Behavioural Brain Research 344 (2018) 1–8

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

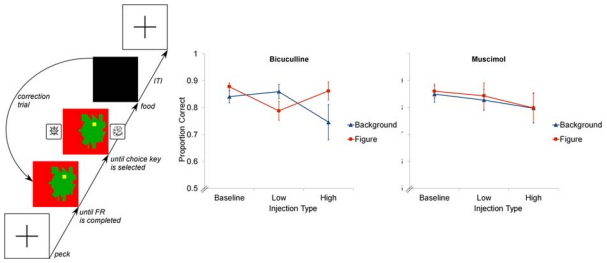
Research report

Pharmacological manipulation of GABA activity in nucleus subpretectalis/interstitio-pretecto-subpretectalis (SP/IPS) impairs figure-ground discrimination in pigeons
Running head: SP/IPS in figure-ground segregation

Martin J. Acerbo[a,*], Olga F. Lazareva[b]

[a] Iowa State University, United States
[b] Drake University, United States

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Visual processing
Inhibitory regulation
Nucleus rotundus
SP/IPS
Figure-ground segregation

ABSTRACT

Figure-ground segregation is a fundamental visual ability that allows an organism to separate an object from its background. Our earlier research has shown that nucleus rotundus (Rt), a thalamic nucleus processing visual information in pigeons, together with its inhibitory complex, nucleus subpretectalis/interstitio-pretecto-subpretectalis (SP/IPS), are critically involved in figure-ground discrimination (Acerbo et al., 2012; Scully et al., 2014). Here, we further investigated the role of SP/IPS by conducting bilateral microinjections of GABAergic receptor antagonist and agonists (bicuculline and muscimol, respectively) and non-NMDA glutamate receptor antagonist (CNQX) after the pigeons mastered figure-ground discrimination task. We used two doses of each drug (bicuculline: 0.1 mM and 0.05 mM; muscimol: 4.4 mM and 8.8 mM; CNQX: 2.15 mM and 4.6 mM) in a within-subject design, and alternated drug injections with baseline (ACSF). The order of injections was randomized across birds to reduce potential carryover effects. We found that a low dose of bicuculline produced a decrement on figure trials but not on background trials, whereas a high dose impaired performance on background trials but not on figure trials. Muscimol produced an equivalent, dose-dependent impairment on both types of trials. Finally, CNQX had no consistent effect at either dose. Together, these results further confirm our earlier hypothesis that inhibitory projections from SP to Rt modulate figure-ground discrimination, and suggest that the Rt and the SP/IPS provide a plausible substrate that could perform figure-ground segregation in avian brain.

Abbreviations: TeO, optic tectum; Rt, nucleus rotundus; SP/IPS, nucleus subpretectalis/insterstitio-pretecto-subpretectalis

* Corresponding author at: Department of Psychology, Iowa State University, Ames, IA 50011, Office: W161 Lagomarcino Hall, United States.
E-mail address: macerbo@iastate.edu (M.J. Acerbo).

https://doi.org/10.1016/j.bbr.2018.01.033
Received 28 August 2017; Received in revised form 9 January 2018; Accepted 30 January 2018

1. Introduction

The ability to separate object from its background termed figure-ground segregation is essential for any successful visual system as it allows selecting and attending to the objects that are relevant to the current task. In comparison to backgrounds, figures have a privileged status in primate vision: figures are more likely to be attended, remembered, and acted upon than backgrounds [1–4]. Figure-ground segregation in primate brain occurs relatively early in a course of visual processing, most likely in areas V1 and V2 that contain cells sensitive to figure-ground status or to border ownership [5–7].

Recent evidence suggests that figures have privileged status in avian vision, just as they do in primate vision [8]. Moreover, pigeons more readily perceive smaller areas as figures [9], a result consistent with the effect of smaller area on human figure-ground perception. Given these similarities, it seems reasonable to expect that figure-ground segregation in avian brain will also occur at early stages of visual processing.

Unlike primates, birds process most of their visual input in the collothalamic, or retino-collicular pathway which appears to be functionally analogous to the mammalian lemnothalamic, or retino-geniculate-striate pathway [10,11]. Collothalamic pathway begins by transmitting retinal input to a contralateral optic tectum (TeO), and then to the thalamic nucleus rotundus (Rt).

The TeO maintains precise retinotopic organization with narrowly tuned receptive fields in outer layers [12–14] and progressively wider receptive fields in deeper layers [14–17]. In contrast, visual information is segregated functionally in the Rt, with color-sensitive cells in the dorsoanterior region, motion-sensitive cells in the posterior region, and luminance-sensitive cells in the central region [18]. In addition to excitatory input from TeO, the Rt also receives inhibitory input from several thalamic nuclei, with the nucleus subpretectalis/interstitio-pretecto-subpretectalis complex (SP/IPS) providing the main source of inhibitory modulation of rotundal activity [19–21].

Immunohistochemical data show that the cells of SP/IPS receive GABAergic as well as glutamatergic input [22]; in addition, the cells themselves have been shown to be GABA-reactive [19,20]. Finally, thalamic areas of avian visual system contain GABA receptors [19,23–25] as well as the AMPA receptors [22], although the exact distribution of these receptors in the pigeon SP/IPS is unknown.

Our previous research has shown that figure-ground discrimination was associated with a strong metabolic activity of the Rt and the SP/IPS complex [26]. Furthermore, we reported that chemical lesions of the SP/IPS complex significantly impaired figure-ground discrimination but had no appreciable effect on color discrimination or shape discrimination [27], again suggesting that the Rt and its inhibitory complex, the SP/IPS, are likely to be critical structures involved in figure-ground segregation in avian brain. This hypothesis is consistent with the current understanding of figure-ground segregation in primate brain that is thought to involve excitatory feedforward projections as well as inhibitory lateral and feedback projections [5,7,28,29].

The goal of the current research was to further investigate this hypothesis by conducting a pharmacological manipulation of the SP/IPS complex during figure-ground discrimination task. Specifically, we employed the microinjections of bicuculline and muscimol to manipulate inhibitory GABA input from the SP/IPS to the Rt and the microinjections of CNQX to manipulate excitatory input from the TeO to the SP/IPS. If figure-ground segregation in avian brain involves an interaction of inhibitory and excitatory input as it does in primate brain, then all of these microinjections should impair pigeons' ability to discriminate figures from grounds.

2. Method

2.1. Subjects

Thirteen mixed-breed pigeons (*Columba livia*) purchased from local pigeon breeders were housed in a well-ventilated room on a 12:12 h light/dark cycle at Drake University. Pigeons were housed in individual home cages, with grit and water were available *ad lib*. The birds were maintained at 85% of their free-feeding body weight by the delivery of millet during experimental sessions and mixed grain as needed after experimental sessions. All procedures were approved by Drake University Institutional Animal Care and Use Committee and were in accord with the National Institutes of Health guide for the care and use of laboratory animals.

2.2. Apparatus

Four custom-built, 49 × 49 × 47 cm operant chambers were used in the experiment. A 17-in infrared touchscreen with an antiglare acrylic filter (CarrolTouch Model # D27566-001) was placed into a 32 × 22 cm opening on one side of the chamber wall. A 17 in LCD Dell monitor (Dell UltraSharp™ 1708FP producing 300 cd/m^2 white luminance) was placed directly behind the touchscreen, so that pigeons could see most of the display area. The monitor was set to a 1280 × 1024 px resolution. Pecks to the touchscreen were processed by a USB controller board (CarrolTouch 4000U USB controller, Model # E053303).

A second chamber wall opposite the touchscreen contained a 7.6 × 7.6 cm opening to accommodate a grain hopper (MedAssociates Model # ENV-205M) located outside the operant chamber. A house light (an incandescent 28V 0.4 Amp lamp, model 1819, with filament type C-2F producing 4 lumens) mounted above the grain hopper provided illumination during the experiment. The grain hopper and the house light were controlled via a relay board (NuDAQ® PCI-7250, Model # DAQ144). Millet grains served as the food reinforcer.

The relay board and stimulus presentations were controlled by four Dell computers (Optiplex 330 desktop, Intel® Pentium® Dual Core Processor E2160 @ 1.80 GHz, 2 GB DDR2 SDRAM, integrated video card Intel® GMA3100). All experimental procedures were developed in MATLAB® using functions provided by Psychtoolbox [30].

2.3. Drugs

Drug solutions were prepared in the following concentrations of the salt: muscimol hydrobromide (Sigma, Saint Louis, MO) 4.4 mM and 8.8 mM, bicuculline methiodide (Sigma, Saint Louis, MO) 0.05 mM and 0.1 mM, and 6-cyano-7-nitroquinoxaline-2,3-dione, CNQX (Sigma, Saint Louis, MO) 2.15 mM and 4.6 mM. The concentrations of the drugs were based on previous studies using chicks and rats as no studies using pigeons were available [31–33]; the only paper using CNQX microinjections into nucleus accumbens reported no measurable effect [34]. Muscimol and bicuculline were dissolved in sterile artificial cerebrospinal fluid (CSF) containing NaCl 119 mM, $NaHCO_3$ 26.2 mM, KCL 2.5 mM, NaH_2PO_4 1 mM, $MgCl_2$ 1.3 mM and $CaCl_2$ 2.5 mM (pH 7.4). CNQX was dissolved in CSF containing 20% DMSO.

2.4. Stimuli and design

We used the same design of the stimulus display as in our prior report [27] illustrated on Fig. 1A. Two complex shapes (height = 5 cm, width = 7 cm) were shown at the top, the left side, the right side, or the bottom of a square background (9 × 9 cm). Therefore, two Gestalt cues, smaller area and surroundedness, defined these shapes as figures. The color of figure and background alternated between red and green; therefore, a color or its luminance could not serve as a discriminative cue. A small yellow square (1 × 1 cm), or the target, was presented in four possible locations. Each location was equally often used on figure trials and on background trials, so that the location of the target did not predict the correct choice. In total, we used 64 unique stimulus displays (2 colors × 2 shapes × 4 figure locations × 4 target locations).

The pigeons were randomly assigned to one of the six