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Pigeons discriminate shapes based on topological features

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ABSTRACT

The use of topological features in visual recognition has been demonstrated only in species with global-cue precedence. We investigated whether pigeons, with local-cue precedence, use topological features as cues for discriminating different shapes. The subjects in the topology group were required to discriminate stimuli based on whether the shapes contained one or no holes, whereas the subjects in the pseudocategory group were required to discriminate stimuli based on arbitrary categories. In contrast to the pseudocategory group, which showed little improvement in stimuli discrimination over the sessions, the topology group showed rapid improvement, indicating that the latter group performed better than what was expected from rote learning. Moreover, our data suggest that shape discrimination in pigeons is based on on-off feature information contained in the stimuli. We conclude that certain species with local-cue precedence are capable of perceiving topological features and that this type of perception may be a primitive component of the visual system.

1. Introduction

Despite large variations in perceptual systems across animal species, the common functions that underlie these systems reveal perceptual primitives. In the case of visual perception, some researchers have suggested that discrimination of visual stimuli based on topological properties is a primitive component of object recognition (Chen, 1982; Chen, Zhang, & Srinivasan, 2003).

According to textbooks on geometry (e.g., Fomenko, 1994; Meserve, 1983), topological properties refer to properties that are preserved under one-to-one, continuous transformations. Two shapes that differ in shape or size share topological properties as long as they have the same number of holes. Human visual perception is highly sensitive to topological properties. Chen (1982) showed that at visual threshold, adult humans are better at differentiating visual stimuli that differ in topological properties than in other geometrical features. More specifically, the subjects in their study could correctly differentiate between a disc and a ring (a disc with a hole in its centre) but they could not differentiate a disc and a triangle. There is also evidence suggesting that sensitivity to global topological properties precedes the sensitivity to local properties in the course of human development (Chien et al., 2012; Kibbe & Leslie, 2016). In fact, infants as young as few days old can differentiate shapes with and without a hole (Turati, Simion, & Zanon, 2003). Even 24-hour old chicks have shown predisposed preference for hollow objects over closed objects (Versace, Schill, Nencini, & Vallortigara, 2016) and therefore it is possible that such discrimination ability serves as a functional advantage.

Sensitivity to topological properties may play an important role in defining the presence of objects by differentiating open and closed spaces and distinguishing objects from their backgrounds. Identifying the presence of objects is particularly important for animals that interact with their environment, for example, during locomotion. Closed contours indicate obstacles that need to be avoided, other individuals, including predators and potential mates, or food items. The major advantage of using topological features for object identification is that they remain relatively stable both physically and perceptually. Firstly, topological features are not affected by transformations such as stretching, shrinking, and twisting. Therefore, a chipped rock can still be recognised as the same rock even though its size and shape have changed. Secondly, the perception of topological features is not usually affected by the context. This contrasts with the perception of certain features such as colour and texture that change in appearance depending on the amount and the colour of illumination. The stability of topological perception makes it a useful tool for recognizing objects by different animals, regardless of their environment.

The number of studies on topological perception in nonhuman animals is limited. However, Chen et al. (2003) reported a striking finding in small-brained insects. In their experiment, the authors trained honey

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bees to discriminate between an O-shape (one hole) and an S-shape (no holes) by placing the stimuli at the end of a Y-maze. The bees were rewarded for visiting the O-shape but not for visiting the S-shape. After the training phase, generalisation of the bees' discrimination was tested using novel pairs of stimuli. For the two pairs of stimuli that each contained a shape with one hole and a shape with no holes, and for the third pair that contained a shape with one hole and a shape with four holes, the bees consistently chose the one-hole stimulus. For the fourth pair of stimuli that contained an O-shape and a hollow square, both with one hole, their choice was at random. These findings indicate that honey bees can distinguish shapes based on topological features even if they cannot distinguish shapes with different geometric features that share topological features. The authors concluded that the ability of topological perception in such a simple visual system as that of bees suggests that it is a primitive component of visual perception.

Although the evolutionary history, neural mechanism, and lifestyle of honey bees are very different from that of humans, the two species share other aspects of visual perception. In image processing, both species seem to process global cues before local cues. Global cues refer to the holistic aspects of an object whereas local cues refer to the details or parts. A typical approach to assessing global-local precedence is to use hierarchical stimuli consisting of small components that form larger compounds (Navon, 1977). Both humans (for review, see Kimchi, 1992) and honey bees (Avarguès-Weber, Dyer, Ferrah, & Giurfa, 2015), prefer information provided by larger global compounds over that provided by small local components, which indicate global precedence. Because topological features, which define contours of objects, can be considered as global cues in most contexts, shared global precedence of humans and honey bees is a possible explanation of why both these species are capable of perceiving global topological features. Global precedence is not a shared characteristic of all animal species. For example, despite their close evolutionary proximity with humans, other primates, including baboons (Fagot & Deruelle, 1997), chimpanzees (Fagot & Tomonaga, 1999) and capuchin monkeys (Spinozzi, De Lillo, & Truppa, 2003), show local precedence. If indeed topological perception relies on global processing, species with local precedence might not have the ability to extract topological features.

Pigeons are another species that show local precedence. They are sensitive to both local and global cues but prioritise local information when both are available (Cavoto & Cook, 2001; Sekiguchi, Ushitani, & Jitsumori, 2011). Although local-global precedence of pigeons differs from that of humans, several studies suggest similarities in the visual experience of these two species on other aspects of visual perception. Blough (1982) found that pigeons' classification of letters of the alphabet resembles that of humans. Specifically, letters such as U and V that confuse humans also confuse pigeons. Therefore, both pigeons and humans might be using the same geometric features as cues during stimulus recognition.

Similarities between pigeons and humans in classifying visual stimuli have also been observed for colour photographs. Pigeons can learn to discriminate photographs based on the presence of humans, trees, or water (Herrnstein, Loveland, & Cable, 1976). Furthermore, Wasserman, Kiedinger and Bhatt (1988, Experiment 2) showed that pigeons can classify photographs according to the concept categories of cats, flowers, cars, and chairs. In their experiment, 80 slides were categorised by two groups of pigeons. Those in the category group were rewarded for classifying the stimuli based on their concept categories, whereas those in the pseudocategory group were rewarded for classifying them based on four arbitrary categories, each containing an equal number of stimuli from the four concept categories. Because the only way for the birds in the pseudocategory group to solve the task was to memorise the stimuli in each category, any performance advantage for the category group would have indicated generalisation occurring within the concept categories. The authors found that the performance of the category group increased more rapidly than the pseudocategory group and concluded that pigeons saw a resemblance among stimuli that belong to the same concept category.

The current study investigated whether pigeons perceive resemblances among visual stimuli that share topological features. To overcome the difficulty of preparing two stimuli that differ only in the topological feature, generalisation across a variety of stimuli was studied by requiring pigeons to categorise relatively large sets of stimuli. Using the same approach as Wasserman et al. (1988), the subjects were divided into topology and pseudocategory groups and their performance was compared as the sessions progressed. The pigeons in the topology group were required to classify stimuli based on their topological categories (one-hole or no-hole) and the pigeons in the pseudocategory group were required to classify stimuli based on pre-determined arbitrary categories, each containing equal numbers of one-hole and no-hole stimuli. If pigeons find any perceptual similarities among stimuli that share a topological feature, correct classification should be learned faster in the topology group than in the pseudocategory group.

2. Methods

2.1. Subjects

The subjects were six homing pigeons (*Columba livia*), divided equally into two conditional groups (topology group: FDO, HNA, BKL; pseudocategory group: PLT, STB, BEC). They were housed in individual cages in a room with a window that allowed natural sunlight to enter. The pigeons had free access to water and grit and were maintained at 85% of their free-feeding weights for the duration of the experiment. This experiment was approved by the Animal Care and Use Committee of Chiba University and was conducted according to the Guidelines for Animal Research of Chiba University. All of the birds had previous experience with behavioural experiments in operant chambers but were naïve to tasks involving stimulus discrimination.

2.2. Apparatus

Three operant chambers (approximately 30 × 35 × 35 cm) were used, one for one bird from each group. A 15-inch Acoustic Pulse Recognition touchscreen monitor (ET1529L-AUJA-1-BG-G, Tyco Electronics, Kanagawa) with the resolution of 1024 × 768 pixels and a refresh rate of 60 Hz was attached to the exterior of each chamber and the birds could view the stimuli and respond via an opening on the chamber wall (approximately 16 × 10 cm). The feeder was located beneath the opening and the feeder light was turned on whenever food became accessible. A houselight illuminated the chamber during the intertrial intervals (ITI).

2.3. Stimuli

The sample stimuli to be categorised consisted of 80 white shapes (see Fig. 1), each adjusted to fit into 100 × 100 pixel square (estimated visual angle: 15.9 × 15.9° at a viewing distance was 10 cm), and they were displayed individually on a black background. These shapes were created to provide a variation in features (e.g., in terms of the symmetricity and whether edges were composed of straight or curved lines). For the topology group, the shapes were divided into Category A or Category B based on the topological feature of the stimuli. Category A contained 40 shapes without any holes, whereas Category B contained the remaining 40 shapes with one hole, which appeared as a black area inside the shape. The classification of the stimuli in the pseudocategory group was arbitrary, and each category contained 20 shapes with one hole and 20 shapes without any holes. Red (100, 0, 0) and green (0, 100, 0) 80 × 80 pixel squares were used as comparison stimuli to indicate the category choice of the subjects.

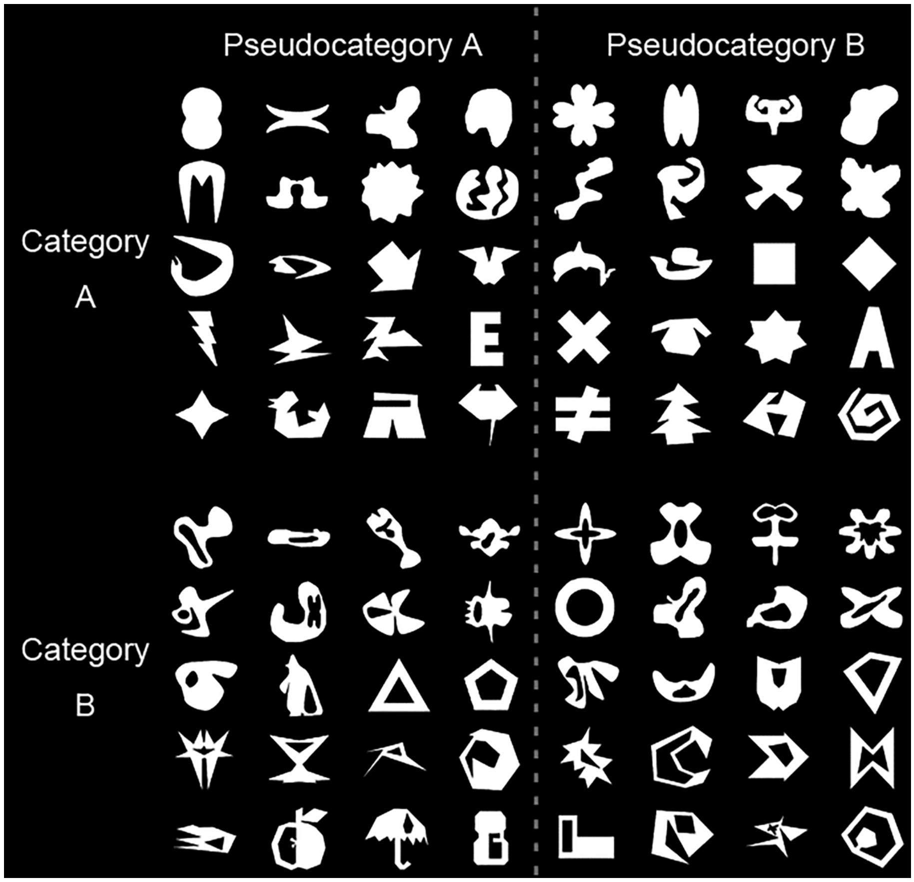

Fig. 1. The 80 shape stimuli used in the experiment. Category A contained shapes without holes and Category B contained shapes with one hole. Pseudocategories were decided arbitrarily.

2.4. Procedure

2.4.1. Pretraining

The pigeons were given pretraining trials after they had learned to eat from the feeder. One of the two comparison stimuli were presented in each pretraining trial, such that the red stimulus appeared on the left side of the display and the green stimulus on the right for all subjects. Responding to the available comparison stimulus always resulted in 3-second food delivery. An ITI of 3 s was included after the subjects completed a session with 30 trials. The subjects moved on to the test trials after they completed one session of 30 trials with the ITI.

2.4.2. Test

Each test trial began with the presentation of a sample stimulus in the middle of the display to which the subject was required to respond. The number of pecks required on the sample stimulus was increased from one to three pecks after about five sessions, and to five pecks after about ten sessions. After making the required number of pecks to the sample stimulus, red and green comparison stimuli appeared respectively on the left and the right side of the sample stimulus. A response to either comparison stimulus cleared the display and resulted in 3-second food delivery if the choice was correct, or 3-second blackout if the choice was incorrect, before commencing the 3-second ITI. The correct choices for subjects in both groups were red for Category A shapes and green for Category B shapes (note that categorisation of the shapes differed for the two subject groups; see the stimuli section above). Incorrect choices were followed by correction trials in which the same sample was presented repeatedly until the subject categorised it correctly. Correction trials were omitted from later analysis. Each session consisted of 80 trials, one trial for each of the 80 sample shapes, presented in pseudo-random order according to the Gellermann (1933) series. All subjects completed 40 sessions.

3. Results and discussion

Firstly, to compare the learning rates of the two groups, 40 sessions were divided into 10 blocks, each consisting of four sessions, and the percentage of correct choices were calculated for each block. The average performance of the topology and pseudocategory groups over the 10 blocks of sessions are shown in Fig. 2. The topology group showed a rapid improvement in performance over the first three blocks and reached a maximum performance of 76.9% by Block 9. In contrast, only a slight improvement was observed in the performance scores of the pseudocateogry group, which remained for the most part between 45 and 55%. Correct categorisation was possible in the pseudocategory group only by memorising the category to which each stimulus belonged. Therefore, the performance advantage of the topology group suggests the use of additional stimulus cues for categorisation.

To further explore the performance of the two groups, we created a linear mixed effects model using group (topology or pseudocategory), block (1–10), and their interaction as fixed factors and the bird's identity (6 subjects) as a random factor. The effects were significant for group ($F_{1,4} = 60.249$, $p = .002$), block ($F_{1,52} = 77.318$, $p < .001$), and the group-block interaction ($F_{1,52} = 19.504$, $p < .001$), which confirmed that the difference in performance between the two groups was due to different learning rates over the 10 blocks.

Stimuli with high and low performances in the topology group are shown in Fig. 3. The stimuli with the best performance in each category were discriminated well by all three birds, with individual accuracies of above 75%. This observation suggests that these stimuli contain some

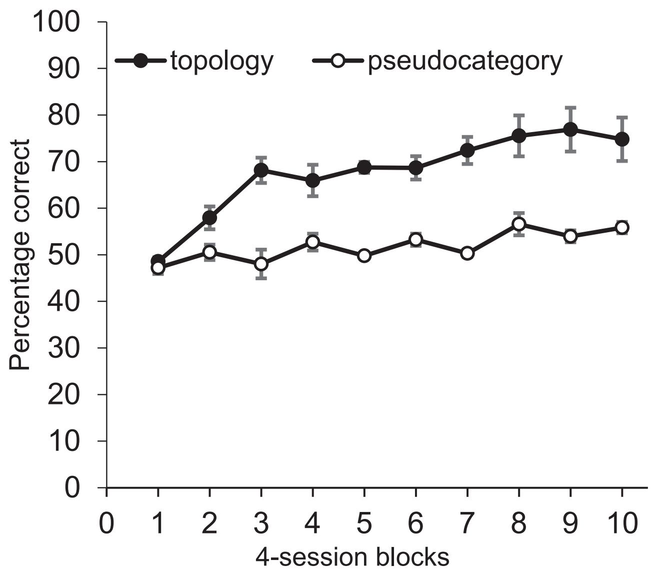

Fig. 2. Percentage of correct trials for topology (n = 3) and pseudocategory (n = 3) groups over 10 blocks of sessions. Error bars represent standard error of the mean.

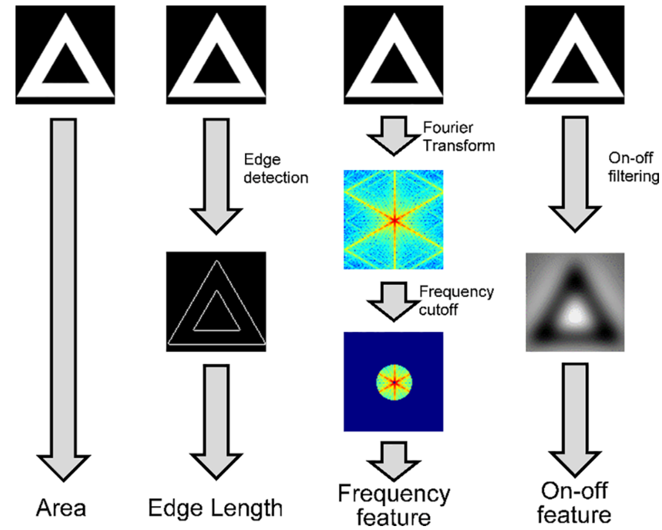

Fig. 4. Examples of four types of image features.

features that make them easy to categorise and that all three birds were using similar strategies to solve the task. The possibility of a shared strategy is also supported by similar learning curves of the birds over the sessions, as indicated by the small error bars on Fig. 2.

The improvement in performance indicates that the birds in the topology group successfully learned the correct categorisation of the stimuli. Then, we examined the stimuli features that the birds in the topology group were using as cues for categorisation by calculating the four types of image features for each of the 80 stimuli: (1) the area, (2) the edge length, (3) the frequency feature value, and (4) the on-off feature value. Fig. 4 shows examples of the image features for a hollow triangular stimulus. The area (Fig. 4a) was calculated from the total number of white pixels in the stimulus. For calculating the edge length (Fig. 4b), edge components of the stimulus were obtained using the Canny edge detector (Canny, 1986), and the total number of white pixels in the edge image was counted. The frequency feature value (Fig. 4c) was achieved by manipulating a stimulus image in the frequency domain. The visual systems of birds have band-pass characteristics in the frequency domain (Ghim & Hodos, 2006). Therefore, it could be assumed that specific frequency bands influenced topology recognition. First, the frequency components of a stimulus were computed to calculate the frequency feature value. Then, we set minimum and maximum cutoff frequencies for extracting specific frequency components by using the most appropriate settings based on the linear fit to the results of topological categorisation as minimum and maximum cutoff frequencies. Finally, the amount of specific frequency components was calculated. The fourth image feature was the on-off feature value (Fig. 4d). Visual systems in the early stage include on-off (centre-surround) mechanisms and we assumed that such on-off visual characteristics were useful for the topology recognition. The DOG (difference of Gaussian) filter (Itti & Koch, 2000) was applied to each stimulus. Similar to the frequency feature value, we used the most appropriate filter sizes based on linear fitting to the topological categorisation. Thus, we employed the sum of filtered image values as the on-off feature values.

We used generalised linear mixed models fit to Laplace approximation with binomial distribution and a logit link function to investigate factors that were associated with the choice of topological Category A (no-hole shapes) in each two-block phase. The bird's identity was included as a random factor in all models. We compared the Akaike information criterion (AIC) from all possible models developed with combinations of the area, the edge length, the frequency feature value, the on-off feature value, and the stimulus category as factors. A smaller AIC value indicates that the model is better at predicting the data. As summarised in Table 1, the model with the lowest AIC value for blocks 1–2 contained the area and the edge length. For all other later phases (blocks 3–4 to 9–10), the best model included the area, the edge length, the on-off feature value, and the stimulus category. These results show the birds were likely to be using the area and the edge length of the stimuli as cues for categorising them at the very beginning of the experiment but, as the sessions progressed, they began using the on-off features and the stimulus category as well. Use of the on-off features and the category in later phases is further supported by the AIC of

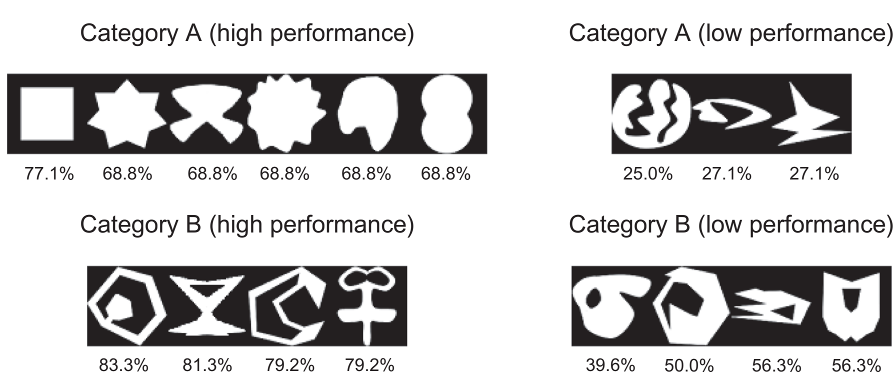

Fig. 3. Hole and no-hole stimuli with highest and lowest average performances for the topology group. Group averages are shown below each stimulus.

Table 1
List of AIC values for models that predicted birds' choice of Category A for the topology group. Asterisks indicate models with minimum AIC value in each two-block phase. Superscripted S letters indicate the single-factor models with a minimum AIC value in each phase.

	Blocks				
Factors in model	1-2	3-4	5-6	7-8	9-10
area, edge, frequency, on-off, category	2584.3	2242.3	2055.0	1787.8	1838.0
area, edge, frequency, on-off	2582.5	2261.9	2064.8	1821.9	1879.2
area, edge, frequency, category	2582.5	2253.1	2062.2	1790.9	1842.6
area, edge, on-off, category	2583.4	2241.9*	2054.1*	1786.2*	1836.3*
area, frequency, on-off, category	2590.3	2258.7	2103.2	1841.6	1895.1
edge, frequency, on-off, category	2583.8	2258.8	2084.9	1824.6	1864.3
area, edge, frequency	2580.7	2274.3	2074.3	1827.1	1885.3
area, edge, on-off	2581.5	2260.0	2062.8	1820.7	1880.5
area, edge, category	2581.7	2252.0	2060.8	1789.1	1841.0
area, frequency, on-off	2588.6	2288.6	2123.5	1879.9	1938.4
area, frequency, category	2592.6	2285.7	2128.8	1861.7	1917.5
area, on-off, category	2590.2	2257.2	2101.2	1839.7	1894.2
edge, frequency, on-off	2581.9	2277.9	2093.5	1849.2	1898.9
edge, frequency, category	2585.1	2307.5	2133.7	1866.2	1907.3
edge, on-off, category	2583.0	2257.9	2083.3	1822.6	1862.6
frequency, on-off, category	2588.3	2262.5	2105.1	1844.4	1894.3
area, edge	2579.7*	2272.4	2072.3	1826.4	1887.6
area, frequency	2592.8	2329.1	2162.7	1913.5	1973.3
area, on-off	2589.0	2287.2	2122.9	1881.8	1942.3
area, category	2593.3	2283.7	2127.2	1860.5	1917.8
edge, frequency	2583.2	2333.9	2151.0	1897.8	1946.9
edge, on-off	2581.0	2275.9	2091.5	1848.1	1899.8
edge, category	2585.0	2305.5	2131.8	1864.5	1906.8
frequency, on-off	2586.6	2289.5	2123.5	1879.5	1936.6
frequency, category	2592.6	2315.7	2154.6	1887.3	1935.8
on-off, category	2588.2	2261.1	2103.1	1842.5	1893.3
area	2598.0	2331.4	2166.8	1920.5	1983.0
edge	2583.4S	2333.4	2151.1	1899.4	1951.4
frequency	2596.1	2358.8	2190.1	1938.1	1993.3
on-off	2587.0	2288.0 S	2122.7 S	1881.0 S	1940.4
category	2595.7	2313.8	2153.4	1886.5	1936.6 S
null	2600.7	2363.3	2196.4	1946.8	2005.0

models that contained a single factor. There were small differences between one-factor models during Blocks 1–2, but from Blocks 3–4, AIC for the on-off factor model showed a sudden decrease. In other words, the on-off factor was the best single factor that explained the pigeons' behaviour from Blocks 3–4 to 7–8. In the final phase, in Blocks 9–10, the smallest AIC is seen in the category factor model. To summarise, the birds' categorisation was initially based on the area, and the edge, followed by on-off features, which finally led to the successful discrimination of topological categories.

As pointed out by Chen et al. (2003), the nature of topology makes it impossible to create two geometrically-equivalent stimuli that differ only in topological features. In fact, our stimuli in the two topological categories differed in area (Welch's *t*-test: $t(74.04) = 2.49$, $p = 0.02$) and edge length (Welch's *t*-test: $t(76.17) = 5.29$, $p < 0.001$) and it is possible that the birds were using these features as cues for categorisation, especially early in training. However, it can be seen in the detailed analysis above that this explanation is insufficient for describing responses in the later phases of the experiment. Another possible feature the birds may have been using for discrimination is the colour found in the centre of stimuli. Category B contained more stimuli with black centre (20/40) than category A (4/40). If the birds were using centre colour as a cue for correct categorisation, they should perform well in categorising category B stimuli with black centre. This was not the case as three out of the four best categorised category B stimuli had white centres (Fig. 3).

The significant role of the on-off mechanisms in vision has already been illustrated in human literature. Itti and Koch (2000) showed that their simulated model consisting of the on-off mechanism and other bottom-up processes outperformed humans when locating objects in visual scenes. They argued that saliency from the bottom-up processes alone could effectively direct attention during visual search in the absence of top-down processes, which can sometimes bias attentional shifts in unwanted directions. In addition to visual search, it has been suggested that the on-off mechanism is capable of processing perception of surface materials (Motoyoshi et al., 2007). Given our results and that the on-off mechanism can be used for solving various visual tasks in humans, it is likely that pigeons relied on this bottom-up process for categorising stimuli based on topological features. The extent to which additional top-down processes are involved has not been clarified but an explicit understanding of the topological concept is unnecessary for categorisation. In fact, exclusive use of bottom-up processes could enable fast processing as has been previously reported in computational models (Itti & Koch, 2000; Motoyoshi et al., 2007).

Pigeons' ability to distinguish topological features seems to contradict the idea that topological perception relies on global processing. One possible explanation is that although pigeons have local precedence, they use global processing for solving the current task. Another possibility is that topological perception relies on the summation of local processing. In support of the latter explanation, pigeons in this experiment had difficulty in categorising specific no-hole stimuli that had local features suggestive of the presence of a hole (Fig. 3).

We have yet to discover whether topological perception provides functional advantages for birds, for example, in locomotion or feeding, or if it is a by-product of other complex visual processes. In any case, topological perception is shared by vertebrate and invertebrate species, or at least by humans, pigeons, and honey bees, which suggests that it is a fundamental part of the visual system. The current observation that a simple bottom-up process could be the primary mechanism of topological perception further supports previous claims that topological perception is a primitive component of the visual system (Chen, 1982; Chen et al., 2003).

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