Experience-Dependent Plasticity for Auditory Processing in a Raptor

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A growing consensus in the neurosciences is that neural plasticity remains open throughout life, often driven by critical experiences (*1*). Almost all of the work on plasticity in vertebrates comes from studies in captivity using restrained animals and neurophysiological preparations; most are based on tasks that are removed from the types of problems these animals confront in nature. Here, we present the results of playback experiments to wild and captive harpy eagles that provide evidence of experience-dependent plasticity in a lateralized response, using a task that taps a specialization for orienting to highly meaningful acoustic stimuli.

Harpy eagles are the principal aerial predator of primates in the neotropics; in Central America, the mantled howler monkey is one of their primary prey species (*2*). Acoustic signals are a primary channel for communication and information gathering in these two species (*3*). Like owls, harpies have specialized facial structures (a ruff) for enhancing sound localization (Fig. 1A).

We compared the orienting responses of adult and juvenile harpies with or without experience preying on howlers. We compared four captive inexperienced harpies (two adults and two juveniles; age: 2 to 50 years) with three experienced wild (Panamanian rainforest) adult (age: 6 to 50 years) harpies, using a task that requires directional orienting to a sound source. The method, previously used with success on free-ranging rhesus macaques (*4*), involved placing a speaker 180° behind a subject when facing a food trough and then playing back an acoustic signal. The assay for evaluating lateralization was the direction of head turning toward the concealed speaker within 2 s of playback.

We concealed a speaker and video camera directly behind the subject and then played one of four different stimulus conditions (Fig. 1B). The acoustic stimuli tested whether the direction of orienting to a sound source was influenced by the following distinctions: conspecific-heterospecific, prey-nonprey, biological-nonbiological, and familiar-unfamiliar. As a conspecific stimulus, we used the harpies' contact call. The heterospecific prey call was a howler roar, used in territoriality. The heterospecific nonprey call was from a tinamou, a common bird in the area. As a nonbiological stimulus, we used a pure tone that fell within the spectro-temporal range of the other stimuli. All subjects had been exposed to the three biological sounds throughout life, but only the experienced harpies had hunted howler monkeys.

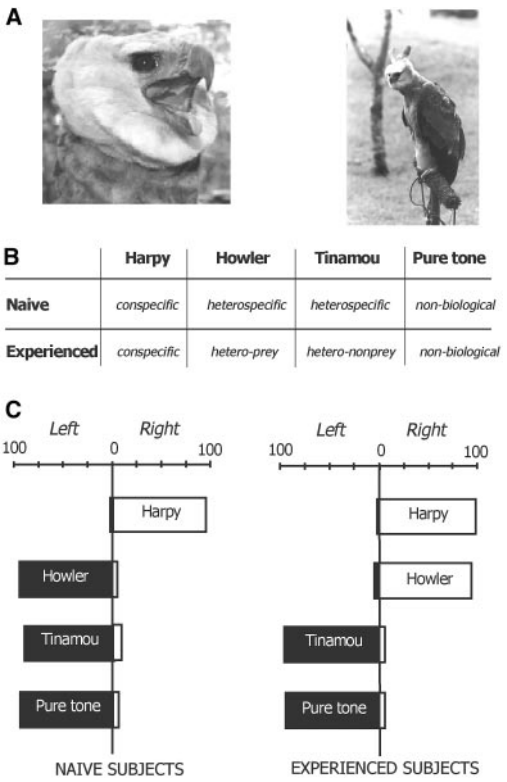

Fig. 1. (**A**) Adult harpy eagle orienting facial ruff to an acoustic signal (left) and captive juvenile on test perch (right). (**B**) Stimulus condition by experience. We presented experienced and naïve harpies with four different stimuli (harpy, howler monkey, tinamou, and pure tone) and measured their orienting responses. The howler is considered a prey species for the experienced harpies because only they have hunted them; naïve harpies have heard howler calls, making them acoustically familiar, but not identifiable as a prey species. (**C**) Percentage of orienting responses (left, black; right, white) to each of the four stimuli as a function of subject experience. Contrast analyses were carried out for lateralization of response and experience for all conditions using eagle as the point of comparison. All contrasts were Bonferroni adjusted to $P = 0.0125$. The only statistically significant contrast was for the howler condition, with naïve harpies orienting left and experienced howlers orienting right.

Each session, separated by 1 to 2 days, consisted of six trials spaced from 10 to 30 min apart and initiated when the head was oriented 180° away from the speaker and immobile for a minimum of 5 min; this ensured that responses were not biased by visual stimuli. We ran 18 trials per condition per subject. Each video trial was digitized and scored blind with respect to condition by first marking the onset and offset of the signal with a label and then turning off the sound and recording the direction of orienting.

Results (Fig. 1C) reveal highly significant effects of experience [repeated measures ANOVA, $F(1,5) = 41.43$, $P < 0.001$] and stimulus condition [$F(3,3)=1394.44$, $P < 0.0001$]. Both naïve and experienced harpies turned significantly to the right when orienting to harpy calls but turned significantly to the left for tinamou calls and pure tones. The effect of experience was only significant for the howler calls: Naïve harpies oriented to the left, whereas experienced harpies oriented significantly to the right [$F(1,5) = 73.673$, $P < 0.0001$]. Thus, for naïve harpies, howlers elicit the same kind of orienting response as do tinamous and pure tones, whereas for experienced harpies, howler calls elicit the same orienting response as do harpy contact calls. Neither age nor familiarity can explain these results because the naïve and experienced harpies overlap in age and all birds have heard howler calls throughout their lives.

These results provide evidence of an orienting asymmetry, altered by explicit hunting experience. As in barn owls, (*5*), our results show that the active experience of hunting, which presumably combines visual and tactile information, modifies auditory processing, shifting an initial left ear bias to a right ear bias. If the asymmetry is in the forebrain, as assumed in behavioral studies of rhesus monkeys (*4*) and human infants (*6*), then the documented right ear/left hemisphere asymmetry for harpy and howler calls presents a challenge to the claim that this bias evolved for language as opposed to some more general auditory or cognitive function.

References

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