

CATEGORIES IN THE PIGEON BRAIN: A REVERSE ENGINEERING APPROACH

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Pigeons are well known for their visual capabilities as well as their ability to categorize visual stimuli at both the basic and superordinate level. We adopt a reverse engineering approach to study categorization learning: Instead of training pigeons on predefined categories, we simply present stimuli and analyze neural output in search of categorical clustering on a solely neural level. We presented artificial stimuli, pictorial and grating stimuli, to pigeons without the need of any differential behavioral responding while recording from the nidopallium frontolaterale (NFL), a higher visual area in the avian brain. The pictorial stimuli differed in color and shape; the gratings differed in spatial frequency and amplitude. We computed representational dissimilarity matrices to reveal categorical clustering based on both neural data and pecking behavior. Based on neural output of the NFL, pictorial and grating stimuli were differentially represented in the brain. Pecking behavior showed a similar pattern, but to a lesser extent. A further subclustering within pictorial stimuli according to color and shape, and within gratings according to frequency and amplitude, was not present. Our study gives proof-of-concept that this reverse engineering approach—namely reading out categorical information from neural data—can be quite helpful in understanding the neural underpinnings of categorization learning.

Key words: categorization, avian brain, NFL, single unit recording, key peck, pigeon

Rochon-Duvigneaud (1943) defined pigeons as animals that are nothing else but two eyes with wings. Indeed, humans have only 40% of the retinal axons of pigeons (Binggeli & Paule, 1969), discern fewer colors (Emmertson & Delius, 1980), and fail to discriminate subtle luminance differences that are easily distinguished by pigeons (Hodos, Bessette, Macko, & Weiss, 1985). Pigeons are also well known for their ability to categorize all kinds of diverse objects like “humans” (Herrnstein & Loveland, 1964; Yamazaki, Aust, Huber, Hausmann, & Güntürkün, 2007), man-made objects (Lubow, 1974), impressionist versus cubist paintings (Watanabe, Sakamoto, & Wakita, 1995), and “good” versus “bad” children’s drawings (Watanabe, 2011). Pigeons are also able to differentially categorize pictures according to 16 different categories in parallel (Wasserman, Brooks, & McMurray, 2015). Moreover, they can solve cognitively challenging same versus

difference tasks (Young & Wasserman, 2001; for a review see Wasserman & Young, 2010). But how do pigeons master these diverse tasks?

The classical way to investigate pigeon’s discrimination abilities is to train them to give distinct behavioral responses to stimulus categories that were previously defined by the experimenter. In the present study, we decided to test a radically different procedure. We employ a reverse engineering approach in which we confront our subjects with various stimuli that do not have to be discriminated. The animals just have to peck on them to obtain food. By simultaneously recording from visual forebrain neurons, we plan to deduce the inherent order of visual objects in the pigeon’s brain.

To our knowledge, Kriegeskorte et al. (2008) were the first to deploy this approach by using a large number of images depicting real-world objects; these images were shown to both human and nonhuman primates and neural responses were measured in the inferior temporal cortex (IT) using fMRI and single cell recording, respectively. Depicting the differences between activities elicited by stimuli, representational dissimilarity matrices (RDM) revealed segregation between the semantic categories of animate and inanimate objects (Kriegeskorte et al., 2008). Hence, categorical

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information is represented on a neural level in humans' and monkeys' IT—even without the need to perform a behavioral categorization task. The possibility of using such a method is not restricted to the visual association cortices, but can also be applied to frontal areas for an analysis of segregation of eye movement direction clusters (Kiani *et al.*, 2015).

The present study is the first to use a similar approach in pigeons. At the brain level, we decided to target the nidopallium frontolaterale (NFL), a higher visual area within the pigeon's visual system where the tectum and the thalamofugal visual pathways come together (Husband & Shimizu, 1999; Shanahan, Bingman, Shimizu, Wild, & Güntürkün, 2013; Shimizu, Cox, & Karten, 1995). An overview of the visual pathways in the pigeon brain, including the position of the NFL, is illustrated in Figure 1.

Thus, the present study explores the hypothesis that neurons of the NFL distinguish between different categories of visual stimuli without any task-dependent need of discrimination. As our experiment is the first of its kind in birds, we decided to use artificial stimuli of

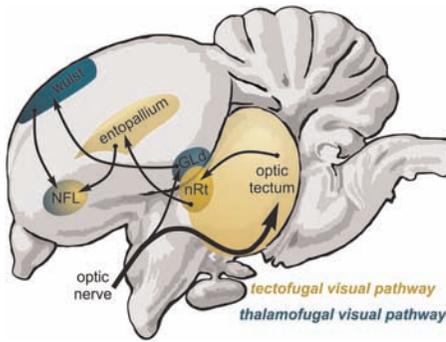


Fig. 1. Visual pathways in the pigeon brain. Avian tectum (yellow) and thalamofugal pathways (blue) are homologous to the mammalian extrageniculocortical and geniculocortical pathways, respectively. Avian and mammalian systems, however, differ at the functional level. The avian tectofugal pathway is mainly responsible for both object and motion vision in the frontal visual field. Information travels from the eye to the optic tectum, the nucleus rotundus (nRt) in the thalamus, the entopallium in the telencephalon (primary visual area), and then to multiple higher visual areas of which our targeted area, the nidopallium frontolaterale (NFL), is shown. The thalamofugal pathway is mainly directed towards the lateral field of view. Information travels from the eye to the nucleus geniculatus lateralis, pars dorsalis (GLd) in the thalamus, to the visual wulst in the telencephalon (primary visual area) and then to the NFL.

low visual complexity to see whether we can find such clustering of NFL activity that reflects categorical structures. These artificial stimuli consist of pictorial stimuli differing in color and shape (see Fig. 2A) as well as gratings differing in spatial frequency and amplitude (see Fig. 2B)

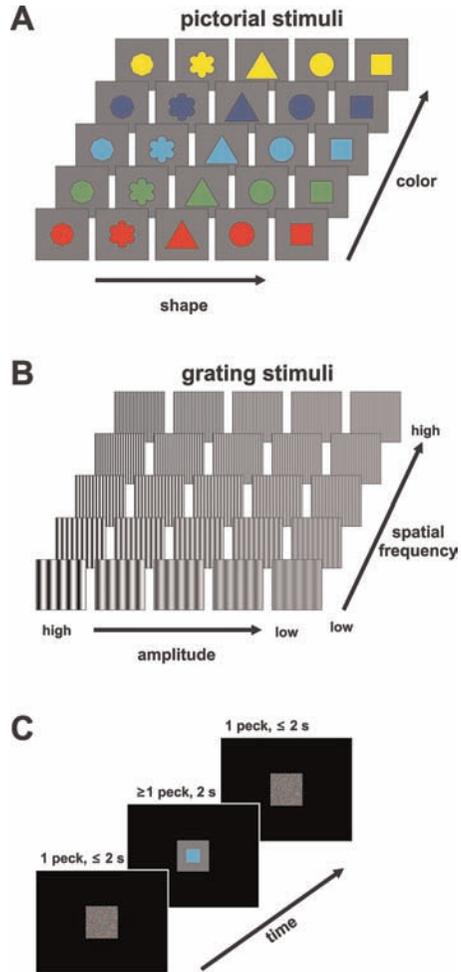


Fig. 2. Stimuli and behavioral paradigm. (A) All 25 pictorial stimuli used. Stimuli differ according to color (blue, yellow, green, red, turquoise) and shape (octagon, stylized flower, triangle, circle, square; same surface area). (B) All 25 grating stimuli used. Stimuli differ according to spatial frequency (0.11, 0.23, 0.34, 0.46, 0.58 cpd) and amplitude (0.2, 0.4, 0.6, 0.8, 1.0). (C) Sequence of one trial. The initialization key was visible for up to 2 s and disappeared if pecked once. After a 0.2 s delay, one of 50 sample stimuli (pictorial or grating stimuli) was shown for a fixed interval of 2 s and had to be pecked at least once. After another 0.2 s delay, the initialization key was presented again for up to 2 s and had to be pecked once. After pecking at all three stimuli, a food reward was delivered and the intertrial interval (6 s) followed.

to cover a broad set of properties within these types of simple stimuli. Using these simple stimuli, we aim to unravel basic principles of neural coding.

Method

Subjects

The subjects were three adult homing pigeons (*Columba livia*) obtained from local breeders that had previously participated in unrelated experiments. They were housed in individual wire-mesh cages with a 12 to 12 light-dark cycle beginning at 08.00 hr. They were food-deprived and maintained at 80-90% of their free-feeding body weight and fed with a mixture of different grains. The subjects were kept and treated in accordance with the National Institute of Health Guide for Care for Laboratory Animals and the national authorities of North-Rhine Westphalia, Germany, approved the experiment.

Apparatus and Stimuli

The experiment was conducted in a custom-built operant chamber (35 × 35 × 35 cm) with three horizontally aligned pecking keys (4 × 4 cm, 17 cm above the floor) and a centrally located food hopper that delivered a food reward upon responding. Only the center pecking key was used in this experiment. An LCD flat screen monitor was mounted behind the pecking keys to present the stimuli. The stimuli consisted of 50 artificial images, 25 pictorial stimuli of colored geometric shapes (see Fig. 2A) and 25 grating stimuli (see Fig. 2B). The shapes used were an octagon, a stylized flower, a triangle, a circle, and a square of the same surface, each colored in blue, yellow, green, red, and turquoise (RGB color space). The gratings were modulated in frequency and amplitude. Five different spatial frequencies (0.11, 0.23, 0.34, 0.46, and 0.58 cycles per degree, cpd) were each paired with five different amplitudes (0.2, 0.4, 0.6, 0.8, and 1.0). The overall grayscale value was equal for all grating stimuli.

Behavioral Task

Pigeons were tested once a day. Stimuli were shown in ten consecutive blocks, each consisting of a single presentation of every stimulus in the entire set. The stimuli within each block

were randomized prior to each session, such that each session consisted of 500 trials and each stimulus was presented 10 times. A schematic drawing of the behavioral task is depicted in Figure 2C. Each trial began with an initialization key that was visible for 2 s and which disappeared when pecked once. After a 0.2 s delay, one sample stimulus was presented for a fixed interval of 2 s. The pigeon had to peck at the stimulus at least once. After another 0.2 s delay, the initialization key was again presented for 2 s and disappeared when pecked once. Only if the pigeon had pecked at all three stimuli, 2 s access to food accompanied by turning on the feeding light followed. Food reinforcers were delivered with a probability of 55–70%, adjusted in accord with the weight and performance level of the pigeon. After non-reinforced trials, the feeding light was turned on as a conditioned reinforcer. After the reinforcer period, a 6 s intertrial interval (ITI) followed before the next trial started. If the pigeon failed to peck at either one of the initialization keys or the actual stimulus, then the trial was aborted and the ITI followed. Custom-written Matlab (MathWorks, Natick, MA, USA) code (Rose, Otto, & Dittrich, 2008) controlled all experimental hardware.

Surgery

After training on the task, pigeons were implanted with custom-built microdrives (Bilkey & Muir, 1999; Bilkey, Russell, & Colombo, 2003; Starosta, Güntürkün, & Stüttgen, 2013; Starosta, Stüttgen, & Güntürkün, 2014) with seven electrodes made of 25 μm formvar coated nichrome wires (Science Products GmbH, Hofheim, Germany) and one additional 76 μm heavy polyimide coated stainless steel wire serving as reference (francoCorradi, Milano, Italy) that were connected to microconnectors (Omnetics Connector Corporation, Minneapolis, USA). All pigeons were implanted with one microdrive each in both the right and left hemisphere of the brain. Pigeons were initially anesthetized with a mixture of ketamine and xylazine 7:3 with 0.075 ml per 100 g body weight. Anesthesia was maintained with isoflurane during the whole procedure. Feathers on the scalp and overlaying the ears were cut and the animals were placed in a stereotaxic apparatus. The scalp was cut and retracted to expose the skull. Six stainless steel screws (Small Parts, Logansports, USA) were

placed into the skull to hold the implant. A hole was drilled above the NFL at AP +12 and ML \pm 6 (Karten & Hodos, 1967). The tips of the electrodes were then lowered into the brain to position them above the NFL. An additional hole in the skull was made to insert a 200 μ m teflon coated silver wire (Science Products GmbH, Hofheim, Germany) with its tip melted to a ball that served as ground for electrophysiological recordings. Dental acrylic was used to attach the microdrives to the skull. The incision was sutured and covered with antibiotic ointment. The birds were returned to the home cage when fully alert and mobile. The pigeons received analgesics (Carprofen, 10 mg/kg) for 3 days. They were allowed to recover with unlimited access to food for at least 7 days before recording sessions started.

Neural Recording

We recorded from both hemispheres in the three birds. In every session, we stored the output of eight electrodes, one serving as reference. Signals were fed through a miniature preamplifier (10x), then amplified 1,000x and filtered online (300 Hz high-pass filter, 5 kHz low-pass filter; Multi Channel Systems MCS GmbH, Reutlingen, Germany), and digitized using an analog-to-digital converter (Micro 1401 mkII, Cambridge Electronic Design, Cambridge, UK). Neural activity was recorded with Spike2 Version 7.06a (Cambridge Electronic Design, Cambridge, UK). Spike sorting was conducted offline using amplitude thresholds for initial spike detection and principal component analysis for manual sorting. Sorting quality was examined with custom-written Matlab code. We adopted a conservative approach to classify neural activity as originated from 'single units'. Single units had to show a clearly distinguishable cluster in principal component space, show no sign of overlapping multiple units in the waveform overlay and density plots, show a symmetrical, unimodal distribution of peak waveform amplitudes without evidence of false negative classifications, have interspike intervals larger than 1 ms, and a signal-to-noise ratio of at least 2. The signal-to-noise ratio was calculated as the difference between the maximum and minimum of the averaged waveform, divided by the central 95% range in the noise distribution. Additionally, we visually checked for movement related artifacts (e.g., from wing

flapping and key pecking) and by inspecting peri-peck time histograms for peaks of spiking activity near time point 0. Materials, recording, and spike sorting procedure have been described in greater detail by Starosta *et al.* (2013, 2014).

Data Analysis

To analyze our data, we used custom-written Matlab code. For each pigeon, we constructed a set of response vectors assigned to each stimulus, where the entries represented the activity of one recorded cell. The activity was calculated as the average number of spikes within the 2s window of each particular stimulus presentation based on all completed presentations of this stimulus within a session. To account for different firing rates of cells, the results were taken after vector normalization across all activity measurements for one cell. Based on these vectors, an individual RDM matrix was separately computed for each pigeon, and finally averaged across all pigeons.

The RDM (Figs. 4A and 5) shows the percentiles of $1-r_s$, where r_s is the pairwise Spearman's rank correlation coefficient of the response vectors. Figure 3 explains the rationale behind the RDMs. In the RDM, neural output to each stimulus is correlated with every other stimulus. The diagonal depicts comparison of each stimulus with itself, resulting in the absence of dissimilarity (i.e., total similarity, black color). Across the diagonal, the RDM is mirrored. Looking only at the space below the diagonal, the upper left triangle depicts comparison within the pictorial stimulus set. The lower right triangle depicts comparison within the grating stimulus set. Within the stimulus sets, lower dissimilarity (i.e., higher similarity) is indicated by darker shades of gray. The lower left rectangle depicts the comparison between both stimulus sets. Here, higher dissimilarity (i.e., lower similarity) is indicated by lighter shades of gray (Fig. 3).

We used bootstrap resampling of the stimulus set to answer the question whether significant pairwise similarity level differences occur among the three groups: (a) similarities of items within the pictorial stimulus set, (b) within the grating stimulus set, and (c) comparisons of stimuli between both sets (cf. Fig. 3). This simulates the expected distribution of the mean of dissimilarity measures by repeated sampling from the observed data.

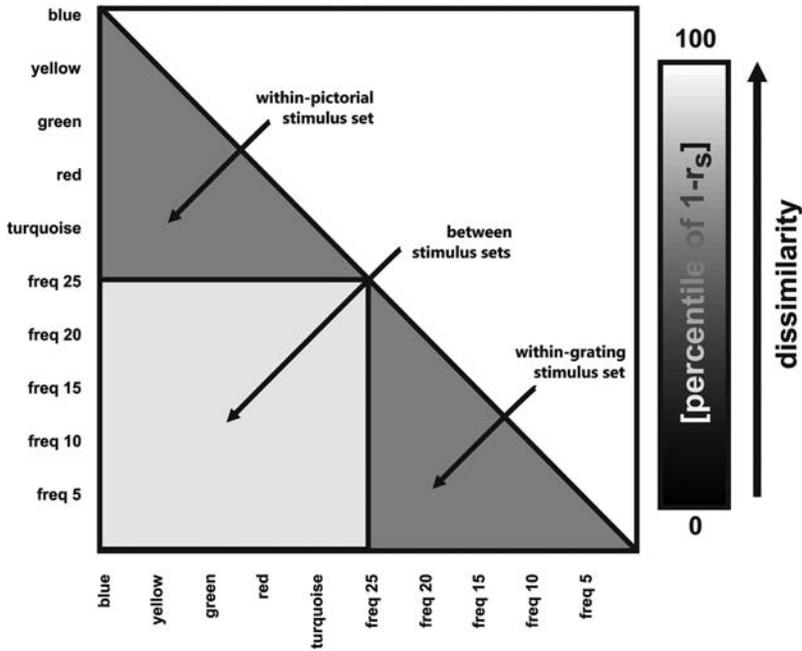


Fig. 3. Explanation of representational dissimilarity matrices. The diagonal depicts comparison of each stimulus with itself, resulting in the absence of dissimilarity, that is, total similarity (black color). Across the diagonal, the RDM is mirrored. Looking only at the space below the diagonal, the upper left triangle depicts comparison within the pictorial stimulus set. The lower right triangle depicts comparison within the grating stimulus set. Within stimulus sets, lower dissimilarity, that is, higher similarity, is indicated by dark gray color coding. The lower left rectangle depicts comparison between both stimulus sets. Here, we indicate higher dissimilarity, that is, lower similarity (light gray).

We performed 1,000 iterations for each group, each time sampling n data points from the observed n data points under the diagonal of the percentile matrix in each group. Mean and variance were calculated on the basis of the obtained samples for each group, respectively. Our test statistic was the mean of percentile points within each of the three groups, computed solely on the corresponding values under the diagonal. As the bootstrap test is optimistic in estimating differences, we set our parameters to conservative values ($p < .001$, 1000 iterations). Additionally, our pairwise correlations ($1-r_s$) were used as distance measurements to perform classical multidimensional scaling to visualize our results in two-dimensional space.

We produced three generalized linear model regressions (GLM) to separately test the predictive capability of the categories pictorial and grating, shape and color, as well as frequency and amplitude on our dissimilarity measures ($1-r_s$), and thus the pigeons' categorical representations. For the first GLM, a vector

was computed using all dissimilarity measures under the diagonal as a dependent variable. As an independent variable we computed a binary prediction vector depicting the value 1 within-pictorial and within-grating stimulus sets and the value 0 between both sets. Doing so, we can answer the questions whether dissimilarity measures differ within stimulus sets and between stimulus sets. For the second GLM, only dissimilarity measures within the pictorial stimuli were examined. A binary prediction vector was computed with the value 1 for same color and the value 0 for different color as well as a prediction vector with the value 1 for same shape and the value 0 for different shape. In doing so, we can examine what predictive capability the properties color and shape have on categorical representation. For the third GLM, only dissimilarity measures within the grating stimuli were examined. Here, two binary prediction vectors coded for frequency and amplitude to examine what predictive capability these properties have on the pigeons' categorical representations.

Moreover, we undertook the same steps to analyze stimulus similarities based on the number of pecks in the 2 s window of stimulus presentation. Note that pigeons were required to peck at least once at the stimulus during this time for it to be counted as a valid trial and to be analyzed, but they pecked an average of 7.95 times (standard deviation = 2.84) in this time period.

Results

We recorded from a total of 33 single units from five hemispheres in three birds (3 from the left and 7 from the right hemisphere of the first bird, 10 from the right hemisphere of the second bird with no suitable units from the left hemisphere, and 7 from the right and 6 from the left hemisphere of the third bird). The cells fired at a mean of 4.93 Hz, ranging from 0.3 to 28.4 Hz.

Figure 4A shows the RDM consisting of all pairwise dissimilarity values (percentile of $1-r_s$; dark gray represents low, light gray represents high dissimilarity) based on the neural responses. Along the diagonal, the neural activity pattern of each stimulus is compared to itself, resulting in total similarity (black). In Figure 4A,

pictorial stimuli are arranged according to color. Hence, the first five lines represent the five blue pictorial stimuli, etc. Grating stimuli are arranged according to spatial frequency. Figure 5 shows the same RDM, but arranged according to shape and amplitude. Note that this is only a difference in presentation, the content is the same. Figure 4B shows the average percentile points with the standard deviation revealed from the bootstrap resampling for the within-pictorial stimulus set, the within-grating stimulus set, and between both sets (cf. Fig. 3). All between-group differences are significant ($p < .001$) according to the conducted bootstrapping test. It can be seen that the dissimilarity within the pictorial stimuli is lowest, followed by the dissimilarity within the gratings, which are both far below the overall dissimilarity value between both sets. Thus, even about 30 neurons are sufficient to reveal a differential representation of pictorial stimuli and gratings in the pigeon brain.

The first GLM revealed a significant influence of stimulus set (pictorial and grating) on categorical representation (i.e., dissimilarity measures: $\beta = -14.19$, $t = -9.25$, $p < .001$). The second GLM showed no influence of either color ($\beta = 0.98$, $t = 0.23$, $p = .82$) or shape ($\beta = 3.80$, $t = 0.86$, $p = .39$) on categorical

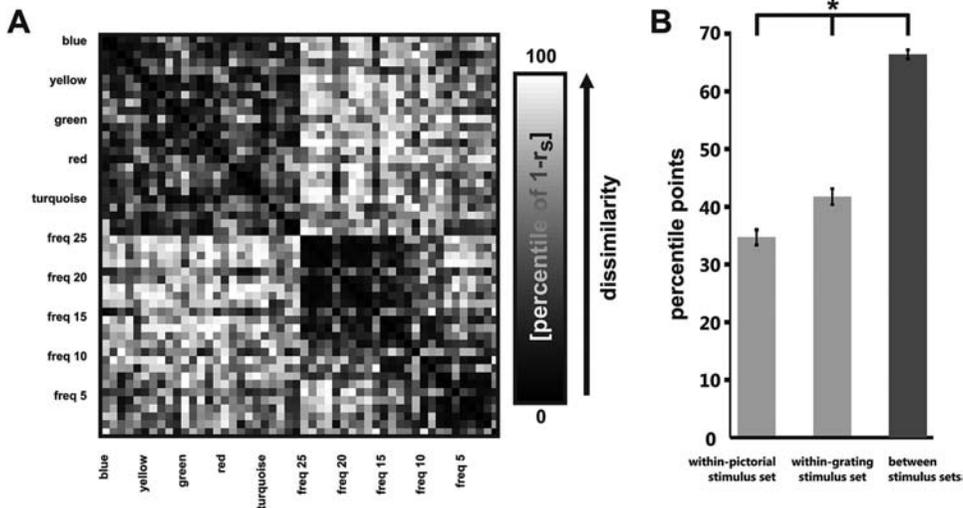


Fig. 4. (A) Representational dissimilarity matrix. For each pair of stimuli, the gray value codes dissimilarity of the response patterns in the pigeons' NFL (dark gray: low dissimilarity, light gray: high dissimilarity). Dissimilarity is measured in percentile of $1-r_s$ (Spearman's rank correlation coefficient). Note that in the diagonal, the neural activity pattern of each stimulus is compared to itself, resulting in total similarity. Thirty-three single units from five hemispheres of three pigeons were recorded. The pictorial stimuli are arranged by color, the grating stimuli are arranged by frequency. (B) Average percentile points within-pictorial stimulus set, within-grating stimulus set, and between both sets. Error bars show standard deviation from bootstrap resampling. All group differences are significant with $p < .001$.

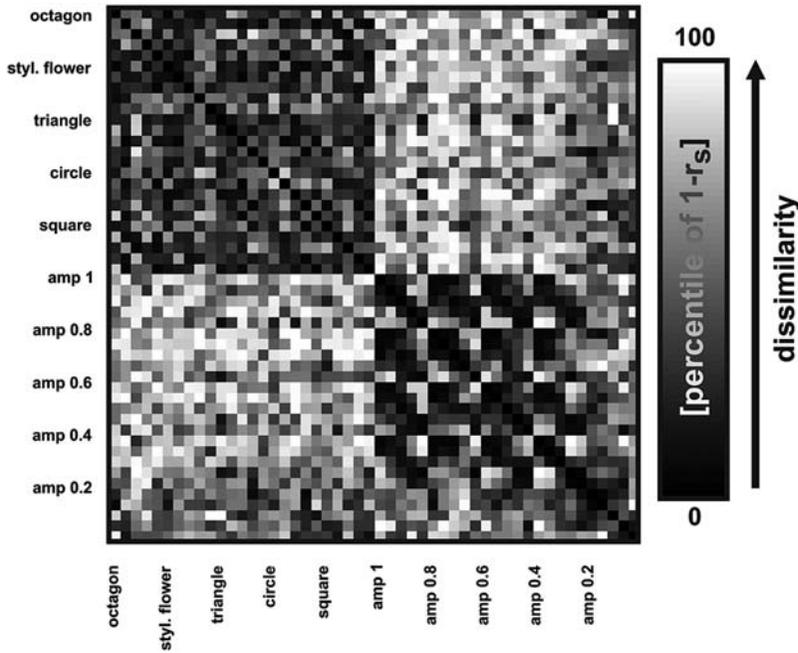


Fig. 5. As in Figure 3A, but pictorial stimuli are arranged by shape, the grating stimuli are arranged by amplitude.

representation within pictorial stimuli. The third GLM revealed no influence of either frequency ($\beta = -3.32$, $t = -0.75$, $p = .45$) or amplitude ($\beta = -1.25$, $t = -0.28$, $p = .78$) on categorical representation of the grating stimuli.

Figure 7A shows multidimensional scaling based on spikes. Each stimulus is depicted as a small picture in the two-dimensional distance space. As there was less dissimilarity within the pictorial stimulus set than within the grating stimulus set (cf. Fig. 4B), we see that the pictorial stimuli cluster more tightly together in this plot than the grating stimuli.

As explained above for the neural data, the behavioral data (pecking responses) can be analyzed in a similar manner. The first bird pecked at each stimulus on average 4.85 times (standard deviation = 0.19), the second bird 11.66 times (standard deviation = 0.38), and the third bird 7.35 times (standard deviation = 0.19) in the 2 s time window. Figure 6A shows the RDM of pecking activity averaged across all birds. Figure 6B shows percentile points within the pictorial stimulus set, within the grating stimulus set, and between both sets. Percentile points within the pictorial stimulus set are significantly different than between both sets. Percentile

points within the grating stimulus set also differs significantly from between both sets (all $p < .001$). Percentile points within the pictorial stimulus set do not differ significantly from within the grating stimulus set ($p = .18$). Figure 7B shows multidimensional scaling based on pecks. Each stimulus is depicted as a small picture in the two-dimensional distance space. As is already apparent in Figure 6, there is no clear sub-clustering according to stimulus dimensions.

Discussion

In the current study, we documented categorical object representation in a visual association area of the avian brain. Categories were deduced from the spike trains of the recorded neurons without conditioning the birds to discriminate one predefined group of stimuli from another. Our data reveal that, in the NFL, pictorial stimuli were differently represented from gratings. Neither pictorial nor grating stimuli revealed sub-clustering according to color or shape, or frequency or amplitude, respectively. We conducted a similar analysis with the number of pecks to the stimuli in the 2 s time window of stimulus presentation as a behavioral marker.

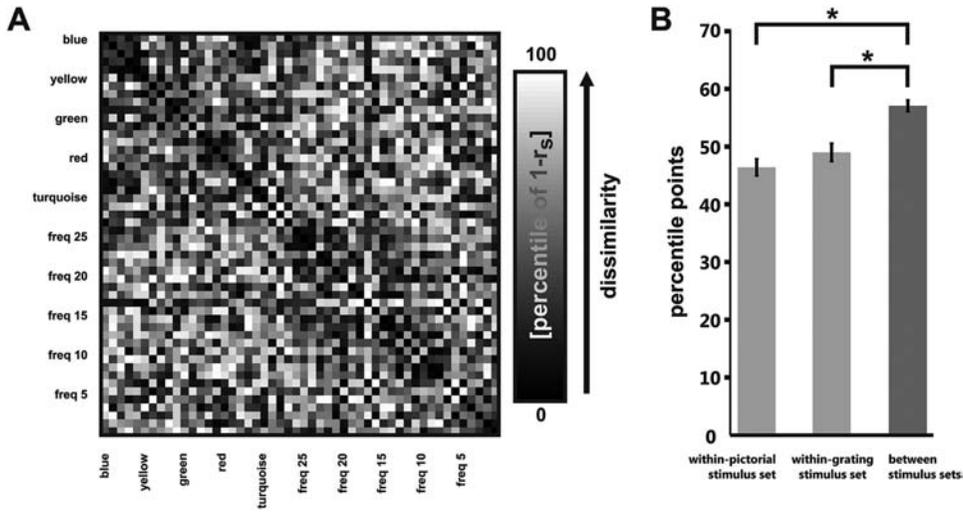


Fig. 6. (A) RDM based on pecking data. For each pair of stimuli, the gray value codes dissimilarity of the pigeons' pecking behavior (dark gray: low dissimilarity, light gray: high dissimilarity). Dissimilarity is measured in percentile of $1-r_s$ (Spearman's rank correlation coefficient). Data is based on 21 recording sessions. (B) Average percentile points within-pictorial stimulus set, within-grating stimulus set and between both sets. Error bars show standard deviation from bootstrap resampling. Both the within-pictorial and the within-grating stimulus sets are significantly different from between both sets ($p < .001$).

This analysis revealed similar, but less differentiated categorical clustering.

Thus, reverse engineering of categorization in birds allows us to draw three main conclusions. First, an RDM analysis reveals object categorizations in the pigeon brain that are independent of previous conditioning along these stimulus dimensions. We are able to show categorization at a neuronal level without

forcing a predefined structure with differential reinforcement contingencies. Second, stimulus clustering based on peck or spike frequencies showed overlapping results; yet, even with our small number of recorded neurons, spike frequencies resulted in sharper category borders. This finding shows that categorical clustering is present in a higher visual structure—namely the NFL—that is at least partially

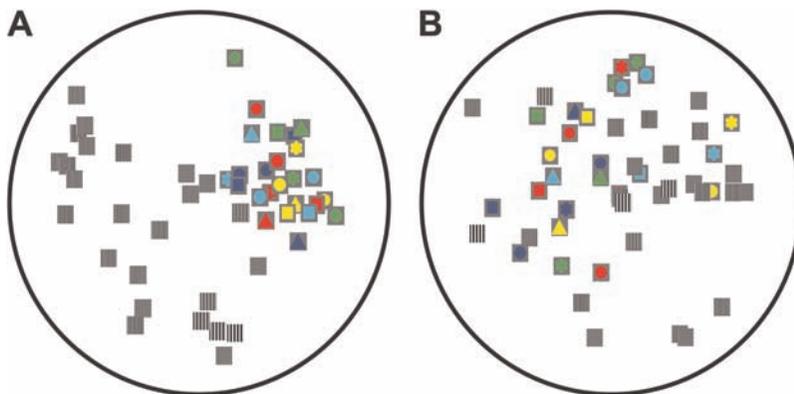


Fig. 7. (A) All 50 stimuli are arranged so that distance reflects similarity of NFL response pattern (multidimensional scaling, dissimilarity $1-r_s$, Spearman's rank correlation coefficient). Stimuli depicted close to each other elicited similar NFL response patterns, stimuli depicted far away from each other elicited dissimilar response patterns. (B) All 50 stimuli are arranged so that distance reflects similarity of pigeons' pecking behavior (multidimensional scaling, dissimilarity $1-r_s$, Spearman's rank correlation coefficient). Stimuli depicted close to each other elicited similar pecking behavior, stimuli depicted far away from each other elicited dissimilar pecking behavior.

independent of the behavioral level. Third, we see this method as a possible new window into the details of categorical representation, regardless of whether novel objects are used, as in our study, or whether conditioned stimuli are employed, as in most category learning experiments. Our approach can be viewed as a new tool to explore categorical representation at a solely neural level.

We did not force the animals to learn a specific behavioral response to a stimulus category to solve a task. Thus, the clusters that we obtained are driven by a combination of stimulus input statistics and possible pre-wired object representations in the bird brain. Visual characteristics can explain categorization processes at both the basic and superordinate level (Gale & Laws, 2006; Gale, Laws, Frank, & Leeson, 2003). Moreover, input statistics can even explain categorization of natural scenes and their representation in the human visual cortex (Stansbury, Naselaris, & Gallant, 2013). Thus, the present finding could simply be based on the perceptual similarity of category members. A simple form of pattern matching would not need an internal conceptualization of categories in the pigeon's brain. In line with the above studies, pigeons perceive members of the same basic level categories as more similar than members of different basic categories (Astley & Wasserman, 1992).

The pictorial and the grating stimuli differed in two dimensions each: namely, color and shape, and frequency and amplitude, respectively. These dimensions did not differ in their ability to predict their neural representation. On a behavioral level, pigeons generally pay more attention to color than to shape in a selective attention paradigm (Farthing & Hearst, 1970) and rely more on color than on shape information when solving a matching-to-sample task (Kirsch, Kabanova, & Güntürkün, 2008). In primates, a parallel representation of human and monkey faces at both behavioral and neural levels can be shown. Confusion errors indicate that human and monkey faces are perceived as highly similar at the behavioral level (Sands, Lincoln, & Wright, 1982), and highly similar representations based on neural output of the IT to human and monkey faces is also seen (Kriegeskorte et al., 2008). Similar to the corresponding of visual judgment and visual neural responses in the primate IT, it could have been expected that the dimension of color

would have had a bigger influence on the neural representation in line with behavioral data in the pigeon. However, a similar correspondence as in primate IT could not be shown for the avian NFL.

Previous studies at the behavioral level already prove that categorical information modifies animal behavior even without the explicit need to do so and without reinforcement contingencies explaining the results. Monkeys make more confusion errors in a same-different judgement when two stimuli belong to the same category; from a set of natural images, pictures depicting humans and monkeys cluster together, as well as different types of fruit (Sands et al., 1982). Hence, objects within these categories are perceived to be more similar than across categories. To apes, pictures depicting humans show even higher intrinsic reinforcing properties than pictures without humans (Fujita & Matsuzawa, 1986).

But not just monkeys and apes use categorical information to modify behavior; pigeons do so, too. Astley and Wasserman (1992) trained pigeons in a successive go/no go discrimination paradigm. Pigeons were more likely to respond to S- stimuli from the same category as the S+ stimuli, than to S- stimuli from a different category. In addition, pigeons seem to perceive stimuli within categories as more similar than between categories, like natural versus artificial objects (Lazareva, Freiburger, & Wasserman, 2004, 2006; Lazareva & Wasserman, 2009). Moreover, pigeons learn semantic categories (e.g., "cat" or "flower") more quickly than random pseudocategories (Wasserman, Kiedinger, & Bhatt, 1988; for a review see Soto & Wasserman, 2014). Thus, pigeons categorize and use the categorical content of visual stimuli without being specifically trained to do so.

Pigeons are also able to categorize flexibly at both the basic level (e.g., humans, flowers, chairs, cars) and the superordinate level (e.g., natural and artificial) within the same task and with the same stimuli (Lazareva et al., 2004, 2006; Lazareva & Wasserman, 2009). Pigeons—as well as children—show an advantage of categorization at the basic level compared to the superordinate level. This effect, however, disappears with increasing between-category similarity of the basic-level categories that form the superordinate category (Lazareva, Soto, & Wasserman, 2010). Whereas basic level categories rely heavily on perceptual similarity,

superordinate categories very likely do not (Hampton, 2001). Therefore perceptual similarity alone cannot account for pigeon's categorization abilities—more abstract and functional relationships also take part.

We see our approach and our findings as a missing link for recent theoretical developments in the field of categorization learning. The “Common Elements Model” of Soto and Wasserman (2010) is an especially relevant theoretical account that combines two strands of experimental findings. On the one hand, this theory assumes that the core of categorization learning rests on the identification of common stimulus elements within the wide diversity of objects that are perceived. Since every stimulus is constituted by a finite set of representational elements, two different stimuli can share some of these features. The perceptual similarity between these stimuli would then be a function of the proportion of shared elements. The second strand of evidence concerns error-driven learning rules, like the one of Rescorla and Wagner (1972), that was later implemented in models that code for neuronal prediction errors (Schultz & Dickinson, 2000). Here, it is supposed that learning is driven by a difference between the actual outcome of an organism's own actions and its predicted outcome, resulting in a prediction error. Dopaminergic neurons appear to code prediction errors and to broadcast them as global reinforcer or teaching signals to diverse brain structures (Montague *et al.*, 2004). It is conceivable that common elements between rewarded objects could be identified as salient category-defining cues by such a broadcasted prediction error. The presence of such common cues in a novel object would then bias the decision of the animal toward accepting this object as member of the reinforced category.

The current finding of neural clustering of basic common elements would be predicted by the Common Elements Model. Because neurons in these clusters are often coactivated when objects containing these elements are perceived, it is likely that they develop stronger synaptic weights within the cluster (Wallace & Kerr, 2010). As a result, common elements of various objects that are strengthened during category learning by reinforcer-based prediction errors could specifically associate clusters of neurons that code for certain basic visual features with the reinforced category. Thus, the

neural clusters discovered in our study could act as basic constituting elements for the neural fundaments of category learning.

Our study can thus be deemed to be a proof-of-concept for a new approach that sees the world from the viewpoint of pigeon brains. The next logical steps would be twofold. First, we plan to study the presence of such neural clusters in various real world objects to reveal the common basic elements of such stimuli (Kiani, Esteky, Mirpour, & Tanaka, 2007). Second, and most importantly, we want to discover the changes in coding for such basic elements during the course of various category learning tasks. Such experiments could combine the rich behavioral (Cook, Patton, & Shimizu, 2013; Lazareva *et al.*, 2004; Soto & Wasserman, 2010) and neurobiological (Güntürkün, 2005, 2012; Shimizu, Patton, & Husband, 2010) traditions of studies on avian learning and cognition.

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