigeons do make use of single features, they do not always 127 select the most predictive feature: a less valid but more salient dimension of stimulus 128 variation may acquire exclusive control over behaviour (Lea et al. 2009). 129 Accordingly, the experiments were designed to enable us to dissociate the effects of 130 cue salience from those of cue validity.

131

132 Von Fersen and Lea (1990) noted that categorization in pigeons can be investigated in 133 two different ways: by using natural photographs, videos and objects, which may be 134 referred to as an analytic approach, and by using artificially designed stimuli, the 135 synthetic approach. The advantage of using artificial stimuli is that structure and 136 feature content can be carefully controlled, but such control is usually at the expense 137 of the richness and detail associated with natural exemplars. The use of photographs 138 or videos enhances the verisimilitude of categorization experiments, because it 139 presumably mimics more closely the kind of discrimination that birds have to make in 140 the wild (though it cannot do so exactly, and it cannot necessarily be assumed that the 141 birds recognize the pictures as representations of the corresponding real objects). In 142 the present paper, we used both techniques, so as to gain the advantages of both, and 143 also to provide systematic replication of our main manipulation. Experiment 1 used

144 natural photographs (though with some artificial modification), while Experiment 2 145 used wholly artificial stimuli In both experiments, the stimuli included a single 146 feature that was a perfectly reliable predictor of category membership; by analogy 147 with the work of Waxman and others cited above, we refer to this as the "label". In 148 addition the stimuli included several other features that were individually imperfect 149 predictors but in combination provided enough information to allow perfect 150 Once good performance had been achieved, probe trials were discrimination. 151 introduced, in which the single, perfectly reliable cue and the remaining cues were put 152 in conflict with each other, allowing us to discern which cues were controlling 153 behaviour more strongly.

154

155 **Experiment 1**

156

157 The first experiment used photographs of everyday objects as stimuli. The two 158 categories were houses and cars, which differ along multiple stimulus dimensions. To 159 provide a single highly salient "label" cue, the roofs of the houses and the windows of 160 the cars were replaced with a standard uniform texture in a contrasting colour. If the 161 pigeons in this situation base their discrimination on the label alone, then when probe 162 stimuli are introduced in which the labels have been reversed between categories, it is 163 expected that probes containing the label previously associated with the positively 164 reinforced category (i.e. positive texture probes) will be treated as positive. If pigeons 165 respond positively instead to probes which contain the label originally associated with 166 the negatively reinforced category (positive picture probes), this would suggest they 167 are attending more to the overall similarity of exemplars. Although the stimuli were 168 based on natural photographs of objects, it was not required by the design that the

pigeons should recognize them as depictions of objects that they had seen;
photographs were used only to ensure that the stimulus sets had the kinds of variation
that are characteristic of functional categories in the everyday world.

172

173 Materials and Methods

174

175 Subjects

176 Twenty pigeons were used. They were acquired as discards from pigeon fanciers, and 177 so had visual experience of the world outside the laboratory. Some had previous 178 experience of the touchscreen arrangement used in the present experiment, but in 179 experiments with monochrome, geometric stimuli and a different training procedure 180 (Wills et al. 2009, Experiment 1a); the remainder were experimentally naive. The 181 pigeons were housed in an indoor aviary, measuring 2.2 m by 3.4 m by 2.4 m, and 182 given constant access to water and grit. Prior to testing, pigeons were held in 183 individual cages in which they had access to water and were released back into the 184 aviary when testing had finished for the day. All pigeons were maintained on a 12:12 185 hr light/dark cycle at 95% of their free-feeding weight.

186

187 Apparatus

Four identical operant chambers (internal size; 640 mm x 430 mm x 470 mm) were used. Each consisted of a plywood box, with a 15-inch (39-cm) touch-monitor (Elo Touchsystems Accutouch (resistive) or CarrollTouch (infra-red) model 1547L) mounted in the front wall. The screen resolution was set to 1024 x 768 pixels. The monitor was controlled by software written in Visual Basic using the Whisker control

193 system (Cardinal and Aitken 2001) running on a computer supplied by Quadvision 194 (Quadvision Ltd., Dorset, UK). Two food hoppers, positioned one on each side of the 195 main screen, could be used to deliver a 2:1 mixture of hemp seed and conditioner to 196 the pigeons, for 2.5 seconds. Each box had a webcam fitted into the side wall, 250 197 mm above the floor, allowing the pigeons' behaviour to be observed from outside the 198 test room using the imaging software ViewCommander (Internet Video and Imaging, 199 Ltd.). Each pigeon was assigned its own test chamber for all stages of the experiment: 200 six pigeons used resistive touchscreens while the remaining pigeons used infra-red 201 touchscreens.

202

203 Stimulus Materials

204 The images used were natural photographs comprising two stimulus sets; houses and 205 cars. There were 24 pictures of each type of object. Photographs were manipulated 206 using the GNU Image Manipulation Program (GIMP ver. 2.2). Each image was 207 isolated from the original setting, placed on a black background and then scaled to 208 ensure images were approximately the same size (160 x 120 pixels). To produce a 209 highly salient "label" feature, similar areas in the upper part of the objects were 210 selected and given a new artificial texture. For houses this was the roof, and for cars 211 the windows. Thus 12 of the houses had their roofs replaced with a leopard-skin 212 texture, and the other 12 had their roofs replaced by a blue "swimming pool" wave 213 texture. Similarly, 12 of the cars had all their windows replaced with the leopard-skin texture and the other 12 had them replaced with the blue wave texture. Figure 1 214 215 shows examples of the stimuli. Fourteen of the pigeons were trained to discriminate 216 the houses with leopard-skin roofs from the cars with blue windows, and for these 217 pigeons probe stimuli consisted of houses with blue roofs and cars with leopard-skin windows. For the remaining pigeons, the training stimuli were the houses with blue roofs and the cars with leopard-skin windows, and the probe stimuli were the houses with leopard-skin roofs and the cars with blue windows. Within each of these groups, some of the pigeons were trained with houses as positive stimuli and the remainder with cars as positive stimuli.

- 223
- 224 General Procedure

225 The pigeons were pre-trained using conventional methods to find food in the grain-226 feeders, and to peck lighted discs on the touch-screen for food reinforcement. They 227 were then trained in a multi-stimulus discrimination procedure similar to that 228 described by Huber et al. (2005) and Wills et al (2009, Experiment 2b). Initially, they 229 were trained using this procedure to discriminate white filled hexagons (8mm across) 230 within a 25-mm diameter black circle, outlined in white, from a blank circle. Those 231 pigeons that mastered this discrimination proceeded to the task involving the house 232 and car stimuli.

233

234 In the multi-stimulus discrimination procedure, each session started when the house-235 lights in the box came on, and a white disc of diameter 4cm (the observing key) was 236 displayed on the screen. When the pigeon pecked the observing key it disappeared, to 237 be replaced by an array of photographs. The array consisted of eight cells, arranged as 238 shown in Figure 2. In order to 'open' a cell, pigeons had to peck it twice in rapid 239 succession, causing the image to disappear. If the opened cell was positive, a side key 240 appeared to one side of the array, in the nearer of the two locations shown in Fig. 2 241 (arbitrarily, the left side key was used when the middle top cell was opened, and the 242 right side key when the middle bottom cell was). The pigeons were required to peck

the side key to activate the food hopper on that side for 2.5 seconds (Figure 2). If a negative cell was pecked this was recorded as a miss; the image disappeared but no side key appeared and the screen became unresponsive for 2.5 seconds. If a pigeon pecked a blank cell this was recorded but there were no scheduled consequences. When all the positive cells had been opened, the array disappeared, to be replaced after an inter-trial interval that varied from 1 to 5 s by the observing key. Sessions consisted of six or seven arrays depending on the stage of the experiment.

250

251 Training

252 Three pigeons failed to complete pre-training and were dropped from the experiment. 253 Of the remaining 17 pigeons, 11 were trained using the houses with leopard-skin roofs 254 and the cars with blue windows; of these, five were assigned houses as the positive 255 stimulus, and six were car-positive. The remaining six pigeons were trained using the 256 houses with blue roofs and the cars with leopard-skin windows, and of these three 257 were house-positive and three were car-positive. Arrays were made up of four cars 258 and four houses, pseudo-randomly arranged, with the constraints that stimuli from the 259 same set were never presented in the same place in more than three consecutive arrays 260 and that no more than three stimuli from the same set were placed next to each other 261 or reinforced on the same side. Each training session contained six arrays, so that each 262 of the 12 positive and negative stimuli was seen twice within a session. 263 Discrimination during the training phase was determined using the p statistic of 264 Herrnstein et al. (1976), which was used to measure the overlap between stimulus sets 265 in terms of the order in which the cells were opened. A ρ value of 0.5 indicates 266 random responding, whereas a value of 1 indicates perfect discrimination (i.e. that all 267 the positive stimuli have been opened before any of the negative stimuli). After each

pigeon had reached a criterion of a ρ value of 0.8 or more in all six arrays in a session,
it was exposed to probe sessions.

270

271 Probe Sessions

272 Probe sessions consisted of four training arrays, alternated with three probe arrays. 273 Each session began and ended with a training array. A probe array contained four 274 training stimuli, two from each stimulus set, and four probe stimuli in which the 275 artificial manipulations were reversed. Two of the probes in each array, one from each 276 stimulus set, were assigned positive reinforcement contingencies and the other two 277 were assigned negative contingencies. Probes that were designated positive the first 278 time they were displayed were not reinforced when next shown. Pigeons were 279 required to open the two positive training cells and all four probe cells in order to 280 complete a probe array. Each pigeon received two probe sessions, which were 281 alternated with training sessions, to ensure pigeons recovered their original training 282 performance. Following the procedure of Wills et al. (2009, Experiment 2b), 283 responses to probe stimuli were categorised according to the order in which the 284 pigeons opened them within the array. A probe that was one of the first four stimuli 285 opened in an array was considered to have been treated as positive, and a probe that 286 was one of the last four stimuli opened was considered to have been treated as 287 negative.

288

289 Results

The pigeons reached criterion in a median of 5 training sessions (range 2-8 sessions). This corresponds to the presentation of a median of 30 arrays, i.e. 240 stimuli. There were no significant differences in the rate of acquisition between the house-positive and the car-positive groups, or the leopard-skin positive and blue-wave positive groups, nor was the interaction between the positive picture and the positive texture significant.

297

298 In probe sessions, responses to training stimuli continued at the same high level of 299 accuracy. Different pigeons behaved differently towards the probe stimuli. Probes 300 included either a positive picture (house or car, depending on which was positive 301 during training) and a negative texture (blue wave or leopard-skin), or a negative 302 picture and a positive texture. Figure 3 shows, for each pigeon, the proportion of 303 probe stimuli that were treated in accordance with the texture cue present (that is, 304 responded to as positive if they included the positive texture or as negative if they 305 included the negative texture). In all, 7 of the 17 pigeons (Ro, Ma, Fr, Sn, Su, Ba and 306 Ze) responded to more than half the probes in accordance with the texture cue, 9 307 pigeons (Io, Le, Ri, Ru, Rs, Ti, Ot, Ry, and Se) responded to more than half the 308 probes in accordance with the picture cue, and the remaining pigeon (At) treated both 309 kinds of probes equally. Chi-square tests were used to determine whether the 310 proportions of probe stimuli treated in accordance with the texture or picture cue 311 differed significantly from 0.5 for individual pigeons. Four pigeons responded to the 312 probes in accordance with the texture cue on significantly more than half the trials (Ro, Fr, Sn and Su; χ^2 values of 15.04, 14.09, 8.52 and 4.34, df=1, p<0.0001, 0.0001, 313 0.01 and 0.05 respectively). Three pigeons responded to the probes in accordance 314 with the picture cue on significantly more than half the trials (Io, Ri, and Ry; χ^2 values 315

of 15.04, 9.38 and 7.04, df=1, p<0.0001, 0.01 and 0.01 respectively). The sum of the individual χ^2 values across the pigeons was 83.05; by virtue of the additive property of the chi-square distribution (Weatherburn, 1957, p. 177), this can be tested as a χ^2 value against the sum of their degrees of freedom. The resulting significance level is < 0.0001, showing that despite the fact that not all results were in the same direction, we can reject the null hypothesis that all pigeons had a 50% chance of treating any probe in accordance with the picture cue.

323

324

325 Discussion

326

327 The rapid learning shown by all the pigeons confirms the conclusion of Huber et al. 328 (2005) and Wills et al (2009) that multi-stimulus training methods are an efficient 329 means of establishing complex pattern discriminations. It is a property of such 330 methods, as they have been implemented previously and in the present experiment 331 that, within an array, a correct response makes the remainder of the task more difficult 332 (because it reduces the ratio of positive to negative stimuli remaining) and an 333 incorrect response makes it easier. This makes the task of predicting the probability 334 of a correct response mathematically more difficult, but is not a cocnern when as here, 335 the intention is to compare the probabilities of choosing different probe stimuli that 336 are presented at the same frequency.

337

338 Responses to probe stimuli were reinforced non-differentially. This was because 339 substantial numbers of probe trials were required, and the alternative, non-

reinforcement, could have led to the pigeons learning that all probe stimuli were essentially negative. Non-differential reinforcement carries the alternative risk that subjects will come to behave at random towards probes. However in the present experiment, sustained non-random behaviour towards probes was observed in most pigeons, showing that non-differential reinforcement had no major effect.

345

346 The pigeons were almost equally split between showing greater control by the picture 347 and showing greater control by the texture (the "label" cue). This was not a result of 348 random behaviour, but of systematic behaviour that differed between individuals. 349 Seven of the 17 pigeons showed significant differences in their responses to probes 350 containing the positive picture rather than the positive texture, but in three of these it 351 was the picture cue that controlled probe responding, and in the other four it was the 352 texture cue. As regards the remaining pigeons, given that performance on training 353 stimuli remained highly accurate throughout the probe sessions, the most plausible 354 conclusion is that they were under the control of both the picture and the texture. The 355 distribution of control by the picture or texture was not even between the groups, and 356 in particular all four of the pigeons that showed a significant trend to texture control 357 had the leopard-skin texture as positive. If the leopard-skin was more salient than the 358 blue-wave texture for the pigeons, this could be accounted for as a feature-positive 359 effect (Jenkins and Sainsbury 1970), but in the absence of independent evidence about 360 relative salience, this can only be a speculation. Furthermore one of the pigeons that 361 showed a significant trend towards control by the picture cue (Io) also had the 362 leopard-skin texture as positive, weakening the argument that the overall pattern of 363 results could be due to high salience of the leopard-skin cue.

364

365 Because the pictures were natural photographs, we cannot easily specify which 366 features were supporting discrimination between them, but inevitably the features 367 available will have varied somewhat between instances. We therefore interpret 368 discrimination based on the picture cue as categorization by overall similarity or 369 family resemblance. The texture cue, by contrast, was (to the human eye at least) 370 highly salient, and it was consistent across the training and probe stimulus sets. Discrimination of the texture cue can therefore be regarded as unidimensional 371 372 categorization. Nevertheless, it only exerted dominant control over behaviour in 373 probe trials for four pigeons.

374

375 It is possible that the pigeons learned to discriminate the categories by learning each 376 exemplar of a house or car separately. Previous results make this unlikely given the 377 number of exemplars used: an experiment by Bhatt, cited by Wasserman and Bhatt 378 1992, showed that pigeons switch from exemplar control to featural control in 379 category discriminations where the number of exemplars rises above about six. In any case it would not matter to the present experiment, whose point was to investigate 380 381 whether the pigeons would come under the control of the single feature provided by 382 the texture cue or the multiple features provided by the picture cue: if the pigeons 383 discriminated houses from cars on the basis of exemplars, that would involve the 384 learning of even more different features than doing so by extracting a few general 385 features that were positively but not perfectly correlated with reinforcement.

386

387 The roughly equal distribution of subjects between control by the texture cue and 388 control by the picture cue is an unexpected result, given that pigeons have a tendency 389 to be dominated by single features (Lea et al. 1993, 2006). However, while it is true

390 that birds rarely use all the features available, they can certainly be trained to use 391 more than one (e.g. von Fersen and Lea 1990; Lea et al. 2006). Indeed, some of the 392 pigeons used in the present experiment had been trained in Experiment 1a of Wills et 393 al. (2009), in which they had to learn to discriminate several different features 394 presented on separate trials (though the stimuli and the procedure were very different 395 from those of the present experiment). In the generalisation tests of that experiment, 396 when the features were combined, the behaviour of one of the pigeons that was re-397 used here (Io) was shown to be under the control of multiple features. However, 398 bringing behaviour under the control of multiple stimulus dimensions often requires 399 special training procedures (as in von Fersen and Lea 1990) or extended training, 400 whereas the pigeons in the present experiment learned very quickly.

401

402 Because the picture cues were based on natural photographs, it remains an assumption 403 that discrimination of the pictures was on the basis of overall similarity. It is possible 404 that within the pictures there were other highly predictive features apart from the one 405 manipulated, which were consistent within each category and which were salient for 406 the pigeons. All the car stimuli, for example, contain wheels and so pigeons might 407 have learnt the discrimination on the basis of the presence or absence of silver 408 ellipses. We did our best to ensure there was no such single predictive feature for 409 each category, for example the angle at which the photographs of the stimuli were 410 taken was varied, as was the colour of the cars (so that although all the cars had 411 wheels, those wheels themselves formed a polymorphous set), but there can be no 412 certainty that such attempts will succeed. Conversely, although the label features 413 were much more consistent, they did have some variability: for example, the shapes of 414 the house roofs and car windows to which the textures were applied varied between

415 instances. To avoid these problems while investigating the question of whether birds 416 are more likely to rely on single features or family resemblance, in Experiment 2 we 417 took the alternative approach of using artificial compound stimuli, and so bringing 418 feature content under control.

419

420 Experiment 2

421

422 Experiment 2 was formally very similar to Experiment 1, but used artificial 423 multidimensional stimuli. The stimuli in the present experiment were made up of four 424 spatially separated elements, each of which constituted a stimulus dimension; they 425 were based on those used by Wills et al. (2009, Experiment 1a) and Lea et al. (2009). 426 The elements are referred to as the Annulus, the Bar, the Checks and the Diamond, 427 and examples are shown in Figure 4. Each element could be used in four graded 428 versions, two of them positively and two negatively correlated with the occurrence of 429 reinforcement. The stimulus sets had exactly the same formal structure as those used 430 by Kemler Nelson (1984) with children and Couchman et al (2010) with rhesus 431 monkeys, but the stimulus dimensions used were different.

432

Corresponding to the reliable, salient, texture cue used as a label in Experiment 1, one of the dimensions was designated as a label cue for each pigeon. This dimension was used only in its extreme versions, and one of these always occurred in the presence of reinforcement while the other one never did. The remaining three dimensions were used to construct a two-out-of-three artificial polymorphous stimulus of the sort introduced by Dennis, Hampton and Lea (1973) and used with pigeons by Lea and

439 Harrison (1978): that is, whenever at least two of the three dimensions took its 440 positive value, the stimulus as a whole was designated as positive. For these 441 dimensions, all four versions were used. These three dimensions collectively 442 corresponded to the picture feature in Experiment 1: if a pigeon was to discriminate 443 on the basis of these cues, it would have to come under the control of the overall 444 similarity of the stimuli to an ideal positive form if it was to achieve 100% correct performance, since each individual dimension within this set was imperfectly 445 446 correlated with reinforcement. These artificial stimulus sets had several additional 447 advantages. First, the spatial separation of the stimulus elements ensured that the 448 dimensions of the stimuli could be manipulated entirely independently. Second, the 449 four dimensions could be used in a balanced way, with each dimension being used to 450 provide the label (reliable) feature for some pigeons. Thirdly, within the set of 451 features used to create the polymorphous concept, it was possible to assess 452 empirically whether all three features were controlling behaviour, and therefore 453 whether it is appropriate to describe the pigeons as coming under the control of 454 overall similarity. Finally, on the basis of results with similar stimuli (Lea et al 2009, 455 Wills et al 2009) we had reason to think that the saliences of the feature differences 456 used on the four dimensions of the stimuli were comparable.

457

458 Materials and Methods

459 Subjects

460 Sixteen pigeons were used in this experiment. None of them had previous experience
461 of this kind of discrimination task. They were maintained under the same conditions
462 as the pigeons used in Experiment 1.

463

464 Apparatus

465 The same apparatus was used as in Experiment 1, except that only infra-red 466 touchscreens were used.

467

468 Stimuli and Experimental design

469 The stimuli were modified from those used in Wills et al. (2009, Experiment 1a) and Lea et al. (2009). Examples are shown in Figure 4. All stimuli consisted of a square 470 471 array of four elements. Elements of the same type were always placed in the same 472 location. The element types were an annulus (A), a horizontal bar (B), a square 473 chequerboard (C), and a diamond shape made up of equal-width stripes (D). There 474 were four versions of each element, designated as the X, x, y, and Y forms. All 475 versions of all elements were placed on a black background, and contained the same 476 number of white pixels (within 2%). The specifications of the four forms of each 477 element are listed in Table 1, and they are illustrated in Figure 4. Note that because of 478 the constraint that all elements should have the same area, some elements varied on 479 two dimensions simultaneously: for example, when the Annulus was made smaller, it 480 was also made wider. With four versions of each of four elements, there were 256 481 possible stimuli, but not all pigeons experienced all stimuli. All versions of all 482 elements fitted within a 60 x 60 pixel square with some black border, so that the entire 483 stimulus including borders fitted within a 120 x 120 pixel square; at a pigeon's typical 484 pre-peck viewing distance, 120 pixels subtended about 25° of arc, and would thus fit 485 within the extent of the pigeon's frontal, binocular viewing field (Martin and Young, 486 1983).

487

488 For each pigeon, one of the four dimensions was designated as Reliable, and either the 489 X or the Y value of it was designated as positive; the less extreme (x and y) values of 490 the Reliable dimension were not used either in training or in probe stimuli. The 491 remaining three dimensions were designated as Unreliable, and either all their X and x 492 values, or all their Y and y values, were designated as positive. Positive training 493 stimuli always included the extreme positive value of the Reliable dimension, and 494 positive values (either extreme or less extreme) of at least two of the Unreliable 495 dimensions. Negative training stimuli always included the extreme negative value of 496 the Reliable dimension, and negative values (either extreme or less extreme) of at 497 least two of the Unreliable dimensions. As an example, consider Pigeon Mo, for 498 which the Reliable dimension was the Annulus and the X values of both the Reliable 499 and Unreliable dimensions were designated as positive (see Table 2). For this pigeon, 500 positive stimuli always contained the X value of the Annulus, and at least two of the 501 other three dimensions (Bar, Chequerboard and Diamond) in either their X or their x 502 forms. The negative stimuli always contained the Y form of the Annulus, and either 503 the y or the Y form of at least two of the other three dimensions. There were 32 504 stimuli in each of the positive and negative categories. These categories could be 505 discriminated perfectly in either of two ways (or by a mixture of them). The pigeon 506 could use the Reliable dimension alone, and ignore the three Unreliable dimensions. 507 Alternatively, it could ignore the Reliable dimension, and respond on the basis of the 508 preponderance of values of the three Unreliable dimensions. Each Unreliable 509 dimension took one of its negative values in a quarter of the positive training stimuli, 510 and a positive value in a quarter of the negative training stimuli, so each Unreliable 511 dimension considered on its own can be described as being 75% valid during training; 512 their collectivity, however, was 100% valid. The Reliable cue thus served as a label,

while the Unreliable cues defined a 2-out-of-3 polymorphous stimulus set. Stimuli that included the positive value of the Reliable dimension with negative values of at least two of the Unreliable dimensions, or the negative value of the Reliable dimensions with positive values of at least two of the Unreliable dimensions, were ambiguous, and were not used in training. There were 64 such ambiguous stimuli for each pigeon, and a selection of these were used as probes, in tests conducted after training was complete.

520

521 The way the categories were used was varied between pigeons so as to balance the use 522 of the different dimensions, as shown in Table 2. Each dimension was assigned as 523 Reliable for four of the pigeons. For two of these, the X value of the Reliable 524 dimension was assigned as positive, and for the other two its Y value was assigned as 525 positive. For one of the pigeons for which each value of the Reliable dimension was 526 assigned as positive, the X and x values of the Unreliable dimensions were assigned 527 as positive, and for the other one the Y and y values of the Unreliable dimensions 528 were assigned as positive.

529

To reduce the risk that the pigeons would learn the contingencies associated with probe stimuli, only 36 probe trials were given to each pigeon, so not all the 64 possible probe stimuli were used. The stimuli used as probes are summarised in Table 3. Four of these stimuli were used 6 times each, so as to provide a strong test of the basic question of whether the pigeons' behaviour was governed by the Reliable or the Unreliable dimensions. These stimuli involved:

536 The positive value of the Reliable dimension, combined with the extreme negative

537 values of all three Unreliable dimensions

538 The negative value of the Reliable dimension, combined with the extreme positive539 values of all three Unreliable dimensions

540 The positive value of the Reliable dimension, combined with the less extreme541 negative values of all three Unreliable dimensions

542 The negative value of the Reliable dimension, combined with the less extreme543 positive values of all three Unreliable dimensions.

544

545 In addition six other probe stimuli, as indicated in Table 3, were used twice each. 546 These stimuli involved the positive value of the Reliable dimension and the extreme 547 positive value of one of the Unreliable dimensions, and the extreme negative values of 548 the other two Unreliable dimensions; or the negative value of the Reliable dimension 549 and the extreme negative value of one of the Unreliable dimensions, and the extreme positive values of the other two Unreliable dimensions. Each of the Unreliable 550 551 dimensions was paired with the Reliable dimension in an equal number of probe 552 stimuli. These stimuli allowed a test of which of the Unreliable dimensions was 553 controlling behaviour. Each probe stimulus was associated an equal number of times 554 with the reinforcement contingencies appropriate to positive and negative stimuli.

555

556 Procedure

557 The pigeons were pretrained as in Experiment 1. They were then trained, using the 558 same procedure as in Experiment 1, to discriminate between two positive and negative 559 training categories. Training was continued for a maximum of 20 sessions, but was 560 stopped earlier if a pigeon reached a criterion of a ρ value of 0.8 or more in all six 561 arrays in a session. Three probe sessions where then given. As in Experiment 1, 562 probe sessions consisted of seven arrays: four training arrays, alternated with three

probe arrays. Each session began and ended with a training array. A probe array contained four training stimuli and four probe stimuli, of which two were associated with the reinforcement contingencies appropriate to positive stimuli and two with those appropriate to negative stimuli. Responses to probe stimuli were classified as positive if they occurred within the first four stimulus cells pecked in an array, and as negative otherwise.

569

570 Results

571 Ten of the 16 pigeons reached criterion before their 20th training session; the number 572 of sessions required ranged from 9 to 18 (median, including the pigeons that did not 573 reach criterion, 17). The other six pigeons were showing no obvious further 574 improvement in performance after 20 sessions, though all but one of them was 575 showing ρ values consistently above 0.5; the performance of the remaining pigeon 576 was erratic.

577

578 For comparison with Fig. 3, Fig. 5 shows the proportions of probe trials in which the 579 response was correctly predicted by the Reliable stimulus dimension rather than the 580 preponderance of the Unreliable dimensions. For 10 of the 16 pigeons, this 581 proportion was greater than 0.5, and over the group as a whole the deviation from 0.5 was significant (1-sample, 2-tailed Wilcoxon test, T = 23.5, N=16, p<0.05). For each 582 583 of these pigeons individually, the proportion deviated from 0.5 significantly (2-tailed 584 binomial test). For one of the six pigeons where the proportion was below 0.5 (Ba), 585 the deviation was significant (2-tailed binomial test, p < 0.001). The pigeons that did 586 not respond according to the Reliable stimulus on the probe trials had taken

587

589

588

 $U = 10.5, N_1 = 6, N_2 = 10, p = 0.03).$

590 Figure 6 shows, for each pigeon, the proportions of probe trials in which the response 591 was correctly predicted by each dimension of the stimulus, whether it was reliable or 592 unreliable for that pigeon. In this figure, any proportion above 0.67 or below 0.33 593 would be significantly different from 0.5 on an individual test, though the number of 594 data points involved and the correlations between dimension values mean that simple 595 significance tests cannot be interpreted directly. It can be seen that for each of the 596 pigeons where the unreliable dimensions predicted the response to probe trials 597 markedly better than the reliable dimension (Mo, Bn and Jk), there was one of the 598 unreliable dimensions that predicted response particularly well (Checks for Mo and 599 Jk, and Annulus for Bn). The same trend can be seen more weakly in two of the 600 pigeons where the dominance of the unreliable dimensions was more marginal, Mr 601 and Sa, where Checks and Annulus respectively seemed to have majority control over 602 behaviour. The remaining pigeon, Cr, showed apparently random behaviour towards 603 probe stimuli. For the pigeons where behaviour towards the probe stimuli was 604 dominated but not 100% predicted by the reliable dimension, there was no evidence 605 that individual unreliable dimensions contributed disproportionately to controlling 606 behaviour.

significantly longer to reach criterion than those that did (2-tailed Mann-Whitney test,

607

Because the values of the unreliable dimensions used in the training stimuli varied, it was possible to examine the relative control over behaviour of these dimensions under training as well as probe conditions. Table 4 shows the results of such an analysis, carried out on the training stimuli that were used within the probe sessions so as to

612 maximise comparability with the probe stimulus results shown in Figures 5 and 6. 613 There were 96 such trials, so any proportion greater than 0.58 or less than 0.42 would 614 be significantly different from 0.5 in a single analysis, though the same cautions about 615 the number of tests and the non-independence of the dimensions must be applied as 616 with Figure 6. These data confirm the dominance of the Annulus dimension for 617 pigeons Sa and Ba, and weakly support the dominance of Checks for Mr, but do not 618 support the dominance of Checks for Mo or Jk. On the other hand they suggest that 619 Cr may have been somewhat under the control of the Bar dimension. It is notable 620 (and logically inevitable) that in those pigeons where one of the unreliable dimensions 621 exerted disproportionate control over behaviour, overall discrimination performance 622 was poorer than in the other pigeons.

623

624 Discussion

625 In Experiment 1, we found that the texture and picture cues (which we interpret 626 respectively as a single reliable dimension, and a collectivity of presumably unreliable 627 cues) were about equally likely to control behaviour, and in many cases individual 628 pigeons probably came under the control of both types of cue. However the two kinds 629 of cues differed in nature. In Experiment 2, where the same cues were used as 630 reliable and unreliable dimensions in a fully balanced way, we found a clear trend for 631 reliable dimensions rather than a collectivity of unreliable dimensions to control 632 behaviour, even though either of them could have enabled the pigeons to perform with 633 perfect accuracy. There were some individuals in which the unreliable dimensions exerted dominant control over behaviour, but in at least some cases it appears that this 634 635 was not because the collectivity of those dimensions was enabling perfect 636 discrimination, but rather because one of those dimensions was controlling behaviour

637 to the exclusion of the others and of the reliable dimension, with the result that the 638 pigeon's discrimination accuracy was limited. The pigeons that did not come under 639 the control of the Reliable dimension were slower to reach criterion (indeed, 4 out of 640 these 6 pigeons did not reach it within 20 sessions, as against only 2 of the 10 pigeons 641 that did show Reliable dimension control), and if they were coming under the 642 exclusive control of a less valid dimension, this is a more or less inevitable result. 643 Our results thus differ from those obtained by Couchman et al (2010), using stimulus 644 sets that were structurally identical to those used here, though with different elements: 645 Compared with humans exposed to the same task, Couchman et al's rhesus monkeys 646 always showed a greater tendency to categorise novel stimuli in terms of overall 647 similarity rather than in terms of the label dimension, and the authors concluded that 648 this was because the monkeys could not use verbal rules to categorize complex 649 stimuli. Since we do not believe that pigeons use verbal rules, yet in our experiment 650 they showed a clear tendency to use the label dimension rather than family 651 resemblance, we conclude that categorization by family resemblance is not an 652 inevitable consequence of failing to use verbal rules. We therefore also conclude that 653 unidimensional categorization is not a reliable sign that a verbal rule is being used, in 654 accordance with the conclusions of Lea and Wills (2008) and Wills et al (2009). The 655 difference between our results and those of Couchman et al may be due to the subject 656 species, or it may be due to differences in the details of the stimuli involved, a matter 657 to which we return in the General Discussion.

658

659 Part of the reason why clear dominance of the reliable dimension was found in the 660 present experiment is that with the values on them used in the present experiment, the 661 salience of the four dimensions seems to have been, if not equal, at least comparable,

662 as we predicted on the basis of our previous results with similar stimuli (Wills et al 2009, Lea et al 2009). As Table 4 shows, when used as the reliable dimension, all 663 four dimensions achieved dominant control over behaviour in at least one of the four 664 665 pigeons for which they were Reliable; assuming that salience is reflected in the number of pigeons for which this was so, the order for salience was Checks > 666 667 Annulus> Diamond > Bar. The data on dominance by Unreliable dimensions (also shown in Table 4) confirm this pattern, with Checks and Annulus being the only 668 669 dimensions to achieve dominant control when unreliable. Acquisition data also show 670 that the pigeons for which these dimensions were Reliable tended to learn more 671 quickly than the others.

672

673 Learning in Experiment 2 was substantially slower than in Experiment 1. In 674 Experiment 1, pigeons took a median of 5 training sessions (range 2-8 sessions) to 675 reach criterion; in Experiment 2, the median number of sessions to the same criterion 676 was 12, with the number required ranging from 3 to over 20. This difference is consistent with the fact that in several studies where polymorphous concept 677 678 acquisition has been slow or incomplete artificial stimuli have been used (e.g. Lea et 679 al., 1993, 2006), whereas otherwise quite similar studies using natural photographic 680 stimuli have found more rapid acquisition (e.g. von Fersen and Lea, 1990). It may be 681 that there is something about abstract geometric stimuli that makes it hard for pigeons 682 to learn about them. The present results do however rule out one explanation for the 683 ease of learning discriminations based on natural photographs, which is the possibility 684 that natural stimuli contain artefacts that enable the subjects to make an easy singledimensional discrimination, whereas the more fully controlled artificial stimuli do not. 685

In Experiment 2, all the discriminations could have been solved by the use of a singledimension of demonstrated salience, and yet they were not easy for the pigeons.

688

689 General Discussion

690 Both of the present experiments examined the effect on pigeons' category 691 discrimination of providing a single, salient dimension, in effect a category label, 692 alongside more variable information that was nonetheless sufficient when taken as a 693 whole to support perfect discrimination. In Experiment 1, the label was a distinctive 694 texture, applied to parts of natural photographs. In Experiment 2, it was one of four 695 artificial geometric elements, distinguished by the fact that it had 100% validity as a 696 cue to reward, whereas the other elements only had 75% validity individually, though 697 collectively they were fully valid. In Experiment 1, some pigeons clearly based their 698 discrimination on the label, but slightly more of the pigeons used the pictorial 699 information instead. In Experiment 2, on the other hand, almost all the pigeons used 700 the label (the Reliable feature); of the small number that did not, most came under the 701 control of just one of the Unreliable features, and were thereby prevented from 702 achieving accurate discrimination.

703

The results of Experiment 1 demonstrate a tendency that is evident in the literature on complex visual discriminations in pigeons; that detailed photographic material can serve as highly effective stimuli in such discriminations, competing in effectiveness with simple unidimensional cues on highly salient dimensions such as colour. On the other hand, taking the results of the two experiments together, they do not support the idea that pigeons discriminate photographs readily because the birds have a strong tendency to integrate the wealth of different and possibly unreliable cues that pictures 711 contain. Rather, the results support the conclusions of Lea and Wills (2008), Wills et 712 al. (2009) and Lea et al. (2009), that pigeons have a strong tendency to come under 713 the control of single salient cues when exposed to complex discrimination tasks. 714 What photographs offer is a wide range of strong cues, so there is a good chance that 715 any pigeon will find one that is salient for it – salience being presumably, in part, a 716 function of the individual's previous experience. The carefully balanced design used 717 in Experiment 2 enables us to conclude that, other things being equal, if there is a 718 fully reliable cue available it is likely that it will achieve dominant control over 719 behaviour. Nonetheless, it is not certain that this will happen; it is possible for more 720 salient but less reliable cues to dominate, resulting in imperfect discrimination. The 721 extreme case of this is the occurrence of position habits in experiments where animals 722 have to make spatial choices in a discrimination task; by the design of the experiment, 723 position is normally a cue that carries no information at all, but it can still achieve 724 dominant control over behaviour that continues despite evidence that an animal has 725 detected the truly predictive contingencies (e.g. Mahut 1954).

726

Despite the strong tendency for pigeons to come under the control of single 727 728 dimensions, it is clearly not the case that they cannot be controlled by more than one 729 dimension. Nor is it the case that control by multiple dimensions only occurs when it 730 is essential for perfect discrimination, as in a compound discrimination. These 731 generalizations were again confirmed in the present experiments: In Experiment 1, it 732 appeared that a majority of the pigeons came under the control of both the picture and 733 the texture, and in Experiment 2 at least a few of the pigeons showed evidence of 734 control by more than one of the unreliable dimensions.

735

736 While control by multiple dimensions is not impossible, it seems from the present 737 results, and previous data, that it is not the natural tendency for pigeons. It may be 738 that it is easier for primates, and this would be one account of the difference between 739 our results and those of Couchman et al (2010) with rhesus monkeys. If 740 multidimensional control does not come naturally to pigeons, tasks that require it, 741 such as polymorphous discriminations, are likely to be difficult for pigeons or other 742 birds to learn, and previous data support this position (e.g. Lea and Harrison 1978; 743 Lea et al. 2006). Lea et al. concluded that the reason was a limitation of attention: any 744 task that requires the processing of more than one stimulus dimension is inherently 745 difficult for a bird. The present data are consistent with that position.

746

747 It is possible that the difficulty of attending to multiple dimensions is exacerbated 748 when the dimensions are spatially separated, as in the present experiments. It is 749 notable that in the stimuli used by Couchman et al (2010), who obtained 750 categorization by overall similarity from rhesus monkeys, the four elements were spatially contiguous, and this could be an alternative account of the difference 751 752 between their results and ours. Spatial grouping does affect pigeons: for example, 753 Sainsbury (1971) found that the feature positive effect in pigeons, which depends on 754 the elements of a stimulus being processed separately, was attenuated when the 755 elements were grouped more closely together. It is also possible that some kinds of 756 stimulus dimension are more separable than others for cognitive rather than perceptual 757 reasons (Soto and Wasserman 2010). However it is not a foregone conclusion that 758 spatial separation or cognitive compatibility will lead to a greater tendency towards 759 categorization by overall similarity: they could instead act to mitigate confusion between the dimensions. This is a matter that would repay experimentalinvestigation.

762

763 The task used in the present Experiment 2 had many points in common with a 764 standard *m*-out-of-*n* artificial polymorphous discrimination task. The essential 765 difference was that there was an additional, completely reliable stimulus dimension (a label in the terms used by Waxman and Markow, 1995), whereas in a standard 766 767 polymorphous task, all dimensions are equally unreliable. It is therefore not 768 surprising that the task was learned relatively quickly, especially when the complex 769 and abstract nature of the stimuli is taken into account. The speed of learning may 770 have been partly due to the multiple simultaneous presentation procedure, which is 771 known to produce faster learning than a simple go/no-go task (Huber et al. 2005, 772 Wills et al. 2009), and it would be interesting to try a standard polymorphous discrimination using this procedure. However the present design does raise an 773 774 intriguing possibility. We normally think of the different dimensions of a stimulus as 775 competing for a subject's limited capacity for attention, and this is the basis of most 776 attention-based theories of discrimination learning, e.g. Sutherland and Mackintosh 777 (1971). Indeed, earlier attention-based theories assumed that animals could only 778 attend to a single stimulus dimension at once (e.g. Krechevsky, 1932). Our results are 779 certainly consistent with the idea that animals' learning of complex stimuli is limited 780 by their attentional capacity. It is conceivable, however, that a highly reliable 781 dimension could act to inform an animal that a task can be learned, and this might 782 heighten attention to other dimensions rather than diminishing it, especially if the 783 reliable dimension was removed once learning had taken place; something of this sort 784 might underlie the "labeling" phenomenon as it occurs in young children (Waxman

and Markow, 1995; Balaban and Waxman, 1997; Plunkett et al., 2008). This possibility gives more potential empirical bite to limited-attention theories, which can seem to add little to the empirical generalization that multiple-dimension discriminations are difficult. It could perhaps be investigated by exploring the mechanisms of attention in more detail by comparing the amount learned about unreliable stimulus dimensions in the presence or absence of more reliable cues.

791

792 Acknowledgements

793 Experiment 1 was carried out by Beth Nicholls in partial fulfilment of the 794 requirements for the MSc degree in Animal Behaviour of the University of Exeter. 795 The experimental work described here was supported by the New and Emerging 796 Science and Technologies activity of the European Community Framework Programme 6, under grant no. 516542, "From Associations to Rules in the 797 798 Development of Concepts" (FAR). We are grateful to Lisa Leaver, Louise Millar, 799 Andy Wills and John Endler for discussion, and to Denis Mareschal and Caspar 800 Addyman (Birkbeck, University of London) for supplying the photographs used as 801 stimuli in Experiment 1. The experimental work was carried out within the terms of 802 the United Kingdom Animals (Scientific Procedures) Act (1986).

803

804 **References**

805 Ashby FG, Alfonso-Reese LA, Turken AU, Waldron EM (1998) A formal

- 806 neuropsychological theory of multiple systems in category learning. Psychol
 807 Rev 105:442-481
- Blough DS (1972) Recognition by the pigeon of stimuli varying in two dimensions. J
 Exp Anal Behav 18:345-367

- Bovet D, Vauclair J (2000) Picture recognition in animals and humans. Behav Brain
 Res 109:143-165
- 812 Cardinal, RN, Aitken, MRF (2001) Whisker (version 2). Cambridge University
 813 Technical Services Ltd, Cambridge
- 814 Couchman JJ, Coutinho MVC, Smith, JD (2010) Rules and resemblance: Their
- 815 changing balance in the category learning of humans (*Homo sapiens*) and
- 816 monkeys (*Macaca mulatta*). J Exp Psychol: Anim Behav Proc 36: 172-183
- 817 Dennis I, Hampton JA, Lea S (1973) New problem in concept formation. Nature
- 818 243:101-102
- Herbranson WT, Fremouw T, Shimp, CP (1999) The randomization procedure in the
 study of categorization of multidimensional stimuli by pigeons. J Exp
 Psychol: Anim Behav Proc 25: 113-134
- Herrnstein RJ, Loveland DH (1964) Complex visual concept in the pigeon. Science
 146: 549-551. doi:10.1126/science.146.3643.549
- 824 Herrnstein RJ, Loveland DH, Cable C (1976) Natural concepts in pigeons. J Exp

825 Psychol Anim Behav Proc 2: 285-302. doi:10.1037.0097-7403.2.4.285

- 826 Huber L (2001) Visual categorization in pigeons. In: Cook RG (ed) Avian visual
- 827 cognition. [On-line], Available www.pigeon.psy.tufts.edu/avc/huber/
- 828 Huber L, Apfalter W, Steurer M, Prossinger H (2005). A new learning paradigm
- 829 elicits fast visual discrimination in pigeons. J Exp Psychol Anim Behav Proc
- 830 31, 237-246. doi:10.1037/0097-7403.31.2.237
- 831 Kemler Nelson, DG (1984) The effect of intention on what concepts are acquired. J
- 832 Verb Lng Verb Behav 23:734-759

- 833 Kirkpatrick-Steger K, Wasserman EA (1996) The what and the where of the pigeon's
- 834 processing of complex visual stimuli. J Exp Psychol Anim Behav Proc 22:60-

835 67. doi:10.1037/0097-7403.22.1.60

- 836 Krechevsky I (1932) Hypotheses in rats. Psychol Rev 39:516-532
- Jenkins HM, Sainsbury RS (1970) Discrimination learning with the distinctive feature
 on positive or negative trials. In: Mostofsky DI (ed) Attention: Contemporary
- theory and analysis. Appleton-Century-Crofts, NewYork, pp 239-273
- Lea SEG, Harrison SN (1978) Discrimination of polymorphous stimulus sets by
- 841 pigeons. Q J Exp Psychol 30:521-537
- Lea SEG, Lohmann A, Ryan CME (1993) Discrimination of five-dimensional stimuli
- by pigeons: Limitations of feature analysis. Q J Exp Psychol 46B:19-42.
- 844 doi:10.1080/14640749308401093
- Lea SEG, Wills AJ (2008) Use of multiple dimensions in learned discriminations.

846 Comp Cogn Behav Rev 3, 115-133. doi:10.3819/ccbr.2008.30007

- Lea SEG, Wills AJ, Leaver LA, Ryan CME, Bryant CML, Millar L (2009) A
- 848 Comparative analysis of the categorization of multidimensional stimuli: II.
- 849 Strategic information search in humans (*Homo sapiens*) but not in pigeons
- 850 (Columba livia). J Comp Psychol 123:406-420. doi:10.1037/a0016851
- Lea SEG, Wills AJ, Ryan CME (2006) Why are artificial polymorphous concepts so
- hard for birds to learn? Q J Exper Psychol 59:251-267 doi
- 853 10.1080/02724990544000031
- 854 Mahut H (1954) The effect of stimulus position on visual discrimination by the rat.
- 855 Canad J Psychol 8:130-138
- Makino H, Jitsumori M (2007) Discrimination of artificial categories structured by
 family resemblances: a comparative study in people (*Homo sapiens*) and

858 pigeons (*Columba livia*). J Comp Psychol 121, 22-33. doi:10.1037/0735-

859 7036.121.1.22

- Martin GR, Young SR (1983) The retinal binocular field of the pigeon (*Columba livia*: English racing homer). Vision Research 23:911-915
- Pothos EM (2005) The rules versus similarity distinction. Behav Brain Sci 28:1-49
- 863 Sainsbury RS (1971) Effect of proximity of elements on the feature-positive effect. J
- 864 Exp Anal Behav 16:315-325
- 865 Smith LB (1981) Importance of the overall similarity of objects for adults' and
- children's classifications. J Exp Psychol Human Percep Perf 7, 811-824.
- 867 doi:10.1037/0096-1523.7.4.811
- 868 Smith LB, Kemler DG (1977) Developmental trends in free classification; Evidence
- 869 for a new conceptualisation of perceptual development. J Exp Child Psychol
- 870 24, 279-298. doi:10.1016/022-0965(77)90007-8
- 871 Soto FA, Wasserman EA (2010) Integrality/separability of stimulus dimensions and
- 872 multidimensional generalization in pigeons. J Exp Psychol Anim Behav Proc
- 873 36:194-205 doi :10.1037/a0016560
- 874 Sutherland NS, Mackintosh NJ (1971) Mechanisms of animal discrimination learning.
 875 Academic Press, New York
- 876 Von Fersen L, Lea SEG (1990) Category discrimination by pigeons using five
- polymorphous features. J Exp Anal Behav 54, 69-84.
- 878 doi:10.1901/jeab.1990.54-69
- 879 Wasserman EA, Bhatt RS (1992) Conceptualization of natural and artificial stimuli by
- 880 pigeons. In: Honig WK, Fetterman JG (eds) Cognitive aspects of stimulus
- control. Erlbaum, Hillsdale NJ, pp 203-223

882	Weatherburn CE (1957) A first course in mathematical statistics, 2nd Edn corrected.
883	Cambridge University Press, Cambridge
884	Wills AJ, Lea SEG, Leaver LA, Osthaus B, Ryan CME, Suret MB, Bryant CML,
885	Chapman SJA, Millar L (2009) A comparative analysis of the categorization
886	of multidimensional stimuli: I. Unidimensional classification does not
887	necessarily imply analytic processing; evidence from pigeons (Columba livia),
888	squirrels (Sciurus carolinensis) and humans (Homo sapiens). J Comp Psychol
889	123:391-405. doi:10.1037/a0016216

Element	dimension	X value	x value	y value	Y value
	of variation				
Annulus	width:radius	5:1	4:1	2:1	1.5:1
	ratio				
Bar	length:width	7.5:1	6:1	3.3:1	2:1
	ratio				
Chequerboard	number of	2 x 2	4 x 4	6 x 6	8 x 8
	elements				
Diamond	orientation	vertical	60°	30°	horizontal
	of stripes				

891 Table 1. Experiment 2: The four forms of each dimension of the stimuli

894 Table 2

Pigeon	Reliable	Positive	Unreliable dimensions	Positive
	dimension	value		values
	(label)			
Мо	Annulus	Х	Bar, Chequerboard, Diamond	X, x
Ct	Annulus	Х	Bar, Chequerboard, Diamond	Y, y
Ch	Annulus	Y	Bar, Chequerboard, Diamond	X, x
Кс	Annulus	Y	Bar, Chequerboard, Diamond	Y, y
Bn	Bar	Х	Annulus, Chequerboard, Diamond	X, x
Mr	Bar	Х	Annulus, Chequerboard, Diamond	Y, y
Sa	Bar	Y	Annulus, Chequerboard, Diamond	X, x
Cu	Bar	Y	Annulus, Chequerboard, Diamond	Y, y
Rg	Chequerboard	X	Annulus, Bar, Diamond	X, x
Ну	Chequerboard	X	Annulus, Bar, Diamond	Y, y
Yw	Chequerboard	Y	Annulus, Bar, Diamond	X, x
Bu	Chequerboard	Y	Annulus, Bar, Diamond	Y, y
Fl	Diamond	X	Annulus, Bar, Chequerboard	X, x
Cr	Diamond	X	Annulus, Bar, Chequerboard	Y, y
Dd	Diamond	Y	Annulus, Bar, Chequerboard	X, x
Jk	Diamond	Y	Annulus, Bar, Chequerboard	Ү, у

895 Experiment 2: Use of stimulus dimensions in training stimuli for each pigeon

896

898	Table 3. Example showing the Probe stimuli used in Experiment 2. In this example,
899	A was the Reliable dimension, with its X value as positive, and B, C and D were the
900	Unreliable dimensions, with their X and x values as positive. The dimensions used as
901	reliable and unreliable, and the values used as positive and negative, varied between
902	birds in a balanced fashion.

	Stimulus	dimension		
Annulus	Bar	Chequerboard	Diamond	Number of times
(Reliable)		(Unreliable)		used
X	Y	Y	Y	6
Y	Х	Х	Х	6
Х	У	У	У	6
Y	Х	Х	х	6
X	Х	Y	Y	2
Y	Y	Х	Х	2
Х	Y	X	Y	2
Y	Х	Y	X	2
Х	Y	Y	Х	2
Y	Х	Х	Y	2

905 Table 4. Experiment 2: Proportions of training trials within test sessions in which the

906 response was correctly predicted by each dimension of the sum

		Proportions of tri	ials correctl	y predi	cted by valu	ue of
Reliable	Pigeon	Positive stimulus Individual unreliable dimensions			nensions	
dimension		(Reliable dimension				
		and majority of	Annulus	Bar	Checks	Diamond
		unreliable dimensions)				
Annulus	Mo	0.64		0.63	0.58	0.58
Annulus	Ct	0.87		0.76	0.67	0.70
Annulus	Ch	0.98		0.77	0.77	0.78
Annulus	Kc	0.98		0.72	0.79	0.79
Bar	Bn	0.70	0.85		0.55	0.50
Bar	Mr	0.64	0.53		0.60	0.58
Bar	Sa	0.66	0.69		0.58	0.53
Bar	Cu	0.95	0.80		0.68	0.73
Checks	Rg	0.88	0.77	0.61		0.73
Checks	Hy	0.98	0.79	0.73		0.77
Checks	Yw	0.89	0.80	0.70		0.66
Checks	Bu	1.00	0.81	0.76		0.77
Diamond	Fl	0.86	0.72	0.68	0.68	
Diamond	Cr	0.46	0.41	0.61	0.38	
Diamond	Dd	0.86	0.74	0.70	0.68	
Diamond	Jk	0.71	0.77	0.64	0.51	

908 Figure Legends

909

Fig. 1. Experiment 1: Examples of stimuli showing each of the two picture types
(house and car) associated with each of the two artificially introduced textures
(leopard-skin and blue wave). Each stimulus measured 160 x 120 pixels. (From
original photographs by Casper Addyman, used with permission)

914

Fig. 2. Diagram of touch screen display, showing size and position of array and two
side keys. Cells were numbered 1-8, clockwise from top left. Cells 3-6 were
reinforced on the right of the screen: cells 7, 8, 1 and 2 reinforced on the left.

918

Fig. 3. Proportions of probe stimuli responded to in accordance with the texture cue.
Data are shown separately for each pigeon, separated by the stimulus type that was
positive in training (*=Difference from 0.5 significant at 0.05 level).

922

Fig. 4. Examples of the stimulus sets used in Experiment 2. The upper two panels
show the A and a versions of each dimension, the lower two panels the b and B
versions.

926

Fig. 5. Experiment 2: Proportions of probe trials in which the stimulus was responded
to in accordance with the Reliable stimulus dimension. Data are shown separately for
each pigeon, grouped by the dimension that was designated as Reliable (*=Difference
from 0.5 significant at 0.05 level).

931

932	Fig. 6. Experiment 2: Proportions of probe stimulus trials on which each of the
933	Unreliable dimensions correctly predicted response. Data are shown separately for
934	each pigeon, grouped by the dimension that was designated as Reliable. Gaps within
935	the cluster of bars for each pigeon correspond to the Reliable dimension

Figure 1.

Fig. 1 Experiment 1: Examples of stimuli showing each of the two picture types (house and car) associated with each of the two artificially introduced textures (leopard-skin and blue wave). Each stimulus measured 160 x 120 pixels. (From original photographs by Casper Addyman, used with permission)





b





Figure 2

Fig. 2 Diagram of touch screen display, showing size and position of array and two side keys. Cells were numbered 1-8, clockwise from top left. Cells 3-6 were reinforced on the right of the screen: cells 7, 8, 1 and 2 reinforced on the left.



Figure 3

Fig. 3 Experiment 1: Proportions of probe stimuli responded to in accordance with the texture cue by each pigeon, separated by the stimulus type that was positive in training (*=Difference from 0.5 significant at 0.05 level).

[see separate file]

Fig. 4. Examples of the stimulus sets used in Experiment 2. The upper two panels show the X and x versions of each dimension, the lower two panels the y and Y versions.



Fig. 5 Experiment 2: Proportions of probe trials in which the stimulus was responded to in accordance with the Reliable stimulus dimension. Data are shown separately for each pigeon, grouped by the dimension that was designated as Reliable (*=Difference from 0.5 significant at 0.05 level). Gaps within the cluster of bars for each pigeon correspond to the Reliable dimension

[see separate file]

Fig. 6. Experiment 2: Proportions of probe stimulus trials on which each of the Unreliable dimensions correctly predicted response. Data are shown separately for each pigeon, grouped by the dimension that was designated as Reliable.



Unreliable dimensions: