

Auditory oddball responses in *Tursiops truncatus*

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Abstract: Two previous studies suggest that bottlenose dolphins exhibit an “oddball” auditory evoked potential (AEP) to stimulus trains where one of two stimuli has a low probability of occurrence relative to another. However, they reported oddball AEPs at widely different latency ranges (50 vs 500 ms). The present work revisited this experiment in a single dolphin to report the AEPs in response to two tones each assigned probabilities of 0.2, 0.8, and 1 across sessions. The AEP was further isolated from background EEG using independent component analysis, and showed condition effects in the 40–60 ms latency range. © 2021 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).

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1. Introduction

Bottlenose dolphins have a remarkable ability to detect and identify underwater objects in complicated acoustic environments based solely on echoic information, and they also use passive listening to identify threats, prey, and individual conspecifics (Au, 1993; Harley and DeLong, 2008; Tyack, 1998). While there is a significant body of electrophysiological investigation into the neurological systems supporting auditory processing of echoes in bats, the majority of dolphin data comes from a relatively small number of dolphins trained for behavioral research. A potential means of expanding this subject pool (ideally including free-ranging dolphins) is the further development of non-invasive electrophysiological methods. Neurophysiological auditory brainstem response (ABR) methods over the past 40 years provide a solid foundation for basic auditory processing in dolphins (Mooney *et al.*, 2012; Supin *et al.*, 2001), but they are not well equipped to answer questions about the role of auditory expectancy in passive or active listening tasks. Advances in human research involve wearable EEG devices and spatial filters like Independent Component Analysis (ICA), which could translate to applications for dolphin auditory neuroscience. Studies of auditory expectancy using oddball paradigms have revealed brain responses generally arising from the cortex in humans (Picton, 2011) and other terrestrial mammals (Nelken and Ulanovsky, 2007).

In general, an auditory oddball response involves an enhanced peak in the auditory evoked potential (AEP) for unexpected sounds compared to the same (or similar) sounds when they are expected. In humans, oddball responses can be categorized by roughly three types of effects: (a) adaptation to a repeated stimulus, mainly affecting the earliest cortical potentials P1, N1, and sometimes P2; (b) pattern-based expectation affecting the N1 and P2, often called the mismatch negativity (MMN); and (c) novelty and target detection affecting a later component often called the P3, or P300 for the third positive deflection occurring ≥ 300 ms after the evoking event (Picton, 2011).

Human AEP components cannot be directly mapped to the dolphin, particularly in terms of traditional long-latency responses; however, the latencies of presumed homologous cortical N1-P2 sensory components seem compressed relative to humans (Schalles *et al.*, 2021; Supin *et al.*, 2001). To date, at least two published attempts have explored a dolphin homolog of the human auditory oddball response and reported oddball responses at different latencies: Woods *et al.* (1986) reported a P300 type oddball effect at a latency of 550 ms, whereas Hernandez *et al.* (2007) reported oddball effects at earlier latencies, approximately 50–75 ms after stimulus onset. The experimental protocols for these two studies differed in EEG acquisition and auditory stimuli; thus, it is not clear what led to such discrepant results.

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Some of the earlier dolphin AEP experiments, including the oddball sessions by Woods *et al.* (1986), made use of electrodes inserted to the skull surface. This recording site offered a relatively high signal to noise ratio (SNR) and could produce reliable AEPs with as few as 64 stimulus presentations (Ridgway, 1980). More recent AEP experiments, recorded from the skin surface, suffer from a significantly lower SNR and require on the order of 300–3000 stimulus presentations for a reliable AEP (Hernandez *et al.*, 2007; Popov and Supin, 1986). The goal of the current study was to revisit the question of how dolphins exhibit auditory oddball responses to an infrequent tone deviant. To increase the SNR of the skin surface recordings, independent component analysis (ICA) was used to spatially filter the AEP (Schalles *et al.*, 2021).

2. Methods

2.1 Subject

OLY, a male dolphin (35 years old, 185 kg) housed in netted enclosures (9×9 to 9×18 m) in San Diego Bay, California participated in this study. Because OLY exhibited high-frequency hearing loss, stimuli were selected to fall within his sensitive hearing range [upper-frequency hearing limit of 70 kHz (Strahan *et al.*, 2020)], at approximately 30 dB above detection threshold for the stimulus frequencies. The study followed a protocol approved by the Institutional Animal Care and Use Committee at the Naval Information Warfare Center Pacific and the Navy Bureau of Medicine and Surgery, and followed all applicable U.S. Department of Defense guidelines for the care of laboratory animals.

2.2 Stimuli

Stimuli were delivered to the acoustically receptive region of the dolphin's left posterior mandible via a jawphone consisting of a hydrophone (ITC-1042) in degassed silicone rubber molded into a suction cup (Rhodia V-1065) (Brill *et al.*, 2001). The jawphone was calibrated underwater, using a Reson TC4013 as a receive hydrophone at a distance of 15 cm, the estimated distance between the pan jaw region and the auditory bulla ANSI/ASA S3/SC1.6 (Animal Bioacoustics Accredited Standards Committee, 2018). Stimuli were presented at a sound pressure level (peSPL) of 120 dB re $1 \mu\text{Pa}$. An NI PXI-6251 data acquisition card (National Instruments, Austin, TX) converted digitally generated signals to analog voltage (16-bit resolution, 512-kHz update rate) which were then bandpass filtered from 5–200 kHz (Krohn-Hite Corporation, Brockton, MA). Stimuli were 300-ms pure tones with 20-kHz or 28-kHz frequencies and linear 5-ms rise/fall times. Stimuli were delivered with a 1000 ms inter-stimulus-interval, plus a pseudo-random temporal jitter, uniformly distributed between 0 and 500 ms. For the initial oddball condition, 20 kHz was designated the standard tone with 0.8 probability on a given trial, and 28 kHz was designated the oddball with a 0.2 probability for a given trial. The second oddball condition reversed the probability assignments. Two control conditions, referred to as “solo” conditions, employed either the 20-kHz tone or the 28-kHz tone as the sole stimulus with a probability of 1 for every trial.

2.3 EEG recording

Sessions were recorded after the dolphin voluntarily beached into a padded, shaded mat. Gold cup electrodes (Natus 10 mm) embedded in silicone rubber suction cups (Rhodia V-1065) were placed on the dolphin with conductive paste. Dolphin skin was prepped with alcohol swabs, and electrode impedance was measured below 5 kOhm. The non-inverting electrodes were placed at 10, 20, and 30 cm, posterior to the caudal lip of the blowhole, along the dorsal midline [as described by Schalles *et al.* (2021)], and a shared inverting electrode was positioned just anterior to the dorsal fin. The signal ground was placed in seawater near the dolphin. The EEG was amplified by three Grass IP511 biopotential amplifiers ($10\,000\times$ gain, bandpass filter of 1–3000 Hz). Amplified signals were digitized using a PXI-6251 card at a 10-kHz sample rate. Stimulus triggers were recorded as the outgoing stimulus voltage onset routed to a fourth analog input.

2.4 EEG analysis

EEG data were analyzed using EEGLAB toolbox (v14.1.2) for MATLAB (Delorme and Makeig, 2004). Data were down-sampled to 1000 Hz using EEGLAB's “resample” function, and then bandpass filtered from 1–50 Hz (3300 point FIR with zero phase). Continuous EEG was segmented into epochs spanning -100 to 1000 ms relative to stimulus onset. The mean voltage value from the pre-stimulus period (-100 to 0 ms) was subtracted from the post-stimulus epoch voltage to baseline correct each trial. High-amplitude artifacts were removed using an adaptive voltage threshold. Initially set at $100 \mu\text{V}$, the algorithm increased the threshold in $25 \mu\text{V}$ steps until at least 1%, but less than 20% of the epochs were rejected. This resulted in a range of rejection thresholds from 850 to $1025 \mu\text{V}$. Remaining epochs were visually inspected, and any non-stationary artifacts were manually removed prior to ICA decomposition (Jung *et al.*, 2000). This process yielded a total of 7085 epochs (1920 standards, 519 oddballs and 1136 solo for 28 kHz conditions; 2017 standard, 393 oddball, and 1100 solo for 20-kHz conditions). The 20-kHz solo condition data were previously published in Schalles *et al.* (2021) as the dorsal referenced montage condition. Independent components were decomposed using the “runica” function from EEGLAB. Reliability for the decomposition was assessed using a split half comparison based on AEP fidelity, as inspired by the algorithm developed by Groppe *et al.* (2009), and explored in more depth as applied to dolphin data by Schalles *et al.* (2021).

Evoked potentials were calculated as the mean in the time domain for sensor-space and component-space data across epochs. The signal amplitude for the SNR was estimated as the root mean square of an AEP from 1–100 ms. The

noise was estimated as the square root of the variance of a single time point randomly selected within the AEP time-window across all epochs, divided by the number of epochs. The SNR was calculated as the square root of the of signal squared divided by noise squared minus 1, and reported in dB, which implies the SNR level, referred to as SNRL (Elberling and Don, 1984; Finneran *et al.*, 2019).

Statistical tests between conditions were performed on the N1-P2 peak-to-peak voltage amplitude for the AEP independent component. The N1 was operationalized as the minimum voltage between 33 and 53 ms, and P2 as the maximum voltage between 58 and 78 ms. This was based on an optimal response window previously published for this dolphin (Schalles *et al.*, 2021), which differed by 8 ms from that originally published by Hernandez *et al.* (2007). The offset N1-P2 was defined as the difference between the minimum voltage between 333 and 353 ms and the maximum voltage between 358 and 378 ms. To account for differences in epoch numbers and variance across conditions, statistics were performed on a bootstrap sample mean distribution for each condition. The onset and offset N1-P2 peak-to-peak difference was calculated from a mean of 300 epochs randomly sampled with replacement from a given condition. The bootstrap distribution of these peak-to-peak values was created over 1000 iterations. For each condition, we calculated the resulting bootstrap distribution mean, standard error, and confidence intervals. Confidence intervals were constructed by first ordering the distribution by voltage, and then selecting the 25th and 975th ranked values to estimate the upper and lower bounds of a two-tailed alpha level of 0.05 (Efron and Tibshirani, 1993). Two conditions were interpreted as significantly different if the means for each condition fell outside of the confidence interval for the other condition.

3. Results

The SNRL for all combined epochs across conditions ($n = 7085$) was larger in component space than in sensor space. The highest sensor space SNRL of 11 dB came from the electrode positioned 30 cm posterior to the blowhole. However, given large heartbeat contamination at this sensor, the AEP N1-P2 complex was not larger than background noise (see supplementary Fig. 1¹). ICA decomposition yielded one component presumably representing an AEP (SNRL = 23 dB), whereas the two other components represented relatively large amounts of background noise (SNRL = 7 and 13 dB). A split half comparison indicated reliability of the AEP component resulting from ICA decomposition (supplementary Fig. 2¹). We therefore focused all subsequent analyses on the AEP component extracted using ICA.

The AEP component was characterized by a prominent N1-P2 complex in the first 40–60 ms post stimulus onset, and at reduced magnitude (but similar latency) in response to stimulus offset at approximately 340–360 ms (Fig. 1). A P1 positive deflection was observed at approximately 20 ms post stimulus onset, followed by a large magnitude negative

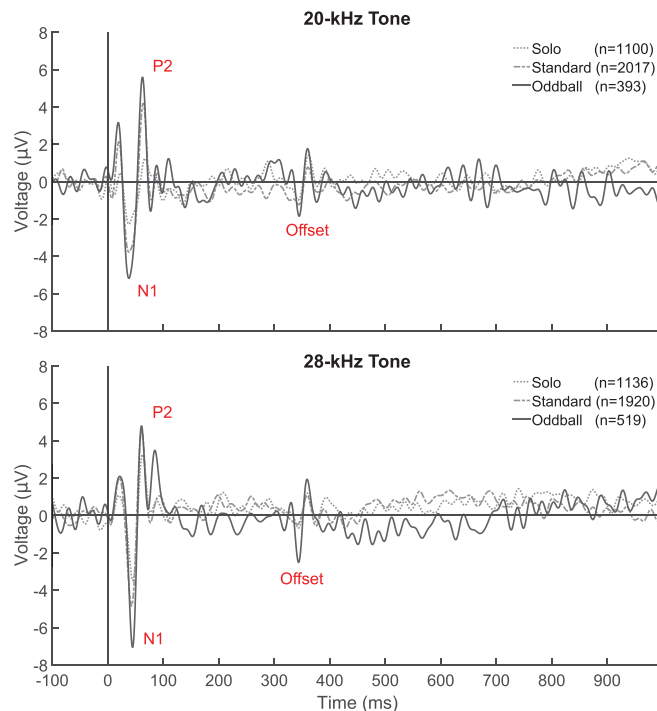


Fig. 1. Event related potentials from the AEP component in response to varying conditions for each stimulus frequency. The oddball condition represents the response to the tone when it had a presentation probability of 0.2 for a given epoch and 0.8 for the standard condition. The solo condition serves as a control for both the standard and oddball, with a presentation probability of 1. The number of epochs in each condition is expressed by “n” in the legend.

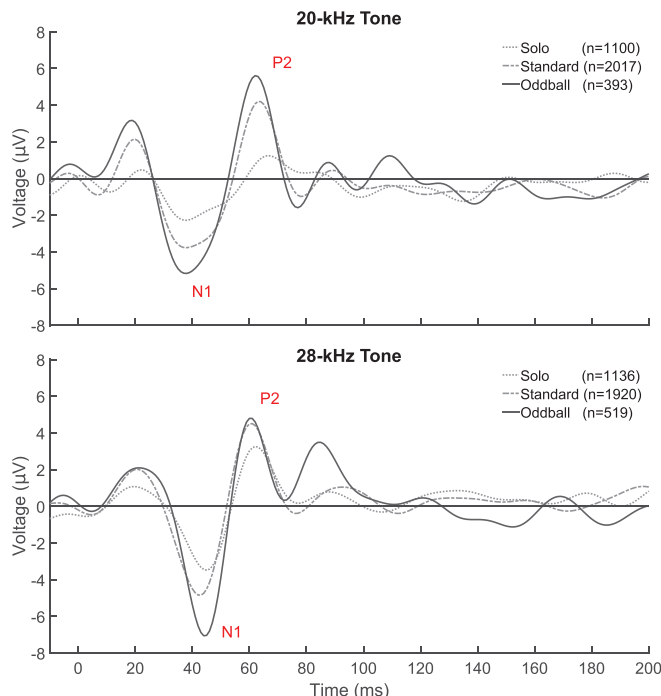


Fig. 2. Event related potentials from the AEP component in response to varying conditions for each stimulus frequency, with emphasis on the N1 and P2 components (Fig. 1 shows the full epoch).

N1 at 40 ms and a P2 at 60 ms (Fig. 2). Across conditions, 20-kHz and 28-kHz tones evoked AEPs with similar morphologies and timings; however, the 28-kHz tone tended to elicit larger N1-P2 magnitude responses, especially for the solo condition comparison (3.04 μ V). No oddball effect was observed at the 200 or 550 ms latencies. Additionally, the effect of condition was stable for even lower numbers of trials, as evidenced by split half comparisons (supplementary Fig. 3¹).

The relative magnitude of N1-P2 peak to peak depended on condition. The amplitude of responses was greatest for the 20% oddball stimulus, lower for the more frequency (80%) standard stimuli and lowest for the solo condition with no oddball (Fig. 3). From the bootstrap sample mean distributions, the effect of condition was significant for each tone: the mean of a given condition fell outside of the upper and lower bounded confidence intervals for each of the other conditions based on a two-tailed alpha level of 0.05 (Table 1). The offset response (approximately 340–360 ms) also exhibited an increase peak-to-peak magnitude for the oddball condition relative to the standard and solo conditions, though only the 28-kHz oddball was significantly different at the 0.05 alpha level (supplementary Table 1¹).

4. Discussion

Using a recently described application of ICA to dolphin EEG (Schalles *et al.*, 2021), we isolated an AEP component that exhibited oddball effects at relatively short latencies (at roughly 40–60 ms). The largest peak-to-peak magnitude of the N1-P2 sensory complex was in response to tones during the oddball condition, and the smallest magnitude was in response to the solo condition tones. This builds on previous oddball research reporting a response with approximately 50 ms latency that was sensitive to the manipulation of stimulus probability (Hernandez *et al.*, 2007). We did not observe any auditory oddball effects around 200 or 550 ms latencies like those previously reported by Woods *et al.* (1986); however, several significant differences in the experimental protocol may also explain this lack of a response, as elaborated below. The present

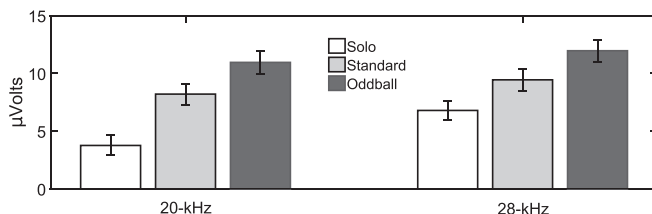


Fig. 3. The bootstrap mean peak to peak amplitude between onset N1-P2 (approximately 40–60 ms post stimulus onset) from the AEP component by condition across stimuli. Error bars represent standard error of the mean of the bootstrap distribution.

Table 1. Bootstrap results for AEP component N1-P2 peak to peak measure. Statistics from the mean of 300 epochs sampled 1000 times from each condition, and displays the resampled mean, standard error, lower- and upper-bound confidence intervals for two-tailed $\alpha = 0.05$.

Tone	Condition	Probability	Mean (μV)	S.E.	CI_l	CI_h
20-kHz	Solo	1	3.76	0.87	2.42	5.34
	Standard	0.8	8.21	0.92	6.54	9.85
	Oddball	0.2	10.96	0.97	8.98	12.67
28-kHz	Solo	1	6.80	0.81	5.57	8.04
	Standard	0.8	9.45	0.96	7.63	11.15
	Oddball	0.2	11.96	0.95	10.21	13.69

study also found an auditory offset response, with similar relative latency (approximately 40–60 ms post-stimulus offset) and oddball sensitivity similar to the onset response. Together these findings support the application of ICA to dolphin EEG to reduce noise, enabling studies of neural auditory processing, at least for early components of the cortical auditory responses.

The N1-P2 magnitudes differed slightly for the 20- and 28-kHz tones. This is likely due to differences in OLY's hearing sensitivity. This difference in N1-P2 magnitudes underscores the importance of comparing AEPs to physically identical stimuli played in different contexts when computing oddball responses. While the present findings exhibit oddball N1-P2 effects in an overlapping time window with the P50 published by Hernandez *et al.* (2007), the polarity of the AEPs are inverted between the two studies [taking into account that ICA can invert the polarity of a given component activation relative to sensor space (Onton *et al.*, 2006)]. However, in this case it is likely due to differences in the relative positions of the recording electrodes (Schalles *et al.*, 2021), as a polarity inversion of the auditory cortical response (ACR) was observed along the anterior-posterior of the dolphin head (Supin *et al.*, 2001). Hence, a more anteriorly recorded P50 could share functional properties with the N1 with latency 40ms that we recorded from a more posterior series of electrodes.

We did not observe a P550 oddball like that previously reported by Woods *et al.* (1986). It is possible that application of ICA could have separated a long-latency cognitive component from the shorter latency sensory N1-P2 in what we term our AEP independent component. Given the relative similarity of the present results with that of Hernandez *et al.* (2007), we consider an ICA separation of AEP components not the most likely explanation, however it warrants follow-up study with a greater density of sensors. The present study differed from these previous reports in stimulus delivery and electrode placement (Schalles *et al.*, 2021), but a more a critical difference may be in the behavioral relevance and salience of the stimuli. Human oddball responses comprise two distinct P3 components, known as the P3a and the P3b (Squires *et al.*, 1975). The P3a is automatic and elicited by any deviant. However, the P3b only occurs when subjects actively attend to behaviorally relevant events, such as the occurrence of a target sound to which the subject must respond (Luck, 2014). Moreover, the overall magnitude of the P3 complex scales with attention (Becker and Shapiro, 1980) and reward magnitude in humans (Yeung, 2004).

One of the oddball tones used by Woods *et al.* (1986) was a tone that the dolphins were conditioned to associate with a food reward, and they reported that the tone associated with food reward elicited an orienting response in their animals (noting that movement could have contaminated the recorded responses). In contrast, the tones presented in our experiment, as well as the stimuli presented by Hernandez *et al.* (2007), had no specifically conditioned behavioral associations, and thus should not elicit a response along the lines of a P3b during passive listening. Further work is needed to confirm whether dolphins exhibit P3b homologous responses when they recognize a behaviorally relevant sound. As there was no way to assess the dolphin's attentiveness during the present study, there is need for follow-up with an active, or directed attention condition.

Rather than a late response that may correspond to a P3 in humans, we found an earlier latency response differences between the standard and oddball tones. This effect could be explained in part by adaptation to a recurring stimulus given the involvement of P1-N1-P2 (Lanting *et al.*, 2013). Adaptation is thought to drive bottom-up responses that reflect automatic processing and do not require attention. This may be related to a mechanism driving the human mismatch negativity (MMN). The MMN presents about 150–200 ms after an oddball (Näätänen *et al.*, 2007), or deviant stimulus, and is attributed to an automatic response that is elicited even when subjects sleep, though it can be modulated by task demands, including top-down effects such as attention (Picton, 2011). Selective auditory attention can affect the magnitude of the N1 response in non-oddball paradigms (Hillyard *et al.*, 1973), and for sufficiently rapid inter-stimulus intervals (410 ms or less in humans), directed attention can increase the magnitude of the MMN (Näätänen *et al.*, 1993). An MMN in humans can occur to a change in frequency between standard and variant tones, for frequencies that are behaviorally above discrimination threshold (Sams *et al.*, 1985). Tonal oddballs elicit an MMN in carnivores such as cats and macaques, but it has not been observed in rodents (Nelken and Ulanovsky, 2007). Depending on the similarity of the standard and deviant, an MMN may overlap with the response latency of the N1 in humans when the difference between stimuli is large (e.g.,

1000 and 3000 Hz), and the latency increases as the difference between stimuli increases (e.g., 1000 and 1050 Hz) (Picton, 2011). Given these properties in humans, and the relative response latencies of the N1-P2 in dolphins, it may be more likely that an adaptive, or automatic deviant detection process in dolphins could occur in the 50–100 ms latency response window, rather than one that could overlap with the N200 described by Woods *et al.* (1986).

Another interpretation of the cross-species MMN analysis by Nelken and Ulanovsky (2007) is that tonal oddballs may not be the ideal stimulus to evoke an MMN in dolphins. Given the segregation of dolphin sound into lower frequency communication tones and higher frequency sonar navigation and foraging clicks, the latter might be more effective in driving an oddball response, given the adaptations and specializations of the dolphin auditory processing system. The extent to which the dolphin auditory system passively segregates incoming sound streams based on features such as frequency is poorly understood. Multiple reports of dolphin auditory oddballs at latencies corresponding to the N1-P2 complex suggest that human MMN paradigms may be a useful tool to further explore dolphin auditory stream segregation. As AEP methods have enabled hearing thresholds in animals without behavioral training, MMN methods may further allow study of more complex auditory processing in animals with minimal training.

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¹See supplementary material at <https://www.scitation.org/doi/suppl/10.1121/10.0005991> for additional results.

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