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Pigeons can learn to make visual category discriminations using either low or high spatial frequency information

Stephen E.G. Lea[a,*], Victoire Poser-Richet[a,b], Christina Meier[a]

[a] University of Exeter, Psychology (CLES), Washington Singer Laboratories, Exeter EX4 4QG, United Kingdom
[b] Institut Polytechnique LaSalle Beauvais, Rue Pierre Waguet, BP30313, F-60026 Beauvais, France

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ABSTRACT

Pigeons were trained to discriminate photographs of cat faces from dog faces, using either high- or low-pass spatial frequency filtered stimuli. Each pigeon was trained with multiple exemplars of the categories, but only with either high-pass or low-pass filtered stimuli. Not all pigeons reached the discrimination criterion. Successful pigeons were exposed in probe trials to test stimuli: cat and dog faces that had been subjected to the opposite kind of filtering from their training stimuli; the unfiltered original stimuli from which their training stimuli had been derived; and new exemplars of the cat- and dog-face categories, with the same filtering as was used in training. There was no transfer of discrimination to the stimuli with the opposite filtering from those used in training. Discrimination transferred, with some decrement, to the original unfiltered stimuli and to new exemplars with the same type of filtering as used in training. These results provide further evidence that both high and low spatial frequency information can be sufficient for pigeons to make category discriminations, and that there is no clear advantage for high spatial frequency information. They also confirm that high-pass and low-pass spatial frequency filtering produce images that have effectively no information in common.

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1. Introduction

The eyes and visual brains of birds differ in many respects from those of mammals, and in particular of humans (Zeigler and Bischof, 1993). Presumably as a result, the processing of complex stimuli seems to follow different rules in birds and humans. For example, a number of lines of evidence converge on the conclusion that pigeons respond more to local details of stimuli in situations where human behaviour is more determined by the Gestalt (Cook, 1993). This is not an absolute rule: both pigeons and humans can be trained to use either local or global features (e.g. Goto et al., 2004), and in studies of object recognition, both detailed "geons" and more global properties such as spatial location can contribute to recognition of an object (Van Hamme et al., 1992). However, there are some striking examples of differences between pigeon and human pattern processing. Faced with hierarchical stimuli like those of Navon (1977), which humans classify in terms of global properties, pigeons classify them in terms of the elements of which they are composed (Cavoto and Cook, 2001). Faced with stimuli in which a small diamond sometimes does, and sometimes does not, fit exactly into a notch in the perimeter of a large square, pigeons detect the notch with equal ease regardless of whether the diamond is fitted into it, whereas humans find the task harder when the diamond fits into the notch, since we then see the image as a diamond superimposed on an intact square (Fujita and Ushitani, 2005). Faced with two long, parallel diagonal lines, one intersected with numerous short vertical lines and the other with short horizontal lines, humans see the lines as converging in one direction (the Zöllner illusion), whereas pigeons and chickens seem them as converging in the opposite direction (Watanabe et al., 2011, 2013). If pigeons are trained to discriminate between images of cats and dogs, and are then faced with chimeras made up of cat heads on dog bodies or vice versa, they classify them in terms of the body (Ghosh et al., 2004, Experiment 1) whereas human infants classify them in terms of the head (Quinn and Eimas, 1996).

Ghosh et al. (2004) and Goto et al. (2011) attempted to draw these and other results together by suggesting that, compared with humans, pigeons may be more sensitive to the higher spatial frequencies in a stimulus. In a direct test of this proposal, Lea et al. (2013) trained pigeons to discriminate cat faces from dog faces, and then tested them with high-pass and low-pass filtered versions of the training stimuli, and with hybrid stimuli in which the

* Corresponding author. Tel.: +44 1392 724612; fax: +44 1392 724623.
E-mail address: s.e.g.lea@exeter.ac.uk (S.E.G. Lea).

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high spatial frequency components of a stimulus from one category were combined with the low spatial frequency components of a stimulus from the opposite category. They found better generalization to the low-pass than to the high-pass filtered stimuli, and furthermore found that the hybrid stimuli tend to be responded to in terms of their low spatial frequency component rather than their high spatial frequency component. These results were opposite to those obtained from humans, and this is surprising given the evidence that pigeons tend to respond in terms of the finer details of stimuli more than humans. Furthermore, in an experiment in which they removed narrow bands of spatial frequencies from images that pigeons had been trained to discriminate, Murphy and Cook (2008) reported that removing high spatial frequencies led to more generalization decrement than removing low spatial frequencies.

Because of the unexpected nature of Lea et al.'s (2013) results, the present experiment was designed to explore further the impact of high-pass and low-pass spatial frequency filtering on pigeons' category discrimination. In particular, it investigated whether high- and low-pass filtered versions of the kind of stimuli used by Lea et al. (2013) contain truly independent information. Fig. 1 shows examples of the kinds of stimuli we used; to ensure that the results obtained by Lea et al. (2013) were not due to any peculiarity of their stimuli, all the stimuli used in the present experiment were new. Because of our past experience of cats and dogs and pictures of them, humans recognize both kinds of filtered stimuli immediately as cat or dog faces, and would therefore generalize responses from one kind to the other. However, the pigeons we used had had no known exposure to either cats or dogs, and it is in any case doubtful that they would recognize the pictures as representations of the corresponding real objects (see, e.g. Dittrich et al., 2010), so we would not expect any transfer to the opposite kind of stimulus, unless there is some experimental artefact. To test this prediction, pigeons were trained to discriminate images using high- or low-pass filtered stimuli. The pigeons that had been trained with high-pass filtered stimuli were then tested with low-pass filtered stimuli, and vice versa. Following this test of the independence of the information in the two kinds of filtered stimuli, the pigeons were tested on transfer to the original, unfiltered versions of the stimuli, and on transfer to new exemplars of the cat and dog face categories.

2. Method

2.1. Subjects

Nine pigeons, obtained as discards from local fanciers, were kept in an indoor aviary and maintained at or above 80% of free feeding weight. They had previously served other experiments on visual pattern discrimination, using similar training and testing procedures but with stimuli of completely different appearance. Eight birds were used in the initial design of the experiment; because some of these did not reach the training criterion, an additional pigeon was added later.

2.2. Apparatus

Each pigeon was tested in one of four 71 cm × 50.5 cm × 43.5 cm operant chambers. One long wall of each chamber was fitted with a 31 cm × 23.5 cm (15-in.) touch monitor (Model 1547L 1024 × 768 pixel TFT monitor with CarrollTouch infra-red detector; ELO Touchsystems Inc.), mounted 12 cm above the grid floor of the chamber. Effective pecks to target areas were followed by an immediate bleep from a 50-ohm loudspeaker, which also played white noise into the box. Two 2.8-W white houselights were mounted above and to either side of the screen. Two 6 cm × 5 cm apertures gave access to grain hoppers when solenoids were activated; they were located directly below the houselights and 4 cm above the floor of the chamber. The hoppers were illuminated by a 2.8-W white light when activated, and contained a 2:1 mixture of hemp seed and conditioner. The interior of some of the boxes was monitored by a video camera. The experiment was controlled by a computer (Quadvision Ltd) located in an adjacent laboratory area, using the Whisker control server system (Cardinal and Aitken, 2010) with client programs written in Microsoft® Visual Basic 6.0.

2.3. Stimulus materials

The training stimuli were spatial-frequency filtered versions of full-colour cat and dog face images on medium grey backgrounds. The original images were similar to those used by Lea et al. (2013), but they were newly sourced and prepared for this experiment. Pictures of cats and dogs were downloaded from a variety of Internet sources; the heads were removed and placed on a circular medium grey background, and the resulting head images were converted into 240 × 240-pixel bitmap files, with a colour depth of 24 bits/pixel. In all, 20 cat faces and twenty dog faces were used; ten of each were used for training and ten for transfer tests. The overall brightness (mean of the sum of red, green and blue intensities across all pixels), redness (mean of red intensity minus green pixel intensity across all pixels) and blueness (mean blue intensity minus half the mean of red and intensity and half the mean of green intensity across all pixels) of each stimulus were calculated, and the mean values of these parameters in all four groups of stimuli (training cats, training dogs, transfer cats and transfer dogs) were equated as closely as possible. Their means and standard deviations are reported in Table 1, and it can be seen that in all cases, the variation of the parameters within categories was much greater than the difference of their means between categories: Among the training stimuli, each cat face was paired with the dog face of the same rank brightness for the purposes of assigning stimuli to sessions. Following filtering, all the images were reduced to 120 × 120 pixel bitmaps. They were then further reduced within the Whisker system to 90 × 90 pixels for display on the touchscreens, where the diameter of the background was approximately 3.0 cm. They subtended approximately 53° of arc at the pigeon's eye at the moment of impact, given a typical pecking distance that positioned the bird's eye about 3 cm from the touchscreen. The final reduction for display introduced some visual noise, in the form of occasional single-pixel dots, into all images, but this factor was constant across all stimulus types. Fig. 1 includes examples of the original images, rendered in greyscale.

As in Lea et al. (2013), spatial frequency filtered stimuli were produced using methods recommended by Walisch et al. (2009, pp. 87ff). Low-pass filtered versions of each stimulus were produced by convolving the two-dimensional matrix of its pixel values for each colour channel (red, green or blue) with a square filter kernel. In simple terms, this blends the pixel values across the area of the kernel, and thus removes high spatial frequency information. The convolution was carried out using the *convn* routine within Matlab® R2013a with a 32-pixel filter kernel, thereby removing spatial frequencies above .031 cycles/pixel; following the final reduction in size of the images, the cut-off frequency becomes .083 cycles/pixel. High-pass filtered stimuli were then produced by subtracting the low-pass filtered stimuli from the originals, leaving only the high spatial-frequency information, and adding half the maximal value to all pixel values to restore overall brightness. Fig. 1 includes examples of high- and low-pass filtered stimuli.

The filter kernel size of 32 pixels was chosen because to the experimenters' eyes it appeared to make the high- and low-pass filtered stimuli equally different from the original images. It can

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