Adulthood Adaptive Plasticity of the Barn-Owl Auditory Localization System

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Abstract—Studies of the neural system mediating auditory localization in the barn owl provide insight as to how sensory information is processed across and within multiple brain structures. The current study investigates the ability of the adult barn owl to adapt its auditory orienting behavior in reaction to imposed displacement of its vision. The specific aim is to test the hypothesis that adulthood plasticity that compensates for the discordance between vision and audition is enhanced when the owl engages in active prey capture—a behavior that makes use of combined auditory and visual information. Our observation supports the hypothesis. Behavioral evidence of plasticity is interpreted using a computational model of the neural mechanisms associated with the adaptive response.

INTRODUCTION

The auditory localization system of the barn owl (Tyto alba) has been studied extensively and provides a well-understood model of how sound localization cues are processed in parallel pathways as well as how that information is integrated across brain structures. In the barn owl brain, midbrain and forebrain pathways provide two parallel neural subsystems for processing auditory spatial information. While both pathways process sound localization cues, their neural representations of this information differ. The midbrain auditory pathway converges upon a topographic map of auditory space, offering a predictable site for measuring physiological data that can be systematically compared to behavior. For this reason, the midbrain auditory localization pathway has been extensively studied, with particular interest in how neurons within the pathway learn to operate under variously altered sensory paradigms [1,2]. In contrast, the forebrain pathway has not been found to contain a topographic representation of auditory space, relying instead upon a less understood clustered representation of space [3].

Localizing a stimulus source is of importance to animals and humans. Often, one needs to localize an object producing polysensory stimuli. The observer’s task is to combine the visual, auditory and tactile sensory information and to form a coherent perception of both the identity of the object and its location. The midbrain polysensory structures, the mammalian superior colliculus and its avian homologue, the optic tectum, play a major role in achieving a coherent localization of a novel object and in the control of reflexive orienting movements of the head and eyes toward the target object [2,4]. In both mammals and birds, the superficial layers of the structure are mainly visually responsive and they contain a map of visual space; the deep layers of the structure are polysensory and they contain maps of visual and auditory space that are in register to each other [2,4,5].

Much research has been conducted to examine the nature of the midbrain auditory localization pathway as well as its relationship to the visual system. It has been shown that the processing of auditory cues is experience-dependent, and that the visual system provides an instructive signal for the development and interpretation of these auditory cues [6,7]. Elegant experiments addressing this subject have been carried out with barn owls. A popular approach has involved inducing a shift in the visual field by placing prismatic spectacles on the owls. It has been shown that, under this paradigm, young juvenile barn owls can nearly fully adjust auditory orienting behavior in reaction to the prismatically induced visual displacement [8-10]. The literature suggests that there is an upper age limit for the barn owl to effectively learn new auditory-visual relationships. It has been shown that the ability of the adult barn owl (>200 days old) to adapt auditory localization to altered vision is negligible [8-10].

We investigated whether the reduced ability of adults to exhibit plasticity can be enhanced by an enriched sensorimotor experience of actively capturing live prey. Past studies have all used dead rodents as food to the owls [8-11], eliminating the need for the owl to engage in active prey-capture and reducing the need for the owl to accurately integrate auditory and visual spatial information. It is proposed that, by feeding owls live preys, they must actively engage in prey-capture
behavior and that this more challenging auditory-visual-motor task will facilitate adulthood adaptive plasticity and will allow the barn owl to more robustly compensate for auditory-visual discordance.

METHODS

The current study represents the results of one barn owl. This owl was hand-raised and tamed from the age of three weeks and, from the age of 10 mo, was trained to orient its head to auditory and visual stimuli while perched in a sound-proof room. The testing procedure of auditory orienting behavior is similar to a previous study [12]. At the age of 6 mo, the owl began to receive live-mouse prey. At the age of 1 yr and 5 mo, the owl began to wear continuously a sequence of increasingly strong prismatic spectacles (Press-on optics, 3M, St. Paul, MN) that shifted the visual field of both eyes to the right. The prisms shifted the visual field by 6°, 11°, 17° and 23°. Each set of prismatic spectacles was attached for 3–5 weeks. This sequence of prisms is similar to that used by Linkenhoker et al. in a physiological study [11]. Experiments were carried out in a sound-attenuating chamber (model 1203, IAC, New York). The inner walls of the chamber were lined with sound-absorbing panels (3” Sonex, Illbruck, Minneapolis, MN). The chamber was dimly lighted during test to simulate a dusk or dawn. The owl was perched in the center of a 5-ft cube frame of magnetic field coils (Crist Instruments, Hagerstown, MD) driven by a controller (DNI Instruments, Newark, NJ). Angular orientation of the owl’s head was measured using a custom-made sensing coil (22 mm in diameter) mounted on the owl’s head. Stimuli were presented using an array of speakers and light emitting diodes (LEDs) arranged in an arc of radius 95 cm, with the owl at the center. The range of stimulus azimuths presented to the owl were from 38° left to 38° right of the center in steps of 6.3°; the elevations of the stimuli were within a few degrees from zero. The speakers and inactive LEDs were hidden from view behind a black-cloth curtain. The owl’s head position at the beginning of each test trial was controlled by having the owl look at an initialization light stimulus presented by an LED located at zero azimuth and zero elevation.

The owl received a food reinforcement when its orienting response to a target stimulus was in a clear step toward a general vicinity of the target. It did not require a strict precision. Three types of stimuli were presented to the owl; (1) sound alone, (2) light alone and (3) sound and light presented simultaneously in the same position. The latter was used in order to give the owl additional auditory-visual multisensory experience.

Head-orienting data were collected from the owl prior to placement of prisms as well as during prismatic experience. Data were collected on multiple days each week throughout the experiment to determine both a total change in head-orienting response as well as the time course of change.

RESULTS

We observed that the adult owl was able to adapt its head-orienting behavior to the discordance in auditory and visual stimuli. The auditory orienting response was shifted in the adaptive direction minimizing the auditory-visual discordance. The magnitude of the auditory adaptive shift progressed over the initial period of experience with each set of prisms and reached a plateau at the end of each period. The owl’s visual head-orienting responses were approximately constant throughout each prismatic period.

The magnitude of the adaptive plasticity of the auditory orienting response depended heavily upon the hemifield from which the target stimulus was presented, with the adaptation magnitude being much greater for the left-side targets than for the right-side targets in the owl wearing right-shifting prisms. For the left-side targets, the mean adaptive shift of the auditory orienting behavior of the owl was a large proportion of the shift of the visual response. However, the auditory adaptive shift for the right-side targets was much smaller. The owl’s visual orienting response also exhibited a left-right difference such that the mean shift of the visual response was larger for the left-side targets than for the right-side targets.

DISCUSSION

The main finding of the present study is that, when the adult barn owl is allowed to engage in active prey-capture, the adulthood auditory plasticity can reduce an auditory-visual discordance to a surprisingly low degree, at least for targets in one hemifield. The adulthood plasticity observed in this behavioral study is greater than that observed in a previous physiological study where adult owls underwent a similar incremental sequence of prisms while receiving dead-rodent food [11]. In the studies that used dead-rodent food, adult owls that experienced single steps of 17° or 23° prisms exhibited much less adaptive plasticity than that observed with incremental prismatic shifts [11]. Thus, the present observation supports the hypothesis that adulthood adaptive plasticity of the auditory localization system is enhanced by an enriched sensorimotor experience of active prey-capture. Bergan et al. [13] conducted a physiological study of the optic tectum of adult owls addressing the same hypothesis as the above, and the conclusions of Bergan et al. and the present study are consistent with each other.

The left-right difference in the auditory adaptive plasticity during prismatic experience is a new finding. Data analysis in past research was restricted to examination of average values of adaptive shift in which information about the dependence of the response on the absolute location of the stimulus was lost. The left-right difference in auditory orienting response reported in the present study underscores the importance of explicitly examining the relationship between the orienting responses as a function of the absolute stimulus position. How to explain the phenomenon of the left-right difference in auditory adaptive plasticity is currently unclear.

In conjunction with the current experimental study, a computational model has been developed which intends to
represent the instructive learning of the auditory localization system.

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