

Development of auditory sensitivity in budgerigars (*Melopsittacus undulatus*)

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(Received 24 January 2003; revised 6 March 2004; accepted 15 March 2004)

Auditory feedback influences the development of vocalizations in songbirds and parrots; however, little is known about the development of hearing in these birds. The auditory brainstem response was used to track the development of auditory sensitivity in budgerigars from hatch to 6 weeks of age. Responses were first obtained from 1-week-old at high stimulation levels at frequencies at or below 2 kHz, showing that budgerigars do not hear well at hatch. Over the next week, thresholds improved markedly, and responses were obtained for almost all test frequencies throughout the range of hearing by 14 days. By 3 weeks posthatch, birds' best sensitivity shifted from 2 to 2.86 kHz, and the shape of the auditory brainstem response (ABR) audiogram became similar to that of adult budgerigars. About a week before leaving the nest, ABR audiograms of young budgerigars are very similar to those of adult birds. These data complement what is known about vocal development in budgerigars and show that hearing is fully developed by the time that vocal learning begins. © 2004 Acoustical Society of America. [DOI: 10.1121/1.1739479]

PACS numbers: 43.64.Ri, 43.64.Tk [WWA]

Pages: 3092–3102

I. INTRODUCTION

The auditory brainstem response (ABR) has been an effective tool for studying the development of auditory sensitivity in a wide variety of mammals. ABRs recorded from altricial mammals show elevated thresholds, prolonged latencies, and diminished amplitudes early in development (e.g., Boettcher *et al.*, 1993a, 1993b; Burkard and Voigt, 1989; Burkard *et al.*, 1996b; Jewett and Romano, 1972; Mair *et al.*, 1978; McFadden *et al.*, 1996; Mills *et al.*, 1990; Walsh *et al.*, 1986a,b,c). Developmental ABR studies in precocial birds show the same general trends (Dmitrieva and Gottlieb, 1992, 1994; Saunders *et al.*, 1973, 1974), but there are no ABR studies relating hearing, latency, and amplitude development in altricial birds.

Although there are some similarities in hearing development across vertebrate classes, there can also be large differences in maturational state at birth and in the rate of postnatal maturation with regard to hearing, especially across precocial and altricial species. For precocial birds, like chickens and ducks, auditory sensitivity begins to develop while the animal is still in the egg and is adult-like at low to mid frequencies at hatching (Dmitrieva and Gottlieb, 1992; Saunders *et al.*, 1973, 1974). On the other hand, altricial birds, such as songbirds and parrots, are probably more comparable to altricial mammals than precocial birds in terms of mode of hearing maturation (see Aleksandrov and Dmitrieva, 1992).

The budgerigar (*Melopsittacus undulatus*), a small Australian parrot, is one of the most widely studied altricial parrots and has been the focus of many studies of hearing and vocalizations (see reviews in Dooling *et al.*, 2000; Farabaugh and Dooling, 1996). Budgerigars are open-ended vocal learners who rely on hearing for learning and maintaining their vocal repertoire. Isolation, or other unusual acoustic and so-

cial rearing conditions, has little effect on the budgerigars' long-term ability to produce and imitate species-specific vocalizations (Brittan-Powell *et al.*, 1997). Deafening, on the other hand, causes major disruptions in vocal production (Dooling *et al.*, 1987; Heaton and Brauth, 1999; Heaton *et al.*, 1999). A study of auditory development in this species may set the stage for more refined questions of the role of hearing in vocal learning in this species.

ABR responses to both clicks and tone-burst stimuli in adult budgerigars can be recorded from the scalp and provide a reliable measure of hearing sensitivity in these birds (Brittan-Powell *et al.*, 2002). Little is known about the development of the middle ear, the sensory epithelium with hair cells and accessory structures, or the innervation of the auditory system in budgerigars, and nothing is known about when these structures are mature enough to support synchronous neural activity necessary for the emergence of auditory brainstem responses. Here, we address development of hearing in nestling budgerigars by recording ABRs to determine both the onset and development of hearing sensitivity. In two experiments, we measured ABRs elicited by clicks and tone-burst stimuli in nestling budgerigars. Experiment 1 tracked the maturation of hearing thresholds and other ABR details as a function of age, intensity, and frequency. Experiment 2 examined the effects of increased presentation rate on ABR wave latency and amplitude as a function of development.

II. METHODS

Nestling budgerigars served as subjects in these experiments. The birds were reared in standard wooden nest boxes attached to small wire cages (37.5×30×37.5 cm) and housed in an avian vivarium at the University of Maryland. Over the course of the experiment, there were approximately 70–80 birds housed in the animal colony with all birds tested raised under similar acoustic conditions. Nestlings were

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taken from their nests 5–10 min prior to testing and returned to their nests once they recovered from anesthesia. No supplemental care was given by the experimenters.

All birds used in this study were sedated with either an intramuscular injection (for fledglings and older nestlings) or a subcutaneous injection (younger nestlings) of ketamine (25–50 mg/kg) and diazepam (2 mg/kg) prior to electrode placement. Older animals remained relatively motionless for up to 75 min, whereas younger animals metabolized the anesthetic typically within 30 min. Animals were given up to two supplementary injections, as needed. Body temperature was maintained at $41 \pm 0.5^\circ\text{C}$ for older animals and $35\text{--}38 \pm 0.5^\circ\text{C}$ for younger animals by placing the bird on a heating pad with a thermistor probe placed under the wing (temperature control unit; Frederick Haer and Co., model 40-90-2 and 40-90-5, Bowdoinham, ME).

The procedure for recording ABRs in budgerigars has been described earlier (Brittan-Powell *et al.*, 2002). The bird was positioned so that the speaker (KEF SP 3235, model 60S, frequency range 100 Hz to 20 kHz, KEF Electronics of America, Inc., Holliston, MA) was 30 cm from the bird's right ear (90° azimuth relative to the bird's beak; 0° elevation relative to the bird's right ear). Standard platinum alloy, subdermal needle electrodes (Grass F-E2; West Warwick, RI) were placed just under the skin in the conventional electrode array: high at the vertex (noninverting), directly behind the right ear canal (the ear ipsilateral to the speaker, inverting), and directly behind the left ear canal (the ear contralateral to stimulation, common). The stimulus presentation, ABR acquisition, equipment control, and data management were coordinated using a Tucker-Davis Technologies (TDT, Gainesville, FL) modular rack-mount system controlled by an optical cable-linked 350-MHz Pentium PC containing a TDT AP2 digital signal process board and running TDT BIOSIG software. Sound stimuli were generated using TDT SIGGEN software and fed through a DA1 digital-analog converter, a PA4 programmable attenuator, and a power amplifier (HB6) which directly drove the speaker. The electrodes were connected to the TDT HS4 Headstage which amplified and digitized the signal before being relayed over fiberoptic cables to the TDT DB4 digital biological amplifier. This amplifier also allowed additional filtering and gain to be added. A TDT TG6 timing generator synchronized the A/D and D/A conversion.

Stimulus intensities were calibrated in the free field by placing the $\frac{1}{2}$ -in. microphone of a sound-level meter (System 824; Larson Davis, Inc. Provo, UT) at the approximate position of the bird's right ear. Continuous tones, with the same peak-to-peak amplitude as the subsequently used tone bursts, were generated using the TDT BIOSIG program and measured using the fast-weighting A scale on the sound-level meter (dB SPL). To determine the intensity of the click, we used the peak equivalent SPL of the click. This was determined using an oscilloscope and noting the peak-to-peak voltage of the click. A test tone, e.g., a 1000-Hz tone, was played and adjusted until the peak-to-peak voltage was the same as it was for the click. The SPL required to match the amplitude of the click, as indicated by the sound-level meter, was the peak equivalent SPL (dB pSPL) of the click stimulus.

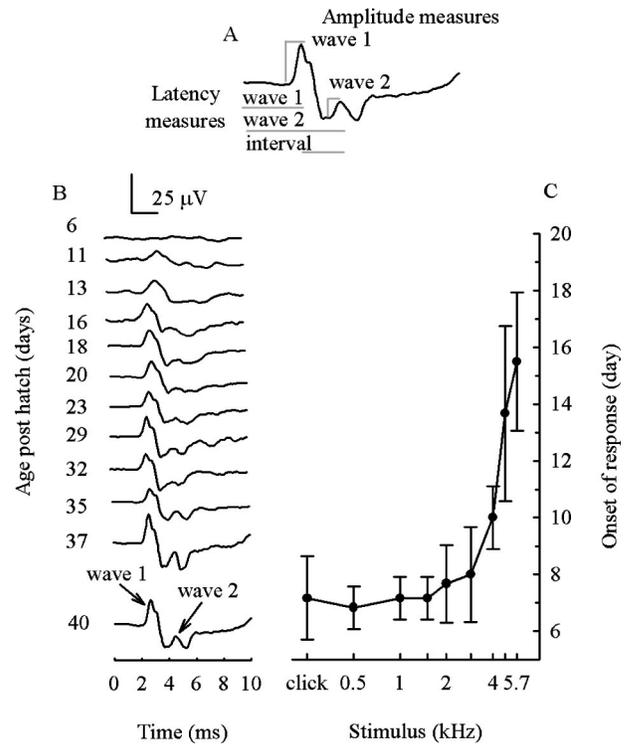


FIG. 1. (A) Schematic showing how latency and amplitude measurements were taken for waves 1 and 2. (B) Typical ABR waveforms in response to the click (85 dB pSPL) for a single nestling. For this bird, wave 1 can be discerned by day 11 and followed as it decreases in latency and increases in amplitude. By 16 days of age, wave 2 can be seen. From day 37–40, there is little change in the waveform. (C) Average age of onset of a response as a function of stimulus frequency. Responses to low and middle frequencies appear first, with high-frequency responses appearing at later ages. The bars are s.d.

For all experiments, only the first two wave components of the ABR waveform, designated by sequential Arabic numerals, were described by their amplitude and latency characteristics [Fig. 1(A); see also, Brittan-Powell *et al.*, 2002]. Positive evoked potential peaks were identified manually by cursor control and associated latencies and amplitudes were automatically stored by the computer. Latencies to wave 1 and wave 2 were corrected for conduction delays between the sound source and the entrance of the ear canal of the animal (0.88 ms). The latency of the interwave interval (referred to as 1–2 interval) was calculated as the difference in latency from the peak of wave 1 to the peak of wave 2. ABR wave amplitudes were measured using baseline-to-peak for wave 1 and peak-to-peak (preceding trough) amplitude for wave 2.

III. EXPERIMENT 1: THE DEVELOPMENT OF AUDITORY SENSITIVITY

A. Subjects

Four of the six birds used in this experiment originated from three different broods produced by the same parents over a span of 6 months. The other two birds were brood mates. Where feasible, ABRs were recorded every 2–3 days during the first 2 weeks posthatching and every 3–5 days

during the last 4 weeks of the study. The day of hatch is denoted as day 0. Each individual bird was recorded a minimum of 13 times, from approximately day 5 until 1 week postfledging (about day 43).

B. Stimuli

The sound stimulation protocol is the same as used in Brittan-Powell *et al.* (2002). Briefly, subjects were presented with multiple intensity stimulus trains that varied in frequency and intensity. Each train consisted of nine single clicks or frequency tone bursts that increased in intensity (5–10-dB steps, depending on age) and were presented at a rate of 4/s. The rectangular-pulse broadband clicks were 0.1 ms in duration, with a 25-ms interstimulus interval (ISI). Each individual tone burst was 5 ms in duration (1-ms rise/fall \cos^2) with a 20-ms ISI. The tone bursts used were 0.5, 1, 1.5, 2, 2.86, 4, 4.8, and 5.7 kHz, with the highest stimulus intensity employed being 95–100 dB SPL. High-intensity tone bursts were played through the speaker and sampled at 40 kHz into the A/D module of the TDT rack. Spectra of these tone bursts were generated using 1024-pt fast Fourier transform (FFT). Spectral analysis showed all second and third harmonics were at least 30 dB down from the peak of the frequency of interest, except for the first harmonic of the 0.5-kHz stimulus, which was 18 dB down.

Each ABR was sampled at 20 kHz for 235 ms following onset of the stimulus train. This allows for 25-ms recording time for each stimulus. Five hundred averages for each polarity/phase were added together to cancel the cochlear microphonic. The biological signal was amplified ($\times 100$ K) and notch filtered at 60 Hz with the DB4 during collection. The signal was bandpass filtered below 0.03 kHz and above 3 kHz after collection using the BIOSIG program.

C. Analysis

ABR waveforms produced in response to high intensities were examined visually to determine which peaks would be used to measure latencies, amplitudes, and thresholds. A response was expected between 1 ms after the onset of the stimulus (travel time from the speaker to the ear) and 15 ms because the response latency tends to be longer in younger animals and also increases at low SPLs in all animals. Using this time window, the wave components were described by their latency and amplitude characteristics.

Response onset was defined as the earliest age at which ABR waves met the following criteria: (1) the response showed at least one positive deflection within the latency range described above [see Fig. 1(B), day 11 for example] and (2) the response was replicable on successive trials (onset of response criteria was modified from Walsh *et al.*, 1986a).

ABR threshold was defined as the intensity 2.5 dB (one-half step in intensity) below the lowest stimulus level at which a response could be visually detected on the trace, regardless of wave (see, for example, Boettcher *et al.*, 1993a). On a few occasions, a response could still be detected at the lowest intensity presented. In all of these cases, the peak amplitudes of the responses to the series of higher

intensity stimuli showed decreasing response amplitudes that indicated that the next intensity step would not evoke a visible response. In these cases, threshold was defined as 2.5 dB below the lowest intensity presented.

All data for the different response variables (e.g., threshold, latency, amplitude) were excluded from the analysis if only one of the six nestlings for that age met the criteria defined above. In other words, at least two birds are represented in every averaged data point and at least two birds for the given time point met the above defined criteria when individual data were used. Individual data were used for all statistical tests. For averaged plots, responses for the nestlings were averaged across 3-day periods (e.g., 4–6-days posthatching), except for the last time period that consisted of a 4-day period (days 40–43). In all figures, the median age of the time period is shown on the abscissa. The dependent variables examined were threshold, latency, and amplitude.

All ABR data collected from the nestling budgerigars were analyzed in a manner similar to that collected from adult budgerigars under the same conditions (as reported in Brittan-Powell *et al.*, 2002).

D. Results

1. Onset

Example ABR waveforms in response to an 85-dB pSPL click are shown for an individual nestling from 6–40 days of age [Fig. 1(B)]. The ABR waveforms from the youngest birds possessed at least one long-duration positive wave which was low in amplitude ($< 2 \mu\text{V}$) and had a prolonged latency (about 4–5 ms). This was the case for all responses, regardless of frequency. This positive-going deflection corresponded to wave 1 of the adult budgerigar ABR waveform. As the animal aged, wave latencies decreased and wave amplitudes increased. The overall waveform was adult-like by 5 weeks of age.

ABR responses could first be evoked by low frequencies and then to increasingly higher frequencies [Fig. 1(C)]. By the end of the first week, responses were typically obtained to frequencies up to 2.86 kHz, and by the end of the second week, the bandwidth of frequencies extended up to 4.8 kHz. Responses could be elicited at all test frequencies by the bird's third week posthatch.

2. Threshold

Figure 2 shows thresholds over time. These data were fitted with exponential decay functions $y = a + be^{-cx}$, where a was the asymptote of the curve, b was the intercept, and c represented the curvature (see Walsh *et al.*, 1986a) (see Table I for parameters). Since a represented an asymptote in threshold improvement, this value most closely corresponded to adult levels of sensitivity as measured by the ABR. When b was large, the values declined along a steep trajectory. The reciprocal of c provided the time constant of the function. In general, frequencies up to and including 4 kHz showed rapid decreases in threshold that stabilized by day 30. Thresholds

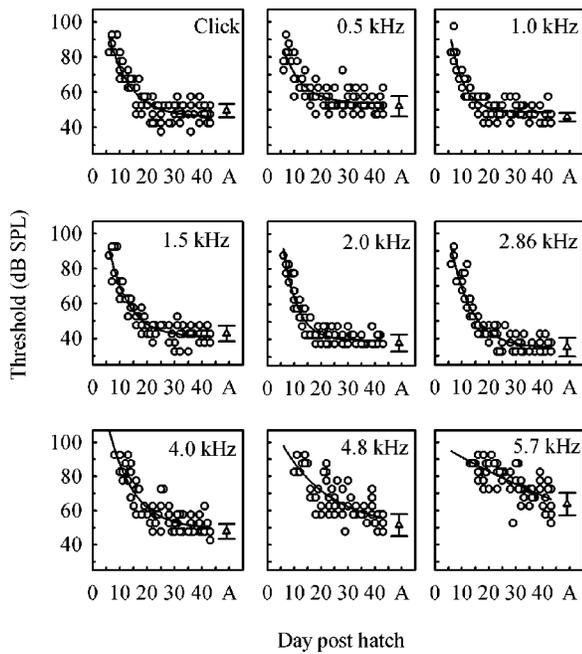


FIG. 2. Exponential decay functions are shown for the individual nestling threshold data (open circles), with parameters presented in Table I. In general, nestlings attain adult thresholds (A=average thresholds for adult with open triangles with s.d. bars; adult data from Brittan-Powell *et al.*, 2002) for most frequencies by 17–20 days of age. Overall, the data were represented well by exponential decay functions except for 5.7 kHz, where the decay was linear ($y = -0.74x + 99.3$).

were more variable at the higher frequencies but still showed decreases as the animal aged. Overall, the exponential decay functions fit the data well ($r^2 > 0.75$; Table I) for the click as well as frequencies between 1–4 kHz.

To determine the ages where nestlings' thresholds differed from the adult budgerigars, one-way ANOVAs were performed on the individual data for each frequency. As expected, there was a significant decrease in threshold at all frequencies as the birds aged (see Table II). *Post hoc* t-tests (Tukey-Kramer HSD) revealed the ages where nestling thresholds differed from the adult thresholds. By 16–18 days of age, ABR thresholds for the click and 0.5, 1.0, 1.5, and 2.0 kHz for nestlings were no longer significantly different from adult thresholds. Thresholds for 2.86 and 4.0 kHz were adult-like by the end of the third week of life, whereas thresholds for 5.7 kHz did not reach adult levels until approximately 1 month of age.

TABLE II. ANOVA results for when nestlings' thresholds differed from adult thresholds.

Stimulus	df	F	P
Click	13, 62	33.32	0.0001
0.5	13, 63	14.65	0.0001
1.0	13, 62	19.30	0.0001
1.5	13, 62	41.05	0.0001
2.0	13, 61	41.42	0.0001
2.86	13, 60	46.70	0.0001
4.0	11, 57	21.03	0.0001
4.8	11, 50	12.60	0.0001
5.7	10, 49	7.09	0.0001

Threshold changed significantly as a function of frequency at different developmental time periods [$F(63,198) = 0.0845$, $p = 0.002$; see Fig. 3]. The ABR audiogram for the earliest ages (e.g., end of the first week) was relatively flat between 0.5 and 2.86 kHz and showed poor sensitivity across frequency. By 14 days, the thresholds improved between 20–40 dB for frequencies below 4 kHz. The smallest improvement in threshold was for 5.7 kHz (20-dB improvement from day 14–42). At approximately 20 days, there was a shift in the frequency of best hearing from 2 to 2.86 kHz. Even though the audiograms for birds 1 month and older were not significantly different from that of adults [$F(35,95) = 0.396$, $p = 0.911$], nestlings' absolute sensitivity above 2.86 kHz remained 15 dB higher than adult values until around the time of fledging.

As a check on the validity of the visual detection level definition of threshold, a second threshold estimate was also used. Here, threshold was defined as the lowest stimulus intensity corresponding to a response amplitude of $0.5 \mu\text{V}$ (at least 1 s.d. above the mean noise level). A one-way multivariate analysis of variance (MANOVA) showed no significant differences between the threshold estimates [$F(1,104) = 0.969$, $p = 0.07$].

3. Latency and amplitude

Latency decreased and amplitude increased with increasing intensity level for all peaks in the ABR waveform. There were also age-dependent effects. As the animal aged, peak latencies to wave 1 and 2 decreased (Fig. 4) and peak amplitude increased (Fig. 5). Peak latencies were the longest during the first 2 weeks posthatch. Latencies for wave 1 de-

TABLE I. Decaying exponential parameters for threshold ($y = a + be^{-cx}$).

Frequency	Asymptote (a)	Y-intercept (b)	Curvature (c)	Time constant (1/c)	r^2
Click	45.75	95.16	0.122	8.2	0.81
0.5	53.50	72.26	0.142	7.0	0.66
1	48.56	137.38	0.200	5.0	0.80
1.5	40.90	115.44	0.138	7.3	0.85
2	39.38	162.51	0.189	5.3	0.88
2.86	34.51	127.49	0.131	7.6	0.88
4	48.88	112.27	0.108	9.26	0.76
4.8	49.36	67.70	0.056	17.86	0.58
5.7	-3.76	104.04	0.009	111.00	0.45

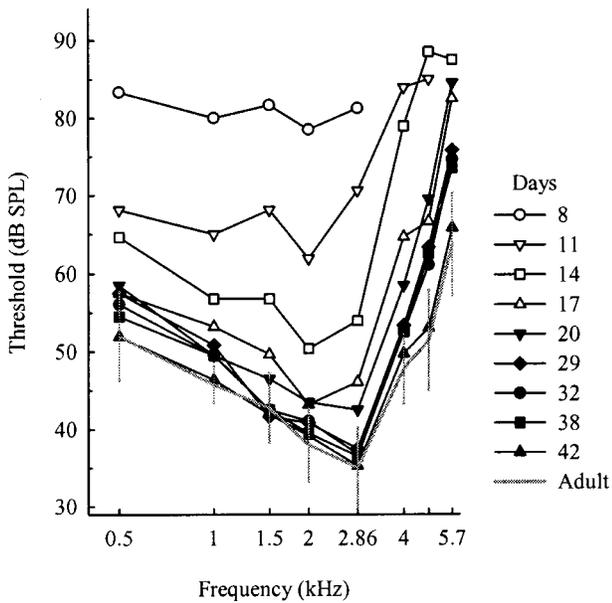


FIG. 3. Average ABR audiograms over development for six nestlings. The solid gray line represents the adult average \pm s.d. (Brittan-Powell *et al.*, 2002). There is a considerable change in threshold from 8–17 days, after which thresholds improve more slowly, with lower frequency thresholds becoming adult-like first, followed by middle and higher frequencies.

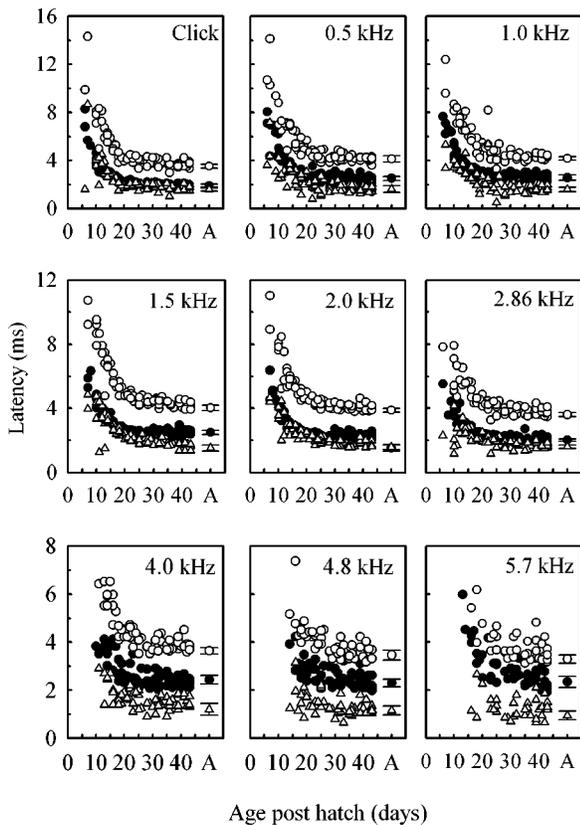


FIG. 4. Latencies to the peaks of wave 1 (closed circles), wave 2 (open circles), and the 1–2 interval (open triangles) plotted as function of age for a constant intensity level of 85 dB SPL. Latency decreases as a function of increasing age, but the 1–2 interval remains fairly consistent throughout development. A=adult average \pm s.d. (Brittan-Powell *et al.*, 2002) with symbols being the same as for the nestlings (e.g., closed circles=wave 1).

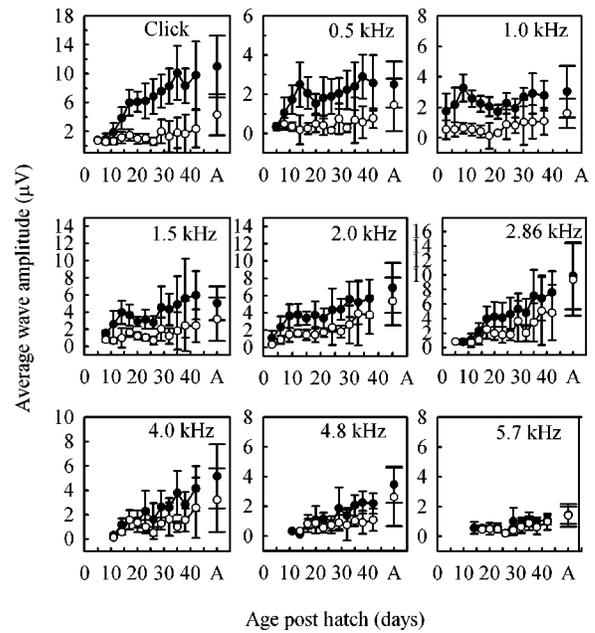


FIG. 5. Average t.s.d. peak amplitudes for wave 1 (closed circles) and wave 2 (open circles) plotted as function of age for a constant intensity level of 85 dB SPL. Amplitude for both wave 1 and wave 2 increases as the animal ages, but the growth of wave 2 amplitude occurs at a later age. A=adult average \pm s.d. (Brittan-Powell *et al.*, 2002) with symbols being the same as for the nestlings (e.g., closed circles=wave 1).

creased from 4–12 ms to the adult average of 2–3 ms by the end of week 3. Similar decreases were seen for wave 2 latencies. Exponential decay functions fit to the data shown in Fig. 4 (see Table III for parameters) revealed that the overall rate of latency decay was high for all frequencies (as indicated by large b term) and that wave 1 matured faster than wave 2, except at 4 kHz (as indicated by smaller time constants). Lower frequencies showed more change in latency than higher frequencies perhaps because responses to lower frequencies were first recorded 7–10 days earlier than responses for higher frequencies. Increasing the intensity level presented to the nestlings at high frequencies may have resulted in similar latency changes at higher frequencies. Even so, latencies and intervals between the peaks were typically within 1 s.d. of the adult values by one month of age for all frequencies (see Fig. 4).

Peak amplitude of wave 1 in young animals ranged from 1 to 8–18 μ V for the frequencies within the birds' best range of hearing. Wave 2 amplitudes were always low (below 2 μ V) in the early weeks and rarely exceeded 4–6 μ V. Figure 5 shows the average peak amplitudes of wave 1 and 2 as a function of age. Linear regressions fit to the individual data showed r^2 that ranged between 0.03–0.51 for wave 1 and 0.04–0.25 for wave 2. Amplitudes increased for all waves with age but by varying degrees. Wave 1 peak amplitudes showed nearly linear increases for the click and 1.5–4 kHz. Compared to the increases seen in wave 1, amplitudes for wave 2 showed little amplitude growth until approximately 1 month of age, especially for low (0.5–1.5 kHz) and high frequencies (4.8–5.7 kHz). Again, the high-frequency data may be accounted for by the lack of a definable response before 15 days posthatch.

TABLE III. Decaying exponential parameters for latency ($y = a + be^{-cx}$).

Frequency	Wave	Asymptote (a)	Y-intercept (b)	Curvature (c)	Time constant (1/c)	r^2
Click	1	1.98	20.20	0.22	4.6	0.96
	2	3.59	23.60	0.17	5.9	0.86
0.5	1-2 interval	1.58	7.30	0.12	8.3	0.53
	1	2.30	14.44	0.17	5.9	0.85
	2	4.10	21.97	0.17	5.9	0.88
1	1-2 interval	1.64	7.48	0.14	7.1	0.60
	1	2.63	18.23	0.21	4.8	0.94
	2	4.19	19.13	0.15	6.7	0.85
1.5	1-2 interval	1.47	6.32	0.10	10	0.59
	1	2.46	13.45	0.19	5.3	0.91
	2	4.14	16.94	0.14	7.1	0.87
2	1-2 interval	1.59	6.31	0.11	9.1	0.73
	1	2.26	14.09	0.21	4.8	0.92
	2	4.02	19.85	0.17	5.9	0.91
2.86	1-2 interval	1.71	7.05	0.13	7.7	0.81
	1	2.06	9.17	0.16	6.3	0.86
	2	3.66	8.91	0.12	8.3	0.80
4	1-2 interval	1.25	1.81	0.04	25.0	0.34
	1	2.24	7.16	0.12	8.3	0.54
	2	3.79	18.10	0.16	6.3	0.79
4.8	1-2 interval	1.48	16.75	0.23	4.4	0.42
	1	2.41	20.18	0.19	5.3	0.42
	2	3.47	13.39	0.13	7.7	0.57
5.7	1-2 interval	1.11	2.90	0.09	11.1	0.21
	1	2.49	35.12	0.19	5.3	0.74
	2	3.57	27.04	0.16	6.3	0.48
	1-2 interval	1.18	4.53	0.14	7.1	0.07

IV. EXPERIMENT 2: EFFECTS OF CLICK REPETITION RATE ON ABR LATENCY AND AMPLITUDE IN DEVELOPING BUDGERIGARS

A. Introduction

The effects of increasing presentation rate on ABRs have been well studied in both developing and mature animals. Generally, ABRs can be elicited to stimulus presentation rates as high as 100 clicks/s in the mature auditory system but not in the immature auditory system of the same animal (Jewett and Romano, 1972). In adult humans and other mammals, reduced ABR amplitudes and increased ABR latencies in response to high presentation rates may be a function of neural fatigue and adaptation (e.g., Burkard and Voigt, 1989; Donaldson and Rubel, 1990; Hall, 1992; Jewett and Romano, 1972). Other studies have shown that increasing the stimulus presentation rate produces greater latency and amplitude changes in young animals as compared to older animals (e.g., Burkard and Voigt, 1989; Burkard *et al.*, 1996a,b; Donaldson and Rubel, 1990; Mair *et al.*, 1979; Shipley *et al.*, 1980). The working hypothesis is that adaptation associated with reduced synaptic transmission (e.g., decreased axon diameter, incomplete myelination, and neurotransmitter reuptake) may be the neurophysiological basis for the interaction between age, rate, and ABR latency and amplitude (Burkard *et al.*, 1996a,b; Hecox, 1975).

As far as we know, a developmental ABR rate study has only been measured in one bird, the chick (Saunders *et al.*, 1973). In the chick, and probably other precocial birds, the relation between stimulus rate and ABR latency and ampli-

tude is almost adult-like at hatch. Such a pattern of development is different from altricial mammals, which do not show adult-like responses to temporal properties of the stimulus at birth. This experiment examined responses to changes in the temporal patterns of the click in five developing budgerigars. All equipment and recording procedures were the same as in experiment 1, except where noted.

B. Stimuli

Short-duration (0.1 ms), broadband clicks were presented at 100 dB pSPL for each of five rates: 5, 10, 30, 60, and 90 per second (Hz). Each ABR represents the average response of 1000 stimulus presentations (500 averages for each polarity), sampled at 20 kHz for 10 ms following onset of the stimulus. As with experiment 1, the biological signal was amplified ($\times 100$ K) and notch filtered at 60 Hz during collection. The signal was bandpass filtered below 0.03 and above 3 kHz after collection.

C. Analysis

As described earlier, latency and amplitude measures were calculated for waves 1 and 2 for all repetition rates.

D. Results

Responses from animals less than 2 weeks of age were poorly developed. The waveform had only one positive-going wave that was relatively low in amplitude (below 3 μ V) and had a latency which exceeded 4 ms. As the animals

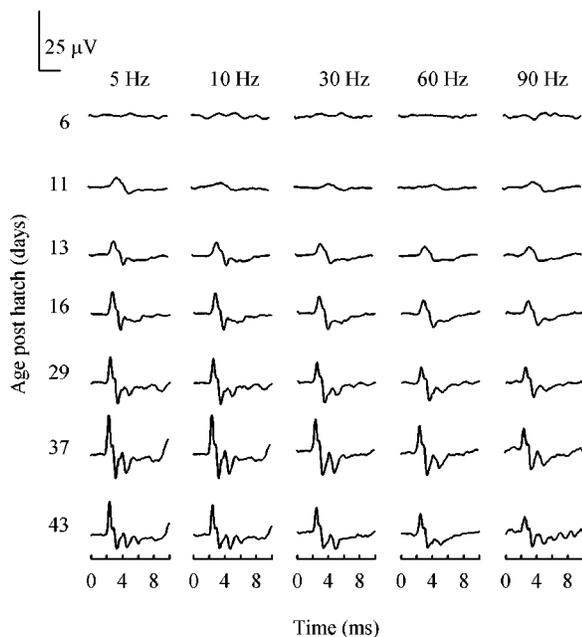


FIG. 6. ABR waveforms for each presentation rate through development for an individual bird. By 11 days of age, peaks in the waveform are visible. As the bird aged, latency increased and amplitude decreased as a function of increased presentation rate.

aged, the waveform increased in sharpness for almost all presentation rates, and all peaks decreased in latency and increased in amplitude (Fig. 6). Typically, a second and possibly a third wave could be identified at later ages.

The youngest animals had the longest latencies and showed the largest changes in latency with increasing presentation rate [open symbols in Figs. 7(a)–(c)]. However, as the animals aged, peak latency decreased for wave 1 when click rate increased from 5 to 90 Hz. For example, shifts decreased, on average, from 0.21 ms at 14 days to 0.12 ms at 42 days. The adult latency change for this same increase in presentation rate was 0.13 ms—similar to the 42-day-old fledglings. This same type of change was seen in shifts for wave 2 peak latencies. For young animals, shifts were 0.33 ms at 14 days and decreased to 0.18 by 42 days of age. Adults showed a latency shift of 0.24 ms for wave 2. The interval between wave 1–2 decreased from 0.15 ms at 14 days of age to 0.06 ms at 42 days; adult birds showed a 0.10-ms shift. In general, latency decreased sharply in the first 2 weeks after hatching. After this age, even though latency shifts were variable, latency shifts exhibited by budgerigars in response to increasing presentation rate were adult-like by about 1 month of age, regardless of presentation rate.

Overall, absolute amplitudes for both wave 1 and 2 increased with age but decreased with increased rate [Figs. 7(d)–(e)]. Responses from older animals had the highest amplitudes, regardless of presentation rate. Between 10–15 days of age, there was a doubling of amplitude for wave 1. Over development, the peak amplitude of wave 1 increased 10–15 μV , and it was within 1 s.d. of adult values by 5 weeks of age. In contrast, the peak amplitude of wave 2 was slower to increase and was still well below adult amplitudes by this age. However, by the sixth week posthatch, nestlings'

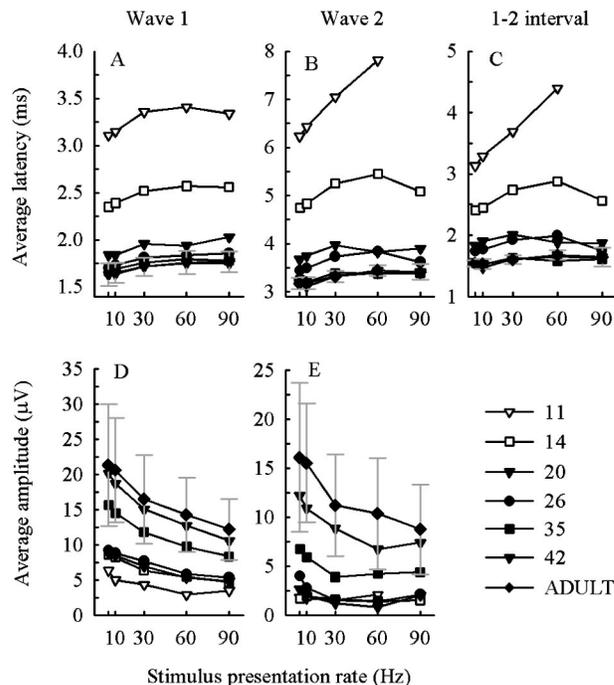


FIG. 7. (Top row) Average latency to the peaks of wave 1 (A), wave 2 (B), and the 1–2 interval (C) plotted as a function of presentation rate. Latency decreases as a function of age for all presentation rates and is more affected in the younger animals (<15 days old) than in the older animals. (Bottom row) Average amplitude for wave 1 (D) and 2 (E) plotted as a function of presentation rate. Amplitude increases as the birds' age but decreases for most ages as a function of increasing presentation rate. Adult measures are averages \pm s.d. (Brittan-Powell *et al.*, 2002).

responses to increases in presentation rate were within 1 s.d. of adult amplitude values for wave 2 as well. The coefficient of variation showed that wave 1 amplitudes were always less variable than wave 2 amplitudes.

V. DISCUSSION

A. Onset of hearing

At high stimulus levels, responses to frequencies up to 2.86 kHz could be consistently evoked by 10 days posthatch, and by 14 days, ABRs could be evoked to almost all test frequencies. An additional nestling budgerigar was presented with tones of intensity levels of at least 110 dB SPL at all frequencies. For this one animal, synchronous responses to 4.8 and 5.7 kHz were elicited at slightly earlier ages (11 and 14 days, respectively), but it is hard to imagine that stimulation by these high intensity levels is biologically relevant to the bird. For example, the parents can produce vocalizations in excess of 100 dB SPL, but they rarely vocalize at such levels within the nest. Also, during the first 7 to 10 days of life, the birds' own vocalizations can barely be heard within 0.2 m of nest box, but after this age, the birds' begging calls could be heard over 6 m away (Stamps *et al.*, 1985).

B. Changes in threshold with development

It is a general property of vertebrates with elongated cochleae that the first auditory responses occur to low frequencies, despite the morphological developmental gradient

of the cochlea from the base (high) to the apex (low frequencies) (see the review in Harris and Dallos, 1984; Manley, 1996; Rubel and Parks, 1988). Like other animals, ABRs in budgerigars follow a similar developmental course—responses are first obtained at low frequencies and then at progressively higher ones. The rates of threshold maturation can differ considerably among animals. Some mammals, such as guinea pigs (Dum, 1984) and humans (see the review in Werner and Marean, 1996), are born with functioning auditory systems, exhibit adult-like thresholds, at most or all frequencies, and are considered precocial with respect to hearing. Other mammals, such as the gerbil (McFadden *et al.*, 1996) or cat (Walsh *et al.*, 1986a), are considered deaf at birth and are thus altricial with respect to hearing. These mammals also show different rates of maturation. For example, threshold development is frequency dependent in cats, with thresholds at high frequencies reaching adult level before low frequencies (Walsh *et al.*, 1986a). Gerbils, however, show faster maturation at the middle frequencies, with low and high frequencies developing at similar but slower rates (McFadden *et al.*, 1996).

Development of high-frequency sensitivity before low-frequency sensitivity in altricial mammals correlates well with the development of the basoapical maturation of the cochlea. Birds, on the other hand, show a different pattern of ABR threshold maturation. Precocial birds show adult-like thresholds to low and middle frequencies by the time of hatching, with sensitivity to higher frequencies continuing to improve after this time (Saunders *et al.*, 1973). Altricial birds, such as the barn owl (Köppel and Nickel, 2001) and the budgerigar (current study), show developmental patterns similar to precocial birds (low to high frequency), except that the maturation occurs after hatching. Like mammals, the basilar papilla of birds develops from the base to the apex (Saunders *et al.*, 1973); however, unlike mammals (but see, for example, Arjmand *et al.*, 1988; Romand, 1987), the physiological threshold development progresses from low to high frequencies such that higher frequency thresholds are the last to become adult-like in birds.

Some mammals show a period early in development where thresholds improve but the ABR audiogram remains relatively flat (McFadden *et al.*, 1996; Walsh *et al.*, 1986a). After this initial period, thresholds across the frequency range improve rapidly. Precocial birds do not show a flat frequency-threshold curve early in development. Young chicks (D12–13 of incubation) exhibit poor sensitivity across frequency but threshold improvement is not equivalent across frequencies. Rather, the audiogram takes on the U-shape appearance by D14–15 (Saunders *et al.*, 1973). This is also true for ducks (Dmitrieva and Gottlieb, 1992). Pied-flycatchers, on the other hand, do show flat frequency-thresholds curves for the first few days after hatching, but respond only to frequencies between 0.3 and 1 kHz. In young budgerigars, the initial audibility curve is relatively flat and thresholds are high (see Fig. 3), but there is rapid improvement from that time on, with 2 kHz becoming the most sensitive frequency by the end of the second week.

In more well-studied animals, the rapid improvement in threshold and the increase in frequency bandwidth to which

the animals respond is correlated with fluid from the middle ear being resorbed and the improvement of middle-ear function as shown in cats (Walsh *et al.*, 1986a), gerbils (McFadden *et al.*, 1996), and chickens (Saunders *et al.*, 1973). In budgerigars, the external ear canal is open by day 10. The opening of the canal is coincident with a dramatic improvement of threshold between 11–17 days of age and an increase in bandwidth of effective frequencies by this time. It is possible that the increase in sensitivity and bandwidth during this phase in budgerigars is partially due to external and middle-ear maturation.

C. Changes in ABR latency and amplitude over development

Latency decreased and amplitude increased with increasing age. Evaluation of latency maturation based on exponential decay functions showed that latencies to wave 1 matured first, followed closely by latencies to wave 2. Wave amplitudes matured slightly later than wave latencies, but this may be a function of variability between subjects. The coefficients of variation in amplitude across development were always greater (>20%) than the coefficients for latency across development (<20%). Wave 1 and wave 2 also showed differences in amplitude growth. For the most part, wave 1 increased in an almost linear fashion, but wave 2 showed little growth across most frequencies until late in development. These results suggest that wave 2 amplitude may still be increasing well after the bird leaves the nest.

As with all species studied to date, increasing intensity level results in shorter response latencies and larger response amplitudes at all ages tested. Even as the animal grows and distances within the papilla and along the VIIIth nerve increase, the latencies to waves 1 and 2 as well as the 1–2 interval show consistent decreases. Explanations offered for these decreases in latency include increasing axon diameter, myelination, and synaptic efficiency which lead to decreases in the time course of action potential generation (e.g., Walsh *et al.*, 1986b). Similarly, increases in amplitude may be due to increased fiber diameter and myelination, resulting in increased neural synchrony (e.g., Walsh *et al.*, 1986c). Nothing is known about whether similar physical changes occur in developing budgerigars. However, the present results, showing that latencies to wave 2 reached adult levels at a slightly later age, do suggest that brainstem development may lag peripheral development in budgerigars, as it does in cats (Walsh *et al.*, 1986b).

Overall, thresholds and latencies tended to stabilize (reach adult levels) at approximately the same age for budgerigars. Response amplitudes, on the other hand, increased in a nonlinear fashion during development for both wave 1 and wave 2. For the highest frequencies (4.8 and 5.7 kHz), amplitudes changed only slightly over the developmental period studied, with birds also exhibiting the highest thresholds at those frequencies. Even though ABR thresholds and latencies stabilize in budgerigars by about 3–4 weeks of age, amplitude did not reach adult values until about 6 weeks of age.

In chickens and kittens, improved mechanical transmission in the external and middle ear is hypothesized to con-

tribute to decreases in ABR latency (Katayama, 1985; Walsh *et al.*, 1986b). In kittens, increased fiber diameter and myelination may also be involved in the continued improvement of latency and amplitude measurements (Walsh *et al.*, 1986b,c). In barn owls, decreasing latencies elicited by click stimuli between P21–23 coincide with the maturation of the endbulbs of Held (Kubke and Carr, 2000)—the innervation between the auditory nerve and cochlear nucleus magnocellularis (NM). Further ABR changes in barn owls are attributed to continuing myelination. Also, synaptic transmission between the auditory nerve and cochlear nuclei is mediated by excitatory amino acids, like glutamate (see the review in Kubke and Carr, 2000), and adult patterns of glutamate expression are attained between P14 and P21. Temporal patterns become adult-like in the barn owl ABR at this same time. On the basis of these data, it seems likely that changes in latency and amplitude in the budgerigar (seen by day 20–26) may be due to increased synaptic transmission between the auditory nerve and the cochlear nuclei, and increased myelination and nerve-fiber diameters as well as the increased transmission function of the middle ear.

D. Effects of click repetition rate on latency and amplitude in developing budgerigars

Temporal aspects of stimulus delivery have a more pronounced effect on younger budgerigars than older budgerigars, as has been found in mammals and chicks (e.g., Burkard and Voigt, 1989; Burkard *et al.*, 1996a; Saunders *et al.*, 1973). Latency to individual waves of the budgerigar ABR increased with increasing rate, even while latency decreased as a function of increasing age. In nestling budgerigars, higher rates of stimulus presentation resulted not only in longer latencies, but showed greater effects in younger animals. The interval between waves was greater at younger ages, suggesting that young budgerigars, like mammals, show greater adaptation which was cumulative across synapses (Burkard *et al.*, 1996a; Donaldson and Rubel, 1990; Jewett and Romano, 1972; Lasky, 1997; Mair *et al.*, 1979; Salamy *et al.*, 1978; Shipley *et al.*, 1980).

Peak-to-peak ABR amplitude increased with age, but ABR amplitude in budgerigar ABR waveforms decreased with increasing rate. This is similar to what was seen in the adult budgerigar data (Brittan-Powell *et al.*, 2002), as well as data shown in mammals, such as gerbils (Burkard and Voigt, 1989; Donaldson and Rubel, 1990), kittens (Burkard *et al.*, 1996a; Mair *et al.*, 1979; Shipley *et al.*, 1980), and human infants (Lasky, 1997; Salamy *et al.*, 1979). In sum, these data suggest that younger budgerigars show greater neural adaptation than older budgerigars, resulting in a greater reduction in ABR amplitudes at higher stimulus rates.

E. Hearing and vocal development

Vocal learning in songbirds has been suggested as a model of vocal development in humans. Studies of ABR development in human infants show that by 6 months of age, hearing thresholds have reached adult values (see the review in Werner and Marean, 1996). This is about the time that the first signs of babbling in infants occur, suggesting that hear-

ing is necessary for this stage of vocal production to occur at this age. The inability to hear one's own voice delays or discourages babbling—deaf infants do not begin this stage until 10–11 months of age (Oller and Eilers, 1988). Thus, normal vocal development in human infants depends on the ability of the baby to hear adult models and feedback from its own vocalizations by 5–10 months of age.

In birds, the first stage of song learning is totally dependent on hearing. Studies of the sensitive period of song learning show that birds tutored with song before P10–13 never produce the tutored song (see the review in Catchpole and Slater, 1995). This parallels developmental studies of hearing in songbirds showing that hearing in altricial birds is not fully developed at hatching but continues to improve even into the nestling period (Aleksandrov and Dmitrieva, 1992; Khayutin, 1985).

The budgerigar is an open-ended learner (i.e., it retains the ability learn vocalizations throughout adulthood), but the sensory and sensory motor phases of vocal learning have yet to be precisely determined. Through studies of budgerigar contact call development (Brittan-Powell *et al.*, 1997; Hall *et al.*, 1997; Heaton and Brauth, 1999), we know that these birds require auditory feedback in order to produce species-specific vocalizations. Deafening birds between 9–11 days of age has a profound effect on the bird's vocal behavior (Heaton and Brauth, 1999) but does not affect all calls equally. Food-begging calls from these birds progressed from high-frequency vocalizations (stage I—stages refer to Brittan-Powell *et al.*, 1997) to the harsh noisy calls observed at later ages (stage II). The birds, however, never produced patterned food-begging calls exhibited by normally hearing birds at 4 weeks of age (stage III) (Heaton and Brauth, 1999). These findings suggest that auditory feedback is important for the transition from stage II to stage III vocalizations.

The present results show that budgerigars hear little, if at all, at hatch. By day 10, the bird's outer ear canals are open and hearing thresholds improved rapidly, primarily at frequencies below 4 kHz. This represents somewhat of a mismatch since the vocalizations of young birds have a peak frequency of 4 kHz or higher. It is unlikely, then, that vocalizations produced before 11 days of age depend on hearing—a conclusion paralleled by what has been found in songbird tutoring studies.

Between days 12 to 28, however, there are dramatic changes going on in both vocal production and hearing development. From 13–27 days, the peak frequency of the nestlings' calls drops to between 3–3.5 kHz, but bandwidth and duration of calls increase. At the same time, the frequency range of hearing increases to include all frequencies tested and sensitivity in the 2–4-kHz range increases by 30–35 dB. It is also during this time that deafening can essentially derail further vocal development. Taken together, these data suggest that stage II may be the start of the sensitive period for auditory feedback in the budgerigar.

By the fourth week of life, the birds' auditory thresholds are near adult levels of sensitivity. During this same time (28–34 days of age), many of the acoustic characteristics of budgerigar vocalizations are stabilizing (e.g., peak frequency

by 1 month and bandwidth and duration of calls at or around fledging). By 1-week postfledging, adult contact calls (a variant of their food-begging call) are readily elicited from the birds (Brittan-Powell *et al.*, 1997). Therefore, adult levels of hearing are reached about a week before of the appearance of the budgerigars' first adult sound (the contact call), but budgerigar vocal development continues beyond the production of the first contact call. Budgerigars show their first signs of vocal mimicry at about 4 weeks postfledging (Brittan-Powell *et al.*, 1997), which is over 2–3 weeks after hearing thresholds are adult-like. Thus, the “sensitive phase” for vocal learning in this species, as in songbirds and human infants, continues well after hearing thresholds reach adult levels.

VI. CONCLUSIONS

This study tracked the development of auditory sensitivity in nestling budgerigars through the auditory brainstem response. We can conclude that in general, changes in the ABR of nestling budgerigars due to changes in intensity, frequency, and repetition rate were comparable to what has been found in other vertebrates, both precocial and altricial. As with all animals tested to date, latency decreases, amplitude increases, and the ABR waveform becomes more complex as the animal ages.

Auditory feedback influences the development of vocalizations in budgerigars, and other vocal learning birds, but until now, little was known about hearing in these birds. This study extends the findings of threshold development in altricial birds to include budgerigars. It shows that budgerigars probably cannot hear at hatching and that auditory sensitivity develops, as in other altricial birds, well into the nestling period (Aleksandrov and Dmitrieva, 1992; Köppl and Nickel, 2001). When combined with what is known about budgerigar vocal development, the present results provide a developmental timetable for future studies pertaining to the anatomical development of the auditory system in the budgerigar as well as direct testing of hearing deprivation at ages where both hearing and vocal ability are now known.

ACKNOWLEDGMENTS

The authors would like to thank C. Carr, O. Gleich, F. Kubke, C. Köppl, D. Higgs, K. Poling, A. Lauer, and M. Dent, as well as two anonymous reviewers, for comments on earlier drafts. This work was supported in part by training grant DC00046 from the National Institute of Deafness and Communicative Disorders of the National Institutes of Health to E.F.B.P. and National Institutes of Health Grant DC00198 to R.J.D. The work described here was in partial fulfillment of the requirement of a doctor of philosophy to E.F.B.P. (University of Maryland, College Park, 2002).

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