Middle- and Long-Latency Auditory Evoked Potentials in Bottlenose Dolphins (*Tursiops truncatus*) Resulting from Frequent and Oddball Stimuli

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Abstract

Middle- and long-latency auditory evoked potentials (AEPs) have not been extensively studied in marine mammals. Differences in longer latency potentials resulting from infrequent "oddball" stimuli inserted within a train of repeated, or "standard," auditory stimuli can potentially be used to detect the discrimination ability of an individual. To investigate the characteristics of evoked responses resulting from the oddball paradigm, AEPs were recorded using 100-ms pure tones as stimuli and recording AEP epochs of 500 ms from two bottlenose dolphins (Tursiops truncatus). The P50 response to a 40-kHz pure tone was attenuated when that stimulus was repeated (the standard stimulus), with an 80% probability of occurrence. When a 30-kHz oddball tone was presented (20% probability of occurrence), however, the P50 response amplitude increased, indicating dishabituation to the novel stimulus. The attenuation of the P50 response to the standard tone was observed when the standard and oddball tones were reversed (30-kHz standard; 40-kHz oddball). The results demonstrated sensory gating, either habituating to a repeated stimulus ("gating out") and/or dishabituating to a novel stimulus ("gating in"). The presence of one or both of these responses suggests that the P50 response to oddball stimuli has the potential to indicate discrimination of a particular set of auditory stimuli.

Key Words: bottlenose dolphin, *Tursiops truncatus*, auditory evoked potentials, middle- and longlatency responses, auditory discrimination

Introduction

Auditory evoked potentials (AEPs) are electrical changes that occur in the auditory system in response to auditory stimuli (Hall, 1992).

Previous AEP research in odontocetes has focused on short-latency responses, generally within 10 to 20 ms of the stimulus onset, which are generated by the auditory brainstem. These shorter latency AEPs have been used by numerous researchers to qualify and quantify characteristics of the odontocete auditory system (Ridgway et al., 1981; Popov & Supin, 1990, 1992, 1997; Bibikov, 1992; Supin et al., 1993; Supin & Popov, 1995; Dolphin, 1997; Popov et al., 1997, 2001; Szymanski et al., 1999). In contrast, long-latency AEPs have not been extensively studied in marine mammals, but have been used to study perceptual as well as cognitive processes in humans (McPherson, 1996). Longlatency AEPs may therefore have similar potential for assessing cognitive processes in odontocetes.

The definitions for the latency range of middleand long-latency AEPs are varied. Hall (1992) defined middle-latency responses as occurring between 12 and 50 ms, and long-latency responses from 50 to 250 ms. McPherson (1996) identified long-latency responses between 90 ms and 200 ms in humans as being largely exogenous—that is, they resulted from neural responses to the stimulus itself. Responses after 200 ms were considered endogenous, or originating from cognitive processing of the auditory information. Evoked responses have been reported as late as 500 ms after stimulus onset.

Research with long-latency AEPs in odontocetes has been limited. Bullock et al. (1968) reported some of the first AEPs from anesthetized cetaceans and found that the location of the electrodes affected the amplitude, as well as the shape of the waveform, depending on the frequency being tested. After testing 29 cetaceans, including three *Tursiops gilli*, with the active electrode surgically inserted into the collicular region, the authors proposed that AEP responses with latencies greater than 4 ms originated in the medial geniculate body or the colliculus and resulted from higher-order neuronal activity. Seeley et al. (1976) applied the long-latency AEP method to hearing threshold estimation. Recording with electrodes inserted at the vertex of the skull, a clear, long-latency AEP waveform was interpreted as a detection of the test tone. The stimuli in this study were 500-ms tones with a 5-ms rise/fall time; recording epochs were 1 s in duration. The audiograms obtained using this method were reliable between and within sessions, and the results were consistent with previously obtained behavioral audiograms of bottlenose dolphins (Johnson, 1966, as cited in Seeley et al., 1976). Ridgway & Seeley (1979, as cited in Ridgway, 1980) described long-latency AEPs resulting from 500-ms tones with a 10-ms rise/fall time in unrestrained bottlenose dolphins, which were recorded from implanted electrodes. Ridgway & Seeley observed a positive peak at a latency of approximately 30 ms and a negative peak at a latency of approximately 100 ms, with a strong stimulus "off" response at about 500 ms.

Supin & Popov (1990) reported long-latency AEPs recorded using needle electrodes that were placed 2 to 3 mm into the dolphins' skin. Tone bursts with a linear rise-time of 1 ms, a plateau of 1 ms, and linear fall-time of 1 ms were used as stimuli. The authors reported auditory cortical responses with latencies of about 10 ms and durations of about 30 ms. The electrode placement with the optimal response in this study was along the midline, approximately 20-cm posterior to the blowhole. The auditory cortical response was used in the context of tonal masking to determine the width of auditory filters.

Woods et al. (1986) investigated long-latency responses to variable stimuli in the bottlenose dolphin (T. truncatus). In this study, the auditory stimuli consisted of two different pure tones, two different dolphin whistles, and a bridge tone (used to signal a reward for the animal). For each trial block, the standard stimulus was presented 80% of the time, and two different types of stimuli were each presented 10% of the time-the oddball stimuli. The evoked responses to the standard and oddball stimuli were very similar except that the oddball response had a much higher amplitude positive wave at approximately 550 ms post-stimulus, designated as the P550 response. The greatest amplitudes of the P550 were seen when the bridge tone was the oddball in test tone blocks and when the second dolphin whistle was the oddball when the first dolphin whistle comprised the standard. These results demonstrated that the P550 response was greatest when signals of biological significance were interspersed with signals without biological significance. The P550 response to oddball whistle stimuli observed in the study was likened to the P300 response in humans, which is an endogenous AEP that indicates categorical discrimination but depends on the attention of the participant (Iliadou & Iakovides, 2003).

Differences in mid-latency AEP waveforms resulting from changes in acoustic stimuli have also been used to study sensory gating. Sensory gating is the process of habituating to repeated stimuli ("gating out") or dishabituating to novel stimuli ("gating in"). Sensory gating has been proposed to result from two different neural processes, either or both of which could be responsible for higher amplitude 50-ms response waves (P50) resulting from the presentation of novel stimuli in humans (Boutros et al., 1995). The measure of sensory gating used by Boutros et al. was the P50 amplitude for the infrequent stimulus (IF) divided by the P50 amplitude to the frequent stimulus (F). Higher IF/F presumably reflects stronger sensory gating. In humans, sensory gating has been described as a neural mechanism of biological sensitivity to context, a proposed component of biological reactivity to novel or stressful events (Boyce & Ellis, 2005). The ability to filter out repeated auditory stimuli and dishabituate to novel stimuli is important for survival and could be essential to detecting and distinguishing predators and prey.

The purpose of the current study was to characterize middle- and long-latency AEPs in the bottlenose dolphin and the variability in AEP waveforms resulting from novel stimuli presented via the oddball paradigm. Results were used to determine the possibility of using middle- and longlatency AEPs to study signal discrimination and sensory gating in bottlenose dolphins. Given that detecting changes in the acoustic environment is likely very important to a dolphin's survival, using evoked potential audiometric methods for rapidly assessing discriminatory ability would provide valuable information that could be used to better contextualize dolphin behavior and ecology.

Materials and Methods

Subjects

The subjects were two female bottlenose dolphins: BLU (40-y-old, 200 kg) and SAY (27-yold, 245 kg). The subjects were housed in floating netted enclosures (9×9 to 12×24 m), located in San Diego Bay, California. The study followed all applicable U.S. Department of Defense guidelines for the care of laboratory animals.

Previous AEP and behavioral tests revealed significant hearing loss above 40 kHz in BLU (Finneran & Houser, 2006). AEP tests with SAY (unpublished, but see Houser & Finneran, 2006, for methods) revealed "normal" hearing with an upper cutoff frequency above 130 kHz.

AEP System and Stimulus Delivery

A portable evoked potential recording system was used to deliver acoustic stimuli and record AEPs in this study (Finneran & Houser, 2006). Sound stimuli were generated using a multifunction data acquisition board (National Instruments PCI-MIO-16E-1), housed in a personal computer. Outgoing stimuli were generated at 12-bit resolution using a 500 kHz update rate, then attenuated (TDT PA-5), filtered (0.1 to 150.0 kHz, Krohn-Hite 3C module), and amplified (Hafler P10000) before being presented to the sound projector.

All tests were performed in air while the dolphin was resting on a padded mat. A jawphone (Moore et al., 1995; Brill et al., 2001), consisting of a B&K 8105 spherical piezoceramic transducer embedded in a degassed silicone rubber (Rhodia V-1065) suction cup was used to present the stimuli (Finneran & Houser, 2006; Houser & Finneran, 2006). The jawphone was attached to the lower jaw over the pan region, a pathway that is important to sound transduction in the bottlenose dolphin (Bullock et al., 1968; McCormick et al., 1970, 1980; Brill et al., 1988; Møhl et al., 1999). Received stimulus levels were estimated by measuring the underwater rms sound pressure levels (SPLs) 15 cm from the center of the jawphone, as previously described (Finneran & Houser, 2006; Houser & Finneran, 2006). The 15-cm distance between jawphone and calibration hydrophone was based on the distance between the jawphone attachment point and the auditory bullae as estimated via computed tomography (Houser et al., 2004). Previous comparisons between in-air AEP thresholds obtained with the jawphone (as calibrated here) and underwater behavioral thresholds confirmed that the in-air AEP measurements are useful proxies for underwater hearing sensitivity and accurately reflect the main characteristics of the audiogram (Finneran & Houser, 2006). In the present study, the main emphasis is on comparisons between AEP recordings using frequent and infrequent stimuli, so the use of the jawphone is acceptable.

AEPs were measured using 10-mm gold cup electrodes (Grass FH-E6G series) embedded in 25-mm diameter silicon (Rhodia V-1065) suction cups. The noninverting electrode (+) was placed approximately 4 cm posterior of the blowhole and 4 cm contralateral of the ear being tested. The inverting electrode (-) was placed opposite of the ear being tested, just behind the external auditory meatus. A ground electrode was placed either on the dolphin's back, near the dorsal fin, or on the dorsal fin. For each recording session, approximately 200 averages of the response to the oddball tone and 600 averages of the response to the standard tone were acquired. Testing for each condition took place over several recording sessions on different days until a minimum of 450

averages of the response to the oddball tone were obtained.

A series of four experiments was performed to investigate middle- and long-latency AEPs resulting from standard and oddball stimuli. In Experiment 1, a control condition, epochs were recorded under the same conditions as the later experiments, but all stimuli were identical 40kHz pure tones. For Experiment 2, the standard was a 40-kHz pure tone and the oddball was a 30-kHz pure tone. Experiment 3 was an oddballonly condition, in which the 30-kHz oddball was presented in the same manner as Experiment 2, but with silence in the place of the standard tone. Experiment 3 was not a true oddball condition because there was only one type of stimulus. Experiment 4 was a counterbalanced version of Experiment 2, where the standard was a 30-kHz pure tone and the oddball was a 40-kHz pure tone. Due to constraints on access to the subjects, only BLU participated in Experiment 4. Stimuli were presented at 130 dB re 1 µPa for 100 ms, with 10ms rise/fall time, in all instances.

The standard tone occurred approximately 80% of the time, and the oddball tone occurred approximately 20% of the time during each data collection phase. Presentation of the tones was pseudorandomized so that there were at least two consecutive standard tones following each oddball. All tones were 100 ms in duration. AEPs were recorded with bandpass filter settings of 1 Hz to 100 Hz, a gain of 2×10^4 , and an epoch window of 500 ms following stimulus onset. Stimuli were presented at the rate of approximately 2 stimuli/s. An epoch window shorter than that required to observe the P550 response reported by Woods et al. (1986) was chosen because the P550 response was not observed in a pilot study using the same electrode placement as the current study. Each standard following an oddball was excluded from the grand average of the waveform evoked by the standard. This exclusion is fairly common in studies using the oddball paradigm, particularly those studying mismatch negativity (e.g., Novitski et al., 2004). Mismatch negativity is an index of change detection present 100 to 250 ms after stimulus onset in humans, and it is thought to reflect the central sound representation (Näätänen, 2001).

Amplitudes at P50 were defined as the maximum positive amplitude occurring between 40 and 60 ms. Once the point for the P50 amplitude was determined, the P50 latency was determined by the time after stimulus onset at that point. Amplitudes at N75 were defined as the maximum negative amplitude occurring between 64 ms and 86 ms, with latencies computed as they were for P50. Sensory gating was measured following the method of Boutros et al. (1995) by calculating the IF/F by dividing the P50 peak amplitude in response to the oddball stimulus by the P50 peak amplitude in response to the standard stimulus. There were no baseline corrections for the measurements of peak amplitude.

Results

Experiment 1

When all stimuli were 40-kHz tones, the resulting waveforms were nearly identical for the dolphin BLU (Figure 1) and more variable for the dolphin SAY (Figure 2). The amplitude of the P50 evoked by the standard was $8.77 \mu V$ for BLU and 8.17



Figure 1. AEPs resulting from 40-kHz pure tones presented in 80% of trials (standard tone) vs AEPs resulting from identical 40-kHz pure tones presented during 20% of trials (oddball tone) during a control condition in the bottlenose dolphin, BLU



Figure 2. AEPs resulting from 40-kHz pure tones presented in 80% of trials (standard tone) vs AEPs resulting from identical 40-kHz pure tones presented during 20% of trials (oddball tone) during a control condition in the bottlenose dolphin, SAY

 μ V for SAY. The amplitude of the P50 evoked by the oddball was 9.00 μ V for BLU and 9.66 μ V for SAY. The P50 peak latency for this condition was 50 ms for BLU and 48 ms for SAY. Both BLU and SAY also had a negative peak at approximately 75 ms after stimulus onset (N75) and a slight positive peak at approximately 150 ms after stimulus onset (P150). The amplitude of the N75 evoked by the standard was -6.03 μ V and -4.71 μ V, with a latency of 70 ms and 82 ms for BLU and SAY, respectively. The amplitude of the N75 evoked by the oddball was -6.11 μ V and -4.96 μ V, with a latency of 70 ms and 76 ms for BLU and SAY, respectively.

Experiment 2

When the standard tone was 40 kHz and the oddball tone was 30 kHz, the P50 amplitude evoked by the oddball tone was 17.7 µV for BLU (Figure 3) and 16.1 µV for SAY (Figure 4). The P50 amplitude of the waveform evoked by the standard tone (40 kHz) was 6.46 µV for BLU and 5.83 µV for SAY. The resulting IF/F was 2.75 for BLU and 2.76 for SAY. The P50 latency for the waveform evoked by the oddball tone (30 kHz) was 48 ms for BLU and 44 ms for SAY, whereas the P50 latency evoked by the standard tone was the same as the oddball for BLU (48 ms), but was 2 ms earlier for SAY. The N75 amplitude of the waveform evoked by the standard was -5.09 μ V and -3.83 μ V, with a latency of 70 ms and 80 ms for BLU and SAY, respectively. The N75 amplitude for the waveform evoked by the oddball was -8.71μ V and -4.05μ V, with a latency of 70 ms and 68 ms for BLU and SAY, respectively.

Experiment 3

In this oddball-only condition, the 30-kHz oddball-only tone was presented at the same rate of probability as the oddballs in Experiments 1, 2, and 4 (20%) but with no intervening standard. The results are overlaid with the results from the 40kHz standard and the 30-kHz oddball pairing in Figures 3 and 4. The P50 amplitude and latency was 15.4 μ V and 48 ms for BLU and 18.8 μ V and 44 ms for SAY, respectively.

Experiment 4

Only the dolphin BLU participated in Experiment 4. The P50 peak amplitude evoked by the oddball tone (40 kHz) was 16.7 μ V at a latency of 48 ms. The P50 peak amplitude evoked by the standard tone (30 kHz) was 7.42 μ V at a latency of 44 ms. The IF/F ratio for this condition was 2.25. The N75 peak amplitude evoked by the standard tone was -3.98 μ V at a latency of 64 ms. The N75 peak amplitude evoked by the oddball tone was -6.31 μ V at a latency of 66 ms.

The peak amplitudes of the P50 responses to the standard and oddball tones are compiled in Table 1, along with the number of averages for each waveform and the IF/F ratio for sensory gating estimation.



Figure 3. AEPs resulting from 30-kHz pure tones presented during 20% of trials (oddball tone) vs AEPs resulting from 40kHz pure tones presented in 80% of trials (standard tone) vs AEPs resulting from 30-kHz oddball-only pure tones presented at the same rate of probability as an oddball but with no intervening standards in the bottlenose dolphin, BLU



Figure 4. AEPs resulting from 30-kHz pure tones presented during 20% of trials (oddball tone) vs AEPs resulting from 40kHz pure tones presented in 80% of trials (standard tone) vs AEPs resulting from 30-kHz oddball-only pure tones presented at the same rate of probability as an oddball but with no intervening standards in the bottlenose dolphin, SAY



Figure 5. AEPs resulting from 40-kHz pure tones presented during 20% of trials (oddball tone) vs AEPs resulting from 30-kHz pure tones presented in 80% of trials (standard tone) in the bottlenose dolphin, BLU

Discussion

Based on previous research of frequency difference limens (Thompson & Herman, 1975; Supin & Popov, 2000), a bottlenose dolphin should easily be capable of discriminating between the 30 kHz and 40 kHz tones. Sensation levels for the 30 and 40 kHz, 130 dB re 1 μ Pa tones were approximately 55 and 65 dB, respectively, for SAY and 60 and 40 dB, respectively, for BLU. This difference in sensation level may introduce differences in loudness perception between the standard and oddball tones. This will continue to be of concern until equal loudness curves are

Subject	Test frequency of the standard (repeated) tone	P50 amplitude (µV)	Number of averages	Test frequency of the oddball tone	P50 amplitude (µV)	Number of averages	IF/F ratio
BLU	40 kHz	8.77	2,421	40 kHz	9.00	813	1.03
BLU	40 kHz	6.46	1,391	30 kHz	17.7	457	2.75
BLU	30 kHz	7.42	1,351	40 kHz	16.3	452	2.25
SAY	40 kHz	8.17	1,328	40 kHz	9.66	458	1.18
SAY	40 kHz	5.83	1,338	30 kHz	16.10	453	2.76

Table 1. Amplitudes at P50 to standard and oddball tones, and the IF/F ratio for two bottlenose dolphins

established for bottlenose dolphins. The conditions were counterbalanced for BLU, however, who received both 30 kHz and 40 kHz acting as standards. In each condition (Experiments 2 & 4), the IF/F was similar. Accepting that the animals could discriminate the 40 kHz and 30 kHz tones in the oddball tests, the difference in P50 amplitudes in these oddball conditions may indicate that it is a means by which sensory gating can be assessed.

There are two main theories to explain sensory gating: (1) "active gating" and (2) the refractory period. The active gating hypothesis states that the auditory stimuli activate comparator neurons in the hippocampus, and these neurons inhibit the response of the pyramidal neurons to subsequent identical stimuli (Freedman et al., 1991, as cited in Boutros & Belger, 1999). Boutros et al. (1995) argued that the active gating hypothesis was a more likely explanation than refractory periods (the period after firing during which the neuron cannot yet fire again) because the time required for neurons to recover is usually several milliseconds rather than the 500-ms interstimulus intervals that are often employed in studies of sensory gating. The exact mechanisms of sensory gating have not been found.

In the current study, the higher amplitude response for the 30-kHz oddball cannot be explained as merely the normal response evoked by a 30-kHz tone. In Experiment 4, the standard and oddball were reversed so that 30 kHz was the standard and 40 kHz was the oddball. In this case, the standard had the attenuated P50 response, and the oddball had a much larger P50 response. In both Experiments 2 and 4, the amplitudes of the P50 evoked by oddball stimuli were similar in amplitude to those in the oddball-only condition (Experiment 3), where there was no intervening standard tone. These results could be explained by gating in the novel stimuli, gating out the repeated stimuli, or the effect of short-term adaptation of the peripheral auditory system. Prior to conclusively determining the impact of sensory gating, studies need to determine the presence and/or degree of amplitude attenuation that might occur as a result of adaptation.

If habituation to the repeated stimulus were the sole mechanism of sensory gating, it would be most prominent in Experiment 1 where the same 40-kHz tone was presented approximately 2,000 times consecutively for SAY and over 3,000 times for BLU. In fact, the P50 peak amplitude was several microvolts higher in Experiment 1 than in Experiments 2 or 4, suggesting that gating out is not the only process involved. The oddball P50 response, when the oddball was 10 kHz higher or lower than the standard, had a much greater amplitude but a similar latency to the standard P50 response. Since the P50 responses to oddball stimuli were similar in amplitude to when the P50 was presented periodically with no intervening standard, the higher amplitudes were likely due in part to gating in the relatively novel sound. Regardless of whether the stimuli were being gated in, gated out, or both, the difference in long-latency responses to the standard and oddball stimuli indicated that differential auditory processing of the stimuli occurred.

The differing P50 responses within and between subjects may be partially explained by the number of averages for each condition and electrode placement. For example, the IF/F for Experiment 1, where the standard and oddball were identical, was 1.03 for BLU and 1.18 for SAY. There were approximately twice as many averages of both the standard and the oddball for BLU than for SAY, which may have contributed to this difference. When a more comparable number of averages were computed for each animal in Experiment 2, the IF/F ratios were 2.75 and 2.76 for BLU and SAY, respectively. Although the IF/F ratios were similar, the amplitudes and latencies of these P50 responses often differed between the two subjects. The differing number of averages for the standard and oddball conditions may have also affected the results. Because the oddball was presented in approximately 20% of trials, there were less averages of the oddball in the analysis. Future studies

should include an equal proportion of artifact-free epochs of the standard as the oddball so that the number of averages will be more comparable and the potential for peripheral auditory system adaptation can be better ascertained.

The recording conditions of Woods et al. (1986) precluded comparison to the P550 of this study, if it were recorded, since the active electrode in that study was implanted in the primary auditory area of the parietal cortex, with reference electrodes on the ipsilateral mastoid process and snout. To a lesser degree, it must be acknowledged within this study that differences in electrode placement may also contribute to some variability of P50 responses between sessions and subjects. Some measurement differences may have occurred due to slight differences in the shape and size of the subjects' heads so that slightly different regions of the brain were recorded. Despite these difficulties, using an oddball paradigm to study long-latency responses to differences in repeated stimuli appears to have promise for studying sensory gating and sensory memory. Future studies should focus on the N75 and P150 responses as well as the more prominent P50 response. These measurable neurophysiological processes may be correlated with discriminatory ability, but more research is needed to determine the exact nature of the sensory gating results.

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