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Research report

Functional organization of telencephalic visual association fields in pigeons

Martin Stacho[a,*], Felix Ströckens[a], Qian Xiao[b,**], Onur Güntürkün[a]

[a] Ruhr-University Bochum, Institute of Cognitive Neuroscience, Faculty of Psychology, Department Biopsychology, 44801 Bochum, Germany
[b] State Key Laboratory of Brain and Cognitive Sciences, Institute of Biophysics, Chinese Academy of Sciences, Beijing 100101, China

HIGHLIGHTS

- Pigeons were trained to discriminate form/color or motion stimuli.
- Activity in higher visual areas was measured by ZENK expression.
- Higher visual areas in pigeons process both form/color and motion information.
- Integration of form/color and motion within one region might minimize long-range connections.

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ABSTRACT

Birds show remarkable visual abilities that surpass most of our visual psychophysiological abilities. In this study, we investigated visual associative areas of the tectofugal visual system in pigeons. Similar to the condition in mammals, ascending visual pathways in birds are subdivided into parallel form/color vs. motion streams at the thalamic and primary telencephalic level. However, we know practically nothing about the functional organization of those telencephalic areas that receive input from the primary visual telencephalic fields. The current study therefore had two objectives: first, to reveal whether these visual associative areas of the tectofugal system are activated during visual discrimination tasks; second, to test whether separated form/color vs. motion pathways can be discerned among these association fields. To this end, we trained pigeons to discriminate either form/color or motion stimuli and used the immediate early gene protein ZENK to capture the activity of the visual associative areas during the task. We could indeed identify several visual associative telencephalic structures by activity pattern changes during discriminations. However, none of these areas displayed a difference between form/color vs. motion sessions. The presence of such a distinction in thalamo-telencephalic, but not in further downstream visual association areas opens the possibility that these separate streams converge very early in birds, which possibly minimizes long-range connections due to the evolutionary pressure toward miniaturized brains.

1. Introduction

Pigeons display excellent visual abilities [25]. They acquire complex visual concepts [101], memorize hundreds of abstract visual symbols [89], and extract numerical rules from visual stimuli [74]. The visual information in the avian tectofugal visual pathway runs from the retina via the optic tectum to the thalamic nucleus rotundus, which in turn projects to the entopallium, the primary telencephalic visual area of birds [76]; Fig. 1). The entopallium further projects to multiple visual associative areas including the nidopallium frontolaterale (NFL), mesopallium ventrolaterale (MVL), area temporo-parieto-occipitalis (TPO) and nidopallium intermediale pars lateralis (NIL; [37,46]. Although a few studies revealed important insights into the functional organization of the thalamic and primary telencephalic visual structures [90,65,100,97,87], we have practically no knowledge of the

* Corresponding author at: Ruhr-University Bochum, Institute of Cognitive Neurosciences, Faculty of Psychology, Department of Biopsychology, Universitätstraße 150, Bochum 44801, Germany. Fax: +49 2343214377.
** Corresponding author at: State Key Laboratory of Brain and Cognitive Sciences, Institute of Biophysics, Chinese Academy of Sciences, 15 Datun Road, Beijing 100101, China.
E-mail addresses: Martin.Stacho@rub.de (M. Stacho), qianxiao@moon.ibp.ac.cn (Q. Xiao).

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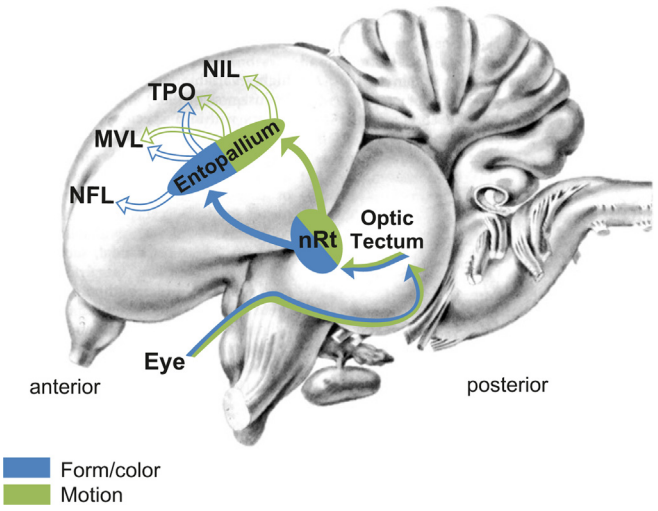

Fig. 1. Functional subdivisions of the avian tectofugal pathway. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Blue and green colors represent the stream processing form/color and motion, respectively. The avian tectofugal pathway runs from the retina via the optic tectum to the thalamic nucleus rotundus (nRt) and then to the entopallium (shaded arrows). The entopallium projects to further tectofugal visual associative areas: NFL, MVL, TPO and NIL. Experimental evidence indicates that the rotundus and the entopallium process form/color and motion separately in different subdivisions. However, tectofugal visual associative areas have been identified only anatomically, yet. Are these areas activated during discrimination of visual stimuli? Are some of them specialized for form/color or motion or both? The outlined arrows indicate anatomical projections of the entopallium. The color of the outlined arrows indicates possible functional differentiation in these projections based on the anatomical projections. Abbreviations: MVL—mesopallium ventrolaterale; NFL—nidopallium frontolaterale; NIL—nidopallium intermediale pars lateralis; nRt—nucleus rotundus; TPO—area temporo-parieto-occipitalis.

functional organization of visual areas beyond the entopallium. The first aim of our study was to fill this gap.

Studies on the mammalian geniculocortical visual pathway yielded evidence for at least two functionally dichotomous systems involved in form/color and motion processing, respectively [50,102,41,84,63,91,22,43]. This dichotomy indicates that separate processing of form/color and motion is a general requirement for complex vision [21,73]. Pigeons show excellent performance in visual discrimination of both form/color and motion stimuli [33,14,15,9,66,20,18,98,48]. They possess separate functional subdivisions for color, 2D motion, and looming within the nucleus rotundus [90,55,32,65,96]. Moreover, form/color and motion appear to be differentially organized along the rostro-caudal axis within the entopallium [65,12]. Thus, a form/color vs. motion dichotomy also exists in birds and might differentiate downstream visual association areas into parallel streams. To identify these separate streams was our second goal. Furthermore, visual processes in birds are lateralized and single-unit recordings in entopallium during color discriminations reveal that left entopallial neurons respond with higher spike densities and higher accuracies to the rewarded stimulus [87]. Thus, our third aim was to reveal possible asymmetries along the ascending visual streams.

To sum up, we set out to seek answers to three main questions: First, which of the anatomically defined tectofugal visual associative areas (NFL, MVL, TPO, NIL) can indeed be activated by visual stimuli? Second, are some of the visual associative areas specialized for either form/color or motion stimuli or both? And third, do responses to visual stimuli differ between hemispheres? To answer these questions, we used molecular imaging to visualize activity of the visual associative areas in pigeons performing a visual discrimination of either form/color or motion stimuli.

2. Materials and methods

2.1. Subjects

Twenty-four adult pigeons (*Columba livia*) of both sexes were used in the experiments with 10 pigeons in each experimental group (form/color and motion group) and 4 pigeons in the control group. To motivate these animals during training phase, they were food-deprived to 80% of their normal weight while water was accessible ad libitum. All procedures were in compliance with the national institutes for the care and use of laboratory animals and were approved by the National Committee of North Rhine-Westphalia, Germany.

2.2. Apparatus

Animals were trained in a custom-designed training box with 32 cm height, 34 cm length and 33 cm width. The training box was equipped with 2 square pecking keys (5 cm × 5 cm) where the stimuli were depicted. The pecking keys were located symmetrically at the front panel with a distance of 2 cm between them. The center of each pecking key was 13 cm away from the lateral border and 10 cm under the top of the training box. A magnetic food hopper was located centrally in the front panel and 7 cm above the floor. The food light was located 3 cm above the food hopper. The training box was illuminated by LED lights along the upper left and right edges (Fig. 2A). The visual stimuli, the food hopper and the LED lights were controlled by a custom-written program (Matlab, MathWorks).

2.3. Stimuli

The form/color stimuli consisted of different black shapes (luminance = 1.25 cd/m^2) on a white background (luminance = 107.17 cd/m^2) or a color covering the whole pecking key (luminance of colors: green = 52.1 cd/m^2; blue = 44.28 cd/m^2; red = 45.20 cd/m^2; brown = 47.39 cd/m^2; violet = 59.7 cd/m^2; purple = 13.27 cd/m^2; yellow = 93.59 cd/m^2; light green = 100.70 cd/m^2; darkcyan = 23.22 cd/m^2; Fig. 2B). They were generated in Paint (Windows Vista). We used these stimuli since shapes and colors have been shown to elicit activation in the ventral stream of primates [102,41,82,47]. Although, differences in the subjective perception of colors might exist due to differences in photoreceptors in primates and birds [25], such subjective differences are not relevant in this experiment. Previous studies demonstrated that pigeons can be successfully trained to discriminate colors, patterns and forms [33,9,66,48].

The motion stimuli were comparable to stimuli used in previous studies that aimed to elicit activation of motion-sensitive areas in primates [64,102,81,43] and pigeons [65]. The stimuli were composed of white moving dots (luminance = 107.17 cd/m^2) with the velocity of 7.5 pixels/s on a black background (luminance = 1.25 cd/m^2). Each dot was 10 pixels in size and moved in one of 24 directions with 15 degree apart. Similar to Nguyen et al. [65], we combined coherently and randomly moving dots. The stimuli contained 0%, 50% or 100% noise. The percentage of noise is the proportion of dots moving randomly while the rest of dots move coherently in one direction.

2.4. Training procedure

We used a visual discrimination task to ensure that pigeons keep attention to presented visual stimuli. In the pre-training session, pigeons were trained to peck on a white stimulus presented randomly on the left or the right pecking key for 10 s. Only correct responses were rewarded with 2 s access to food. No pecks and

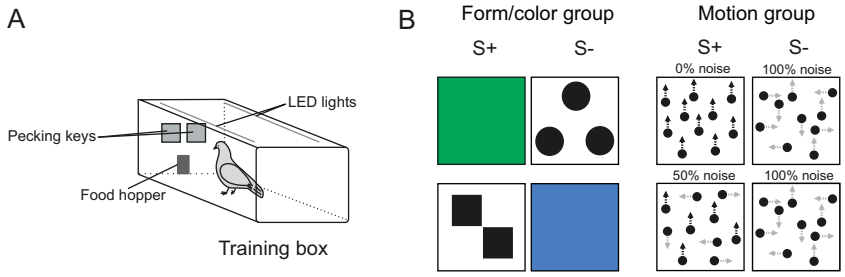

Fig. 2. Training box and visual stimuli. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.) (A) Schematic drawing of the training box. A pair of stimulus (S^+ and S^-) was presented simultaneously on pecking key in each trial. S^+ and S^- were randomly assigned to the left or the right pecking key. Pigeons were required to peck on the S^+ once. Pecking on S^+ was rewarded with food access, whereas pecks on S^- were punished with darkness (10 s). (B) Example of stimuli used in the form/color (left) and motion group (right). The stimuli in the form/color group consisted of either different black forms on a white background or different colors. The stimuli in the motion group consisted of white dots (10 pixels in size each) moving coherently (0% noise) or with 50% or 100% noise on a black background (with velocity of 7.5 pixels/s). The S^+ stimulus contained less noise than the S^- stimulus. Black and gray arrows illustrate coherent and random motion, respectively.

pecks on non-stimulated keys were not punished. Inter-trial interval (ITI) was 20 s. When the animal reached 80% correct responses in two consecutive days, it was randomly assigned to one of the three groups—the form/color, motion or control group.

2.4.1. Training of the form/color group

The animals of the form/color group (10 animals) were trained to discriminate between different pattern/form and color stimuli as illustrated in Fig. 2B. In total, each animal learned 40 stimuli (30 forms and 10 colors). Responses to half of them were (S^+) were rewarded with access to food for 2 s and responses to the rest stimuli (S^-) were punished with 10 s of darkness. S^+ and S^- were identical for each animal. In each trial, a pair of randomly chosen stimuli S^+/S^- was displayed for 10 s with 20 s ITI. Since the S^+ and S^- were chosen randomly, the S^+/S^- pair could be constituted by two colors, two forms or one form and one color. The S^+/S^- stimulus was presented randomly on either the left or the right pecking key. Each animal was given one session (120 trials) per day. If the animal responded incorrectly, the same stimulus pair was repeated up to 5 times to enhance learning (correction loop). When the animal reached 70% correct responses in two consecutive days it proceeded to the final session on the next day.

2.4.2. Training of the motion group

The training paradigm in the motion group (10 animals) was identical to the form/color group. The only difference between them was the type of the stimuli used (Fig. 2B). In each trial, a pair of motion stimuli (S^+ and S^-) was presented. The direction of the coherent motion for each stimulus was chosen randomly. The S^+ and S^- differed in their noise ratios. Similar to the form/color group, the S^+/S^- stimulus was presented either on the left or the right pecking key, which was randomly selected by computer and balanced between trials. The animal was required to peck on the stimulus with less noise (S^+) for reward. A correction loop was applied after a wrong peck to facilitate learning. When the animal reached 70% performance in two consecutive days, the final session followed on the next day.

2.4.3. Training of the control group

Detection of the immediate early genes (see Section 2.5) allows us to identify neurons which were activated at a specific time-point. To make it possible to infer an event-activity correlation, we need a proper control group. Since we were interested in the neuronal activity particularly related to form/color and motion stimuli discrimination, we created a control task which was identical to form/color and motion discrimination in all except of two aspects. First, the control group lacked the form/color and motion stimuli and second, the control task did not include a discrimination component. Other aspects (such as being in the training box, reacting to stimuli, pecking on pecking keys, being rewarded or punished) were identical. Thus, comparing the neuronal activity in the form/color or motion group with the activity measured in the control group should yield the activity related to discrimination of form/color and motion stimuli, respectively. The task for the control group was identical to the pre-training task where the birds were required to peck the lighted pecking key. However, in this task wrong pecks were punished similar to the two discrimination groups. Since this task is much easier than the form/color or motion discrimination, we successively decreased the reward probability from 100 to 80%. In the remaining 20%, the animal was punished despite a correct response. This rendered the control group comparable to the two discrimination groups with respect to amount of reward and punishment. Such counterbalance is necessary to avoid differences in activation based on reward probability. After at least 2 days of training with the 80% reward probability the pigeon proceeded to the final session on the next day. This control task was chosen to better assign the neuronal activity in the form/color and motion group to the discrimination of visual stimuli.

2.5. Activity assessment

We used the protein of the immediate early gene zenk to visualize the activity in the brain. Immediate early genes are genes that are rapidly and transiently expressed in activated neurons, and via their proteins they can affect the transcription of late-response genes [8,51]. The immediate early gene zenk has been associated with synaptic plasticity and long-term memory formation [19,11,95,5,38]. Due to its relatively low basal expression and rapid induction and degradation kinetics [58], it is a useful tool to map neuronal activity [95,61]. ZENK, the protein of the immediate early gene zenk, can be detected in neurons as early as 15 min after stimulation onset with an expression peak between 1 h and 2 h [58]. Therefore, the duration of the final session was prolonged to 60 min (see Section 2.6).

2.6. Final session and tissue processing

The final session for each animal was identical to the last session of each group, with the exception of the omission of the correction loop. After 60 min, the pigeons were immediately sacrificed by decapitation and the brain was dissected and immersed in 5% acrolein in 0.12 M phosphate-buffered saline (PBS; pH 7.4) for 3 h. Afterwards, brains were rinsed in PBS (1×30 min and 2×15 min) and cryoprotected in 30% sucrose solution in PBS for 48 h. To facilitate slicing, brains were embedded in 15% gelatin/30% sucrose

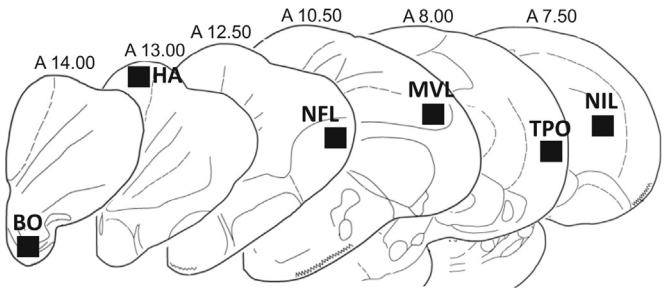

Fig. 3. Schematic drawing of the analyzed regions.
Black squares represent the 300 × 300 μm area where ZENK-positive neurons were counted. Numbers indicate the position at the anterior-posterior axis according to the stereotactic atlas of Karten and Hodos [40].

which was further fixated in 4% paraformaldehyde in phosphate buffer for 24 h. Brains were cut in coronal plane in 40 μm thick slices using a microtome (LEICA) and stored at 4 °C in 0.1% sodium azide until further processing.

2.7. Immunohistochemical procedure

Every tenth slice was used for a free floating immunohistochemistry against ZENK, using a standard DAB (3,3 diaminobenzidine tetrahydrochloride) staining procedure intensified with nickel and cobalt [78,31]. Briefly, slices were incubated in 0.16% sodium borohydride ($NaBH_4$) in PBS for 25 min for antigen retrieval. After rinsing (3 × 10 min in PBS), endogenous peroxidases were blocked by incubation in 0.3% hydrogen peroxide (H_2O_2) in distilled water for 30 min. After further rinsing, unspecific binding sites were blocked with 10% normal goat serum (NGS; Vector Laboratories-Vectastain Elite ABC kit) in PBS with 0.3% Triton-X-100 (PBST). To label the ZENK protein, slices were incubated with a polyclonal rabbit anti-ZENK antibody (Santa Cruz Biochemicals; 1:3000 in PBST with 1% NGS) at 4 °C for 3 days. After rinsing in PBS (3 × 10 min), slices were transferred into a secondary biotinylated anti-rabbit antibody (1:500 in PBST; Vector Laboratories-Vectastain Elite ABC kit) for 60 min at room temperature. After further washing in PBS, slices were incubated in an avidin-biotin complex (Vector Laboratories-Vectastain Elite ABC kit; 1:100 in PBST) for 60 min at room temperature. Slices were rinsed in 3 × 10 min in PBS, 1 × 5 min in 0.1 M sodium acetate buffer (pH 6.0) and then transferred into a DAB solution, containing β-D-glucose, for visualization. Staining reaction was induced by adding glucose-oxidase (100 μl in 50 ml DAB solution). The reaction lasted 30 min and the reaction solution was changed every 10 min. Rinsing the slices in 0.1 M sodium acetate buffer (pH 6.0; 3 × 5 min) stopped the reaction. After washing in PBS (3 × 10 min), slices were mounted on gelatin-coated slides, dehydrated in alcohol and coverslipped with depex (Fluka).

2.8. Quantification of ZENK activity

For the quantitative analysis of the ZENK activity, slices were photographed at 100× magnification using a ZEISS AXIO Imager. M1 equipped with a camera (AxioCam MRm ZEISS 60N-C 2/3″ 0.63×). ZENK-positive cells were counted manually using the software Axio Vision (Version 4.8.1.0, Zeiss) with the counter being blind to group of the animal. Since ZENK-labelling is known to be highly specific [58,95,69,61], we considered all labeled nuclei ZENK positive and counted them irrespective of the intensity of labelling (Fig. 4A). Nidopallium frontolaterale (NFL), mesopallium ventrolaterale (MVL), the area temporo-parieto-occipitalis (TPO) and nidopallium intermediale pars lateralis (NIL) were chosen for analysis since they are the recipients of entopallial efferents [37,46]. The entopallium, the primary target of the avian visual tectofugal

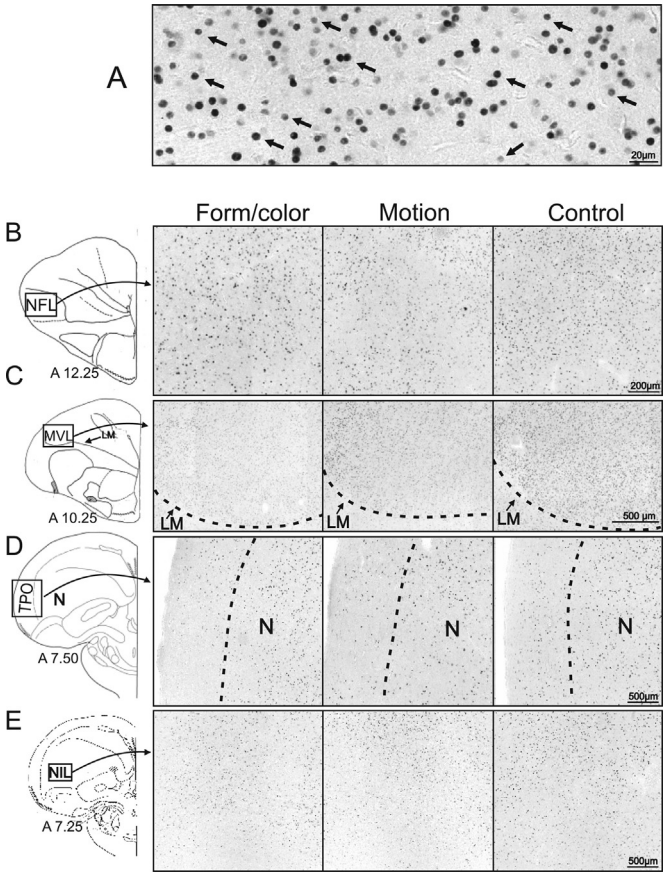

Fig. 4. ZENK expression in tectofugal visual associative areas in form/color, motion and control groups.
(A) Picture of ZENK-positive neurons under higher magnification. Only the nuclei of the neurons are stained, indicating antibody specificity. Arrows point to example of ZENK-positive neurons. Photographs in (B–E) show the stained ZENK positive cells in the NFL, MVL, TPO and NIL in 3 groups. (B–D) The ZENK activity in NFL, MVL and TPO tended to be higher in the control group than in the two other groups. The ZENK expression in NIL did not differ between the groups (E). The schematic drawings depict the positions of the analyzed regions in the pigeon brain. Abbreviations: LM—lamina mesopallialis; MVL—mesopallium ventrolaterale; N—nidopallium; NFL—nidopallium frontolaterale; NIL—nidopallium intermediale pars lateralis; TPO—area temporo-parieto-occipitalis.

pathway, is functionally subdivided along the anterior-posterior axis [65]. Since there is also an anterior-posterior topography in the entopallial projections, it is conceivable that target regions could also functionally differ [37,46]; Fig. 1). The bulbus olfactorius (BO) and the hyperpallium apicale (HA) were used as a control (see below). Cells were counted in the BO at the anterior level (A) 14.00, the HA at A 13.50–13.00, in the NFL at A 12.75–12.25, in the MVL at A 11.25–9.75, in the TPO at A 8.25–7.50, and in the NIL at A 7.50–7.25 [40]; Fig. 3). In each region, cells were counted in a 300 μm × 300 μm square in both hemispheres. The medio-lateral and dorso-ventral coordinates of the centre of the square were as follows: BO: L (lateral) 1.00, D (dorsal) 5.00; HA: L 1.5, D 12.00; NFL: L 6.50, D 9.50; MVL: L 7.00, D 11.00–12.00; TPO: L 8.50, D: 10.00; NIL: L 7.00, D: 11.00; (Fig. 3). To avoid possible artificial differences in cell counts resulting from inaccurate position of the square in different animals, visible landmarks such as lamina mesopallialis, telencephalic ventricle and the pial surface of the telencephalon were taken into account to position the square at the same place in all animals. For instance, the square in NFL was always positioned at a distance 800 μm medial to most lateral edge of the NFL. In MVL, the square was positioned 200 μm dorsal to the lowest point of the lateral aspect of the lamina mesopallialis. TPO was analyzed in a

square located 100 μm medial to the most lateral bulge of the pial surface of the lateral telencephalon in this region. For NIL analysis, the square was positioned 1000 μm medial to lateral pial surface, 1000 μm dorsal to most lateral bulge in this region. HA was analyzed in a square just underneath the dorso-medial curvature of the hyperpallium. The neurons in BO were counted in the subventricular part of the U-shape of the granular cell layer. As outlined above (Section 2.6 and 2.7), the thickness of our slices was 40 μm and every tenth slice was used for analysis. Thus, given the rostro-caudal extent of the entopallial targets [37,46], several slices could contribute to one region, especially for MVL and TPO. In such case, the arithmetic mean of the counts was calculated (see Section 2.9).

2.9. Normalization of ZENK activity

Our aim was to test the hypothesis that the different tectofugal telencephalic areas constitute subsystems that code for either form/color or motion. Our control group conducted a simple visually guided pecking task for food reward. Their data were compared with the experimental groups (form/color and motion group). In addition, we used the HA as a more stringent control. The activities of the diverse tectofugal regions were normalized to the activity level of the HA. This has two important benefits. First, it normalizes variations of ZENK activity at the individual level that may obstruct signal differences between individuals. Second, it provides the possibility to normalize the tectofugal areas with a visual structure. The HA represents the lateral but not the frontal visual field [26]. Although pigeons possess a high visual acuity also in the lateral visual field [29], this field is specialized for distant vision [7,4,6]. The stimuli in our experiment were presented frontally at short distance in an operant chamber. Thus, HA plays no role in the visual discrimination of the critical stimuli but is, nevertheless, part of the visual system of the same animal that is analyzed [53,71,56,34,26,76,92,6,93]. To ensure that HA is indeed not involved in the discrimination task, we compared the activity level of HA between groups. Before that, we normalized the number of ZENK-positive HA neurons by the number of labelled cells in the BO that is a non-visual area involved in odor processing. The HA was analyzed in its dorsal aspect, which contains visual responsive cells [13].

The data of interested area (NFL, MVL, TPO and NIL) were normalized using the following equation $A_{ijh} = X_{ijh} / \left((HA_{i,\text{left}} + HA_{i,\text{right}})/2\right)$ where X is the number of ZENK-positive cells in the region "j" of the animal "i" in the hemisphere "h" and HA is the arithmetic mean number of ZENK-positive cells in two consecutive slices (A 13.50–13.00) in the same animal (i) of the left and right hemisphere, respectively. If several slices contributed to one region, the value (X) was simply the arithmetic mean value of the ZENK-positive cells counted in these slices. Accordingly, if a region was analyzed bilaterally the value was pooled from the left and right hemisphere.

SPSS (20.00 IBM) was used to perform the statistical analysis. We used Kolmogorov–Smirnov tests to check the normal distribution of the data, Levene's test to check the homogeneity of the variance, Mauchly-test to check sphericity and Box's test for the equality of covariance matrices. Mixed analysis of variance (ANOVA) design and multivariate ANOVA were computed to investigate the differences between and within groups. Tukey-HSD test was used for post-hoc comparisons between groups. We compared the amount of reward and performance in the final session with the Kruskal–Wallis test of independent samples (due to computer issues, we could only include 14 animals in this comparison). To estimate the sample size, that would be needed to reveal significant differences between the form/color and motion group, we calculated power analysis with the G*Power (Version 3.1.9.2).

Table 1
Mean values (±S.E.) of the normalized ZENK expression.

Group	HA	NFL	MVL	TPO	NIL
Motion	0.49 ± 0.09	0.49 ± 0.08	0.72 ± 0.15	0.28 ± 0.04	0.51 ± 0.09
Form/color	0.57 ± 0.09	0.50 ± 0.09	0.92 ± 0.18	0.30 ± 0.03	0.57 ± 0.10
Control	0.39 ± 0.06	0.87 ± 0.10	1.78 ± 0.18	0.58 ± 0.01	0.74 ± 0.04

3. Results

All pigeons learned their respective discrimination tasks and no animal had to be excluded from the experiment. No significant differences were observed in the amount of reward in the last session of the two experimental groups (color/form and motion group) and the control group (Kruskal–Wallis test of independent samples; $p = 0.600$; $n = 14$). Similarly, the performance (percentage of correct responses) in the final session also did not statistically differ between groups (Kruskal–Wallis test of independent samples; $p = 0.061$; $n = 14$).

With molecular imaging against the activity marker ZENK, we could simultaneously visualize the brain activity of all areas of interest (NFL, MVL, TPO and NIL) during the visual discrimination task applied in the present experiment. By comparing the ZENK activity between groups, we quantified the contributions of each area to the discrimination of static (form/color) and moving stimuli (Fig. 4). To reduce possible inter-individual differences in ZENK expression unrelated to the experimental variation, the numbers of ZENK-positive neurons of each interested region in the experiment were normalized to that of HA of the same animal (see Section 2.8). We first checked whether the ZENK expression in HA differed between groups. To do this, we normalized the ZENK expression in the HA to that in the BO. As expected, the activity in the HA did not differ between groups (ANOVA; $p = 0.504$; Tables 1 and 2, Fig. 5). Thus, we further analyzed the data for NFL, MVL, TPO and NIL normalized by the ZENK-activation in the HA.

The ZENK activity of NFL, MVL and TPO in the form/color and motion groups was lower than that in the control, whereas the ZENK activity in NIL did not display substantial differences between the groups (Table 1; Figs. 4 and 5). The statistical analysis revealed that the ZENK activity indeed significantly differed between three groups (Mixed ANOVA; $p < 0.01$) as well as between regions ($p < 0.001$; Table 2). However, there were no significant differences between two hemispheres ($p > 0.05$; Table 2). Thus, the ZENK-activity in the analyzed regions (NFL, MVL, TPO and NIL) differed between groups but not between left and right hemispheres.

We then further analyzed the differences between groups (form/color, motion and control group) within the regions (MANOVA; NFL, MVL, TPO and NIL). We found that significant differences exist between groups in NFL ($p < 0.05$), MVL ($p < 0.01$) and TPO ($p < 0.001$) but not in NIL ($p > 0.05$; Table 2, Fig. 5). Post-hoc comparisons revealed significant differences between the control group and two experimental groups in MVL and TPO (Tukey-HSD; all p-values < 0.05; Table 2) and a strong trend in NFL ($p = 0.05$ and $p = 0.056$, respectively; see Table 2). However, the ZENK-activity did not differ between the form/color and motion group (all p-values > 0.05; Table 2). In sum, these results demonstrated that the ZENK activity in MVL, TPO and NFL less activated in the visual discrimination of form/color and motion in comparison to the control task.

Since MVL has a relatively large extent along the rostro-caudal axis (1.5 mm) and its entopallial input follows a topographical organization [46,1], we divided the MVL into rostral (A 11.25) and caudal (A 9.75) part to investigate possible functional differences between the two MVL subdivisions. Consistent with previous analyses, the ZENK activity in rostral and caudal MVL significantly differed between the groups (Mixed ANOVA; $p < 0.01$; Table 2).

Table 2
Summary of statistical results.

Region	*N*	Test	Effect	*F*-value	*p*-value
HA	24	ANOVA	Task	$F_{(2,21)} = 0.708$	$p = 0.504$
NFL, MVL, TPO, NIL	24	Mixed ANOVA	Task	$F_{(2,21)} = 5.877$	$p = 0.009^{**}$
			Region	$F_{(3,63)} = 38.857$	$p = 0.000^{***}$
			Task × region	$F_{(6,63)} = 4.078$	$p = 0.013^{*}$
			Hemisphere	$F_{(1,21)} = 0.311$	$p = 0.583$
			Hemisphere × task	$F_{(3,63)} = 2.541$	$p = 0.086$
			Hemisphere × region	$F_{(2,21)} = 1.394$	$p = 0.270$
NFL, MVL, TPO, NIL	24	MANOVA		Wilk's $\lambda = 0.289$	$p = 0.002^{**}$
NFL				$F_{(2,21)} = 3.586$	$p = 0.046^{*}$
MVL				$F_{(2,21)} = 6.473$	$p = 0.006^{**}$
TPO				$F_{(2,21)} = 15.163$	$p = 0.000^{***}$
NIL				$F_{(2,21)} = 1.022$	$p = 0.377$
		Post-hoc (Tukey-HSD)			
NFL	14	Motion vs. control			$p = 0.050$
NFL	14	Form/color vs. control			$p = 0.059$
NFL	20	Form/color vs. motion			$p = 0.994$
MVL	14	Motion vs. control			$p = 0.005^{**}$
MVL	14	Form/color vs. control			$p = 0.023^{*}$
MLV	20	Form/color vs. motion			$p = 0.651$
TPO	14	Motion vs. control			$p = 0.000^{***}$
TPO	14	Form/color vs. control			$p = 0.000^{***}$
TPO	20	Form/color vs. motion			$p = 0.845$
MVL	24	Mixed ANOVA	Task	$F_{(2,21)} = 6.397$	$p = 0.007^{**}$
			Rostro-caudal position	$F_{(1,21)} = 0.088$	$p = 0.770$
			Hemisphere	$F_{(1,21)} = 3.030$	$p = 0.096$
			Task × position	$F_{(2,21)} = 1.225$	$p = 0.314$
			Position × hemisphere	$F_{(1,21)} = 1.412$	$p = 0.248$
			Task × hemisphere	$F_{(2,21)} = 0.210$	$p = 0.979$

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

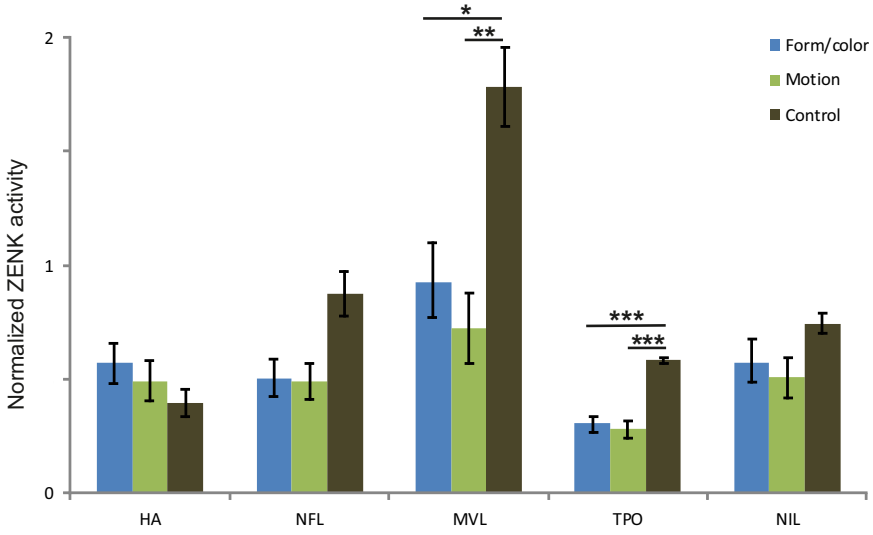

Fig. 5. Normalized ZENK activity across all investigated regions in three groups.
ZENK activity in HA (normalized to olfactory bulb) did not differ between form/color, motion and control group, therefore HA was used to normalize the activity in other investigated regions. ZENK activity was significantly reduced in MVL and TPO in both form/color and motion groups in comparison to the control group. Similarly, ZENK activity in NFL showed a strong tendency toward a reduction in form/color and motion groups compared to the control group. No differences between the groups were found in NIL. The error bars represent the standard error of mean (SEM). Abbreviations: MVL—mesopallium ventrolaterale; NFL—nidopallium frontolaterale; NIL—nidopallium intermediale pars lateralis; TPO—area temporo-parieto-occipitalis; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

However, there was no difference between rostral and caudal MVL ($p = 0.770$). Neither did we found hemispheric differences ($p > 0.05$) or differences between rostral and caudal MVL as a function of hemisphere or task (all *p*-values > 0.05; Table 2). Thus, MVL was equally activated by form/color and motion throughout its rostro-caudal extent and in both hemispheres.

4. Discussion

The present study is the first attempt in birds to reveal the functional architecture of telencephalic tectofugal visual association areas using molecular imaging. Pigeons possess functionally separated parallel streams for color, 2D motion, and looming within their ascending tectofugal pathway [90,55,32,65,96]. We investigated whether visual associative telencephalic areas of birds can be activated by visual discrimination task and whether these areas are specialized for form/color or motion. Our results demonstrate that ZENK expression in NFL, MVL and TPO was reduced during both form/color and motion discrimination task. Thus, these hitherto only anatomically identified areas indeed contribute to the discrimination of static and moving stimuli. However, we did not reveal a stimulus-dependent difference between the analyzed areas, indicating that form/color and motion information is not segregated into different streams. It is conceivable that fusing separate streams at early processing levels serves minimizing long-term connections due to the evolutionary pressure toward miniaturized brains. At the same time, our results imply that maintenance of separate streams throughout most of the ascending visual streams seems not to be a computational necessity for complex vision.

4.1. Reduced ZENK-expression by stimulus familiarity

In songbirds, neurons in the auditory nidopallium decrease their firing rate after becoming familiar with the presented acoustic stimuli [10,70,52]. In particular, this effect is restricted to complex stimuli such as birdsong, artificial words, or complex sound patterns and does not occur with simple tones [10,52]. Moreover, this decreased firing is paralleled by a reduced zenk mRNA expression to basal levels [57]. Similarly, reduced activity after repeated or prolonged visual stimulation was obtained with single unit recordings throughout the primate visual system including primary visual area V1 [62] as well as higher visual areas such as MT [79,42] and inferotemporal cortex [59,49,17]. Furthermore, reduced neuronal response after repeated stimulation was also found with functional imaging in a variety of cortical areas in humans [75,80,16]. This effect is generally assumed to be dependent on prolonged experience to a certain stimulus and was demonstrated with exposure periods up to several months [94]. Most importantly, the response suppression is not due to cellular fatigue but could represent an effective way of stimulus coding and a mechanism of response sharpening [88,83]. Therefore, we assume that the reduced ZENK-expression in our experimental groups reflects a learning-related buildup of stimulus familiarity in these regions [19,11,95,38]. Consistent with this, Huchzermeyer et al. [36] showed that a stimulus imprinted in juvenile zebra finches induced lower levels of ZENK-expression than a non-imprinted stimulus, when presented again at adult stages.

4.2. Lack of hemispheric difference in tectofugal associative structures

Birds are visually lateralized with a left hemispheric superiority for visual discrimination of form details [28,23,86,54]. In pigeons, this functional asymmetry is especially obvious when the animals memorize [89] or categorize stimuli [101] that can only be discerned by attending to small pictorial features. A similar left-right difference is also observed when pigeons discriminate the direction of motion [99]. The tectofugal system of pigeons displays morphological [24] and connectional asymmetries [27] and is the key pathway for visually lateralized behavior. Indeed, single units in the left entopallium discriminate at higher level than the right side between rewarded and non-rewarded colors [87]. We therefore expected to find a lateralized difference of ZENK expression in tectofugal visual associative areas. However, we did not find any hemispheric differences. Presently, we have no strong explanation for the lack of left-right differences in our results. Since the two hemispheres show complementary specializations in all lateralized systems [85,72,67], it is possible that the two hemispheres were differently recruited during the task, so that overall ZENK activity did not differ between hemispheres.

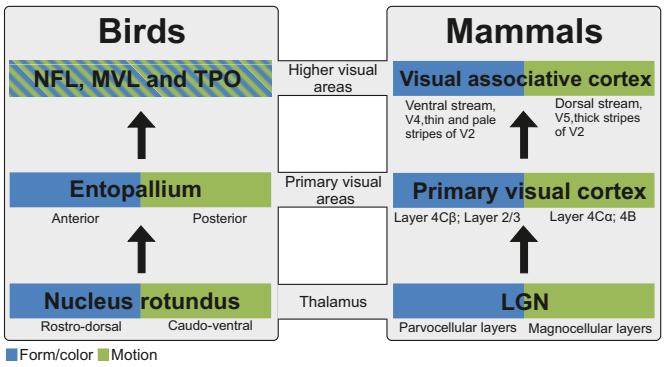

Fig. 6. Comparison of form/color and motion visual stream in the brain of birds and mammals.
Both birds and mammals possess separated functional channels for form/color and motion within their respective thalamic and primary visual telencephalic stations. In birds, the thalamic nucleus rotundus contains different subdivisions involved in color and motion perception, respectively. These different functional channels remain separated along the anterior-posterior axis of the entopallium. Similarly, the mammalian lateral geniculate nucleus (LGN) is constituted of parvo- and magnocellular layers involved in form/color and motion processing, respectively. These different pathways terminate in different sublayers of the layer 4 and remain separated also in other layers of the primary visual cortex as well as in further cortical areas constituting the dorsal and ventral stream. However, our data demonstrated that the functional separation is no longer present in the visual associative areas of birds. Thus, the functional similarities between non-homologous avian and mammalian visual pathways exist at the thalamic and primary telencephalic level but differences occur in the organization of the visual associative areas. This indicates that functional separation in visual associative areas is not a computational necessity for advanced visual behavior.

4.3. Tectofugal associative structures process both form/color and motion

The rostral and caudal entopallium play a differential role in pattern and motion discrimination [65,77,12]. Electrophysiological studies demonstrated that some neurons in caudal entopallium respond to 2D motion and looming stimuli, similar to the posterior nucleus rotundus [100,97]. Thus, the functional dichotomy of the visual thalamus is possibly translated onto the telencephalon. The involvement of TPO in both form/color and motion discrimination possibly results from its afferents from both rostral and caudal entopallium [37,44]. However, NFL and NIL primarily receive input from only the rostral or the caudal entopallium, respectively [37,77]. Thus, we expected to find a differential stimulus-dependent ZENK expression in these two areas. Accordingly, we also expected to see a similar dichotomy for the anterior vs. the posterior MVL, based on its topographical input from the entopallium [46,1]. However, we found that rostral and caudal MVL, TPO and, as a trend, also NFL were significantly involved in both form/color and motion discrimination in comparison to control group. This might indicate that the form/color and motion information is transferred between the rostral and caudal entopallium. Alternatively, the information might be mixed within MVL and due to its interconnection with NFL [2] both kind of information is also present in NFL.

The involvement of visual associative areas in both form/color and motion information is a clear difference to the principle

organization in mammals [50,60,63]. Our findings make it likely that functional tectofugal streams stay separated up to the primary telencephalic level but then fuse (Fig. 6). Presently, we can only speculate about the reason. Birds face a long-standing evolutionary pressure to miniaturize their brains to enable flight [3]. They managed to drastically increase neuron numbers by making their cells smaller, thereby doubling telencephalic neuron density compared to primates [68]. These changes might have resulted in an arrangement where specialization of retinal ganglion cells [30,35] makes separate streams at subtelencephalic [31, Marín et al., 2003 100,97] and first telencephalic entities [65] necessary, while subsequent early integration of parallel streams within pallial association fields saves processing space.

NIL did not show any significant activity differences between groups. Patton et al. [69] could show that NIL-neurons respond to the presentation of live pigeons but not to a video of a pigeon or other species. Thus, NIL might process more complex, living stimuli and was therefore not significantly activated in our task.

In principle, it is conceivable that our method was not sensitive enough to reveal a distinction between stimulus-specific activity patterns. For two reasons we believe that it is unlikely. First, our approach was able to reveal a difference in three visual structures between the experimental and the control group and thus successfully picked up activity changes during the discrimination tasks. Second, power analyses based on our empirical effect sizes revealed that we would need 147 (MVL), 350 (TPO), 439 (NIL), or 9100 (NFL) animals per group to reveal a significant difference between form/color and motion group. Thus, even if there is such a distinction within associative tectofugal subsystems, it is by far more subtle than in the mammalian condition.

5. Conclusions

Taken together, we provide the first evidence that several associative structures surrounding the entopallium process different aspects of the visual signal. In principle, this kind of organization resembles the constellation of cortical fields in mammals where primary sensory areas are usually surrounded by one or several secondary and multimodal sensory fields [39,45]. However, in contrast to mammals, we did not find evidence for a functional separation of form/color and motion. It is important to note that the avian tectofugal and the primate geniculocortical systems are not homologous but functionally comparable. Thus, the present argumentation invokes possible mechanisms of functional convergence instead of common ancestry. The absence of a form/color- vs. motion-subdivision within tectofugal visual associative areas imply that a form/color- vs. motion segregation in birds exists up to the primary telencephalic level but then is processed in combined manner, possibly to save computational space.

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