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Research report

Functional organization of telencephalic visual association fields in pigeons

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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

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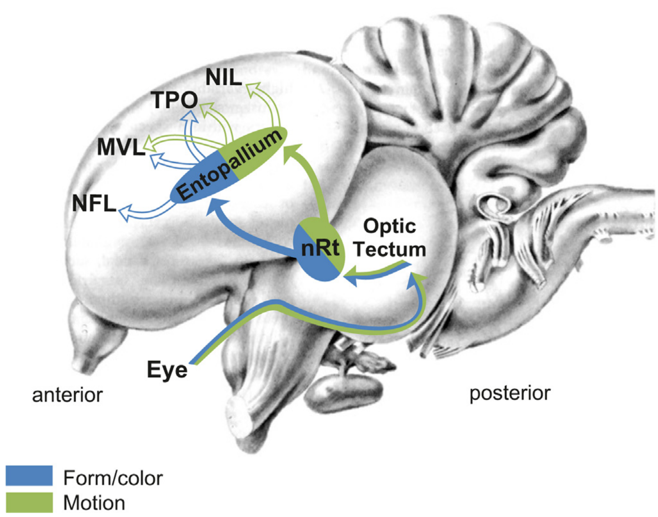

Fig. 1. Functional subdivisions of the avian tectofugal pathway. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Blue and green colors represent the stream processing form/color and motion, respectively. The avian tectofugal 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