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Middle- and Long-Latency Auditory Event-Related Potentials in Dolphins

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INTRODUCTION

Following the presentation of an auditory stimulus a series of electrical deflections, event-related potentials or ERPs, can be recorded from the scalp of humans and other animal species (Corwin, Bullock, & Schweitzer, 1982). ERPs have been widely used for monitoring human sensory and cognitive processing (Hillyard & Woods, 1979), and hold the promise of elucidating sensory and cognitive processes in other species (Bullock, 1981). In the human, short- and middle-latency auditory ERPs (latencies 1.5–30.0 msec) are *exogenous* in that their amplitudes and latencies are determined primarily by the characteristics of the evoking stimulus and are little affected by manipulations in processing strategy. In contrast, long-latency components change with attention and have been related to a variety of higher cognitive functions (Hillyard & Kutas, 1983). One of these components, the P3 or P300, is thought to be wholly *endogenous*, in that it reflects higher order optional cognitive operations which may be elicited by a stimulus (Donchin, 1981).

Short-latency ERPs have revealed specialized mechanisms of acoustic processing in the cochlea, brainstem, and cortex of the bottlenose dolphin and other dolphin species (Bullock et al., 1968; Bullock & Ridgway, 1972; Bullock & Gurevich, 1979; Ladygina & Supin, 1977; Ridgway et al., 1981). Recently,

comparative studies of endogenous long-latency components, particularly the P3 or P300, have been undertaken on other species including the rat (O'Brien, 1982), cat (Farley & Starr, 1983; Wilder, Farley, & Starr, 1981), and monkey (Arthur & Starr, 1984; Neville & Foote, 1984).

One purpose of the current experiments was to determine if P300-like activity might be evident in the dolphin. In humans, the P300 can be elicited when infrequent stimuli are novel and unpredictable or when they cue an infrequent response (Courchesne, Hillyard, & Galambos, 1975). Our first two experiments were designed to determine if P300-like activity would be elicited in the dolphin under either of these circumstances.

Our third experiment was designed to compare the effects of stimulus repetition on dolphin and human ERPs. Recovery functions (changes in amplitude as a function of interstimulus interval) of human ERPs show two properties that have not consistently been reported in the recovery cycles of ERPs from other animal species. First, the duration of the recovery cycle of the human N100-P200 is extremely long; at interstimulus intervals (ISIs) less than 20 sec the N100-P200 is still not fully recovered (Nelson & Lassman, 1973). Second, it is partially specific for the stimulus repeated. For example, when a probe tone is inserted into a train of conditioning tones the amplitude of the ERP that it elicits is increased if it is different in frequency from the conditioning tones (Butler, 1973; Picton, Woods, & Proulx, 1978; Woods & Elmasian, 1984). An examination of the recovery cycle of the dolphin ERP was of particular interest since dolphin ERPs show long-latency components whose relative amplitudes are similar to those of the N100-P200 (Seeley, Flanigan, & Ridgway, 1976). Moreover, since the recovery function of the human N100-P200 has been related to the persistence of short-term acoustic memory (Picton, Campbell, Baribeau-Braun, & Proulx, 1978), it was felt that investigations into the recovery cycle of ERPs in the bottlenose dolphin might also provide some insight into the structure of acoustic memory in this species.

METHODS

A 22-year-old female dolphin was studied. The animal had been used in previous behavioral experiments and was accustomed to the restraining tank used for recording. Brainstem auditory evoked potentials previously obtained (Ridgway et al., 1981) had revealed normal peripheral auditory function.

Experimental Procedure

After the animal was hoisted from its home tank, wire electrodes (0.1 mm Jelliff alloy C) were loaded into a 20 gauge needle which was inserted to the skull. The needle was then gently withdrawn, leaving the bare-tipped wire hooked in place on fascia near the skull surface. The procedure was carried out rapidly

using local anesthetic and focal cooling and resulted in little apparent discomfort to the animal. The electrodes were inserted so as to overlay the primary auditory areas of parietal cortex as mapped by Soviet researchers (Ladygina & Supin, 1977). Reference electrodes were placed on the ipsilateral mastoid process and the snout.

Following electrode implantation, the animal was partially submerged in the restraining tank with the lower jaw underwater (see Seeley et al., 1976 for further details). In order to prevent chafing and irritation of the dorsal skin, the animal was periodically sprayed with cool water. Stimuli were presented in water through an LC-10 hydrophone acting as a speaker 50 cm in front of the lower jaw.

Data Analysis

Wideband EEG (bandpass 1.0–3000 Hz) was recorded on an FM tape recorder along with trigger codes for subsequent analysis by computer. The EEG was digitized off-line (213 Hz/channel) after anti-alias filtering (-3 dB at 100 Hz). Prior to averaging it was scanned for artifacts (excessive peak-to-peak deflections or amplifier blocking).

EXPERIMENT I. EFFECTS OF STIMULUS PROBABILITY

In humans, P300 components are produced by deviant auditory stimuli in ongoing trains of tones (Knight, 1984). In Experiment I, we presented novel auditory stimuli in an effort to produce a P300-equivalent in the dolphin. The stimuli were either computer-synthesized tones (8 or 12 kHz) or sounds which the dolphins had encountered in their environment (dolphin calls or a tone-signal used for training). The environmental sounds were digitized and edited by computer.

All stimuli had 300 msec durations (5 msec rise and fall times) and were presented at fixed 1.5 sec interstimulus intervals (ISIs). There were six conditions (Table 3.1) each lasting 8 min. In each, three stimuli were presented—probable stimuli on 80% of the trials, and two different infrequent stimuli on 10% of the trials each. The stimuli were presented in random order, with probabilities counterbalanced so that the frequent stimulus in one condition was the infrequent stimulus in another. Each condition had been recorded on an audio tape recorder. During the experiment, these were presented through the LC-10 hydrophone after amplification. Trigger pulses indicating the timing and occurrence of different stimuli were recorded along with EEG data for subsequent decoding by computer.

Six stimulus sets were used in all with five different stimuli—tones at 8.0 and 12.0 kHz, two different dolphin calls (FM sweeps), and a 7.5 kHz "bridge tone" which had served as a conditioned reinforcer during the training for experiment II, which follows.

Results

Figure 3.1 shows the grand mean ERPs (averaged over stimuli) recorded from a parietal-mastoid electrode pair in response to frequent (solid line) and infrequent (the two dashed lines) stimuli. The ERPs evoked by both stimulus classes consisted of a sharp P25 component (a relative positivity at the parietal electrode 25 msec after sound onset), a small negative component (N200), and a broad late positivity (P550), followed by a still later negativity (not illustrated) and a positivity which was present prior to the start of the next sample (1.1 sec after sound onset). The P550 component was larger to the infrequent stimuli in every stimulus set (Table 3.1), while the N200 component showed a more variable enhancement. The P25 component was similar in amplitude to frequent and infrequent stimuli.

Although enhanced P550 amplitudes were elicited by infrequent stimuli in every condition of Experiment I, the greatest enhancements were observed in

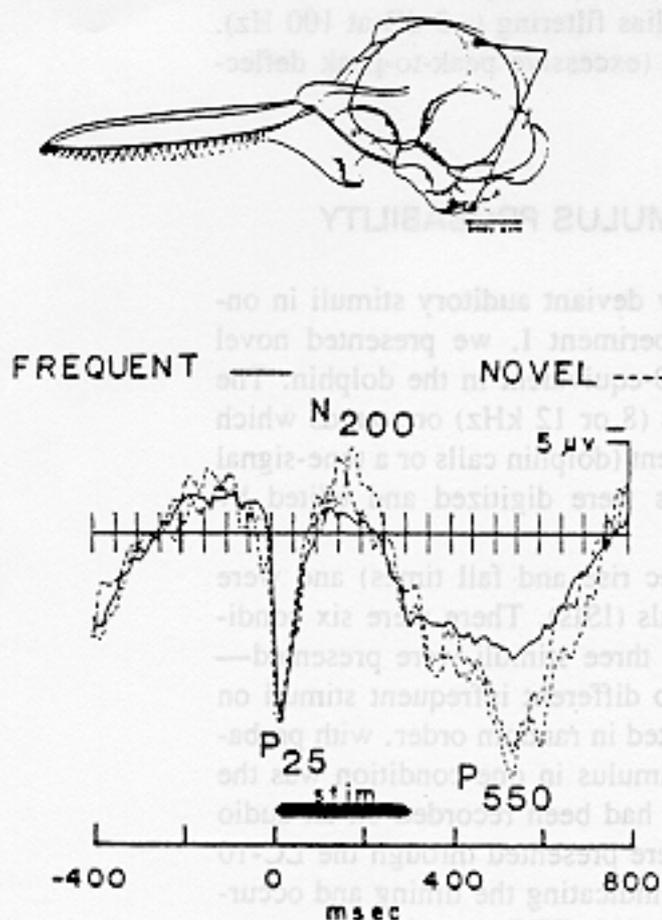


FIG. 3.1. ERPs averaged over the five different stimuli when presented with 80% probabilities (solid line) and when they were presented as deviant stimuli with 10% probabilities (dashed lines). Note the enhanced amplitude of the P550 component to the deviant stimuli. All ERPs from this and following figures are from the parietal-mastoid derivation on the left hemisphere.

TABLE 3.1
Amplitudes (in μV) of the P550 Component Recorded from Parietal-
Left Mastoid Derivations in the Different Stimulus Conditions of
Experiment I

	Condition					
	1	2	3	4	5	6
Frequent stim (80%)	8.0 kHz	12.0 kHz	8.0 kHz	8.0 kHz	Call 1	Call 2
	4.6	6.3	3.7	4.4	3.4	5.7
Deviant-1 (10%)	Bridge tone	Bridge tone	12.0 kHz	12.0 kHz	Call 2	Call 1
	16.6	13.0	8.0	9.4	4.6	15.7
Deviant-2 (10%)	—	8.0 kHz	Call 1	Call 2	Bridge tone	8.0 kHz
	—	11.7	9.4	6.6	8.0	14.3

Peak amplitudes were measured within the latency range of 300–600 msec with respect to the mean voltage during a 400 msec prestimulus interval.

conditions 1 and 2 (where the bridge tone was presented infrequently), and condition 6 (with different dolphin calls serving as frequent and infrequent stimuli, see Table 3.1). Enhanced P550 amplitudes were most prominent in the parietal-mastoid placements, and were not observed at parietal-snout derivations.

EXPERIMENT II. ERPs TO CONDITIONED TONE SEQUENCES

Although the human P300 is usually associated with low probability of stimulus delivery, if one stimulus in a train of low probability stimuli requires a differential response it will elicit larger P300s than equally improbable nontallied stimuli (Courchesne, Courchesne, & Hillyard, 1978). In Experiment II, we examined the response to a differentially reinforced stimulus in a random sequence, in order to determine if it would elicit an enhanced P550 component.

Stimuli

The stimuli were five complex tones which had been synthesized by computer and recorded on a high fidelity audio tape recorder. They consisted of sine waves at a selected fundamental frequency mixed with first and second harmonics of

equal energy and zero phase lag. The fundamentals were selected in one octave steps from 1.0 to 16.0 kHz. Although the tones had comparable RMS voltages, they were not equated in acoustic energy as monitored in the tank near the dolphin's head. All stimuli were 300 msec in duration with 5 msec rise and fall times.

The third tone in the sequence (4.0 kHz fundamental) was differentially reinforced. A series of audio tapes was constructed for the conditioning procedures. First, the animal was conditioned to associate the presentation of the bridge tone (7.5 kHz) with the delivery of fish during the feeding period. Then, the target tone was presented in isolation at long (20–30 sec) ISIs with each presentation followed by the presentation of the bridge tone and fish. Subsequently, two tone sequences were used (tone 3 and tone 1), with differential reinforcement of tone 3. At this point in the training, another tape was constructed with all of the tones except the target randomly presented at 1.5 sec ISIs. This tape was presented periodically between feedings so that responses to non-target tones would not be associated with reinforcement. Finally, the test tape was constructed with all of the stimuli, including the target, presented randomly (20% probability for each) at fixed 1.5 sec ISIs.

Results

The animal developed a conditioned response to the bridge tone characterized by immediate orienting, and was reported by the trainer to orient to the target tone. The ERPs elicited by the equiprobable stimuli are shown in Fig. 3.2. Components with similar latencies and scalp distributions were produced by each of the stimuli. The differentially reinforced target tone (tone 3) elicited enhanced N200 and P550 components in comparison with tones 1, 2, and 5, but somewhat smaller N200-P550s than those elicited by tone 4 (8 kHz). A small late positive component was elicited by tones 1 and 2, while the target and tones 4 and 5 elicited a larger P550 component which was comparable in amplitude for the target and tone 4.

In experiment II, we found enhanced late positive activity (P550) to the target tone and an adjacent nonreinforced tone as well. However, the results are difficult to interpret for several reasons. First, the intensities of the tones possibly differed due to the resonances of the tank. Second, the higher frequency tones would be expected to elicit larger responses at comparable intensities because of the increased sensitivity of the dolphin auditory system to high frequency sounds (Bullock & Ridgway, 1972; Johnson, 1966). Third, because of the harmonic structure of the stimuli they may have been difficult for the dolphin to discriminate, particularly in the restraining tank with acoustic resonances that were unfamiliar to the dolphin. Finally, although only tone 3 was differentially reinforced, the tone which produced the largest N200 and P550 components (tone 4) was closest in fundamental frequency to the bridge tone (7.5 kHz), which had been directly paired with reinforcement.

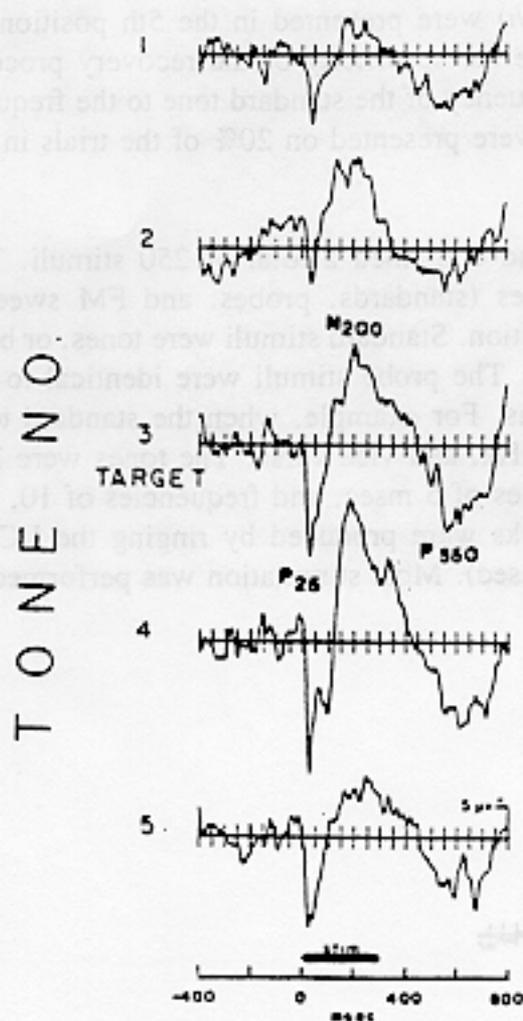


FIG. 3.2. ERPs elicited by the different complex tones used in the conditioning sequence. The tones had been generated by computer and consisted of a fundamental and two harmonics at equal energies. The target tone (no. 3) had been associated with the delivery of a conditioned reinforcer (bridge tone, frequency 7.5 kHz) and with food reinforcement. All tones were presented with equal probabilities.

EXPERIMENT III. THE RECOVERY CYCLE OF THE DOLPHIN ERP

Experiment III was designed to examine the effects of stimulus repetition on auditory ERPs in the dolphin. An audio tape was constructed to control the timing of function generators which delivered tones, clicks, or FM sweeps. Stimuli were presented in trains of six. On 50% of the trials the inter-stimulus intervals (ISIs) within the trains were fixed at 0.5 sec, and on the remainder of the trials ISIs were 1.0 sec. Trains with different ISIs occurred randomly. Longer intertrain intervals (ITIs, also random, and either 2.0 or 6.0 sec) were inserted between trains to permit the ERPs at the beginning of the trains to recover more fully.

Three different stimuli occurred on a random basis in the trains:

1. *Standard stimuli* were presented in the first four positions on all of the trains, on 50% of the trains in the fifth position, and on 80% of the trains in the

6th position. The ERPs elicited by these stimuli were used for evaluating recovery cycles.

2. *Probe tones (of a different pitch)* were presented in the 5th position on 50% of the trains in order to examine the specificity of the recovery process.

3. *FM sweeps* (going from the frequency of the standard tone to the frequency of the deviant tone or vice versa) were presented on 20% of the trials in the sixth position.

Each condition lasted 5.25 min and contained a total of 250 stimuli. The stimuli in each of the three categories (standards, probes, and FM sweeps) remained constant during a given condition. Standard stimuli were tones, or brief clicks similar to dolphin sonar pulses. The probe stimuli were identical to the standard tones used in other conditions. For example, when the standard tone was 30 kHz, the probe tone was 80 kHz, and vice versa. The tones were 200 msec in duration with rise and fall times of 5 msec, and frequencies of 10, 20, 30, and 80 kHz. The broad-band clicks were produced by ringing the LC-10 hydrophone with a square wave (20 μ sec). Most stimulation was performed at 140 dB re 1 micropascal.

FREQUENCY

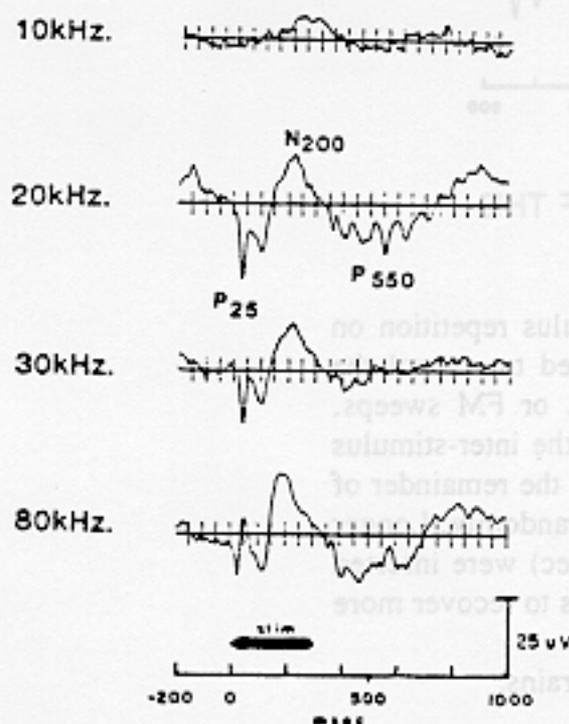


FIG. 3.3. Grand mean ERPs elicited by 300 msec duration tone bursts ranging in frequency from 10 kHz (top) to 80 kHz (bottom). The ERPs were averaged over the different stimulus positions and trains used in Experiment III.

Results

The components typically elicited by the tone burst stimuli are shown in Fig. 3.3 for a parietal-left mastoid placement. At least five components could be reliably identified: middle-latency positive and negative waves (P25 and N65), a small subsequent positivity (P110), and two prominent long-latency components, the N200 and P450. The P450 component was followed by a broad positivity in response to deviant probe tones (P550), which was seen to a lesser extent following the tones at train onset. Comparisons of ERPs from left and right hemisphere sites showed that the components were symmetrically distributed over the two hemispheres. P25, N65 and P110 components were seen at all sites, but N200 and P450/P550 components were more clearly observed in parietal-mastoid than in parietal-snout electrode pairs. A small off-potential, consisting mainly of middle-latency components, occurred at the higher tone frequencies. The 10 kHz tone produced small and delayed late components without evident middle-latency activity, probably in part because of its lower intensity (due to the bandpass characteristics of the hydrophone). The 20, 30, and 80 kHz tones produced middle- and long-latency responses with comparable amplitudes and latencies.

The effects of stimulus intensity were examined on ERPs elicited by 20 kHz tones and click stimuli (Fig. 3.4). Click stimuli elicited prominent middle-laten-

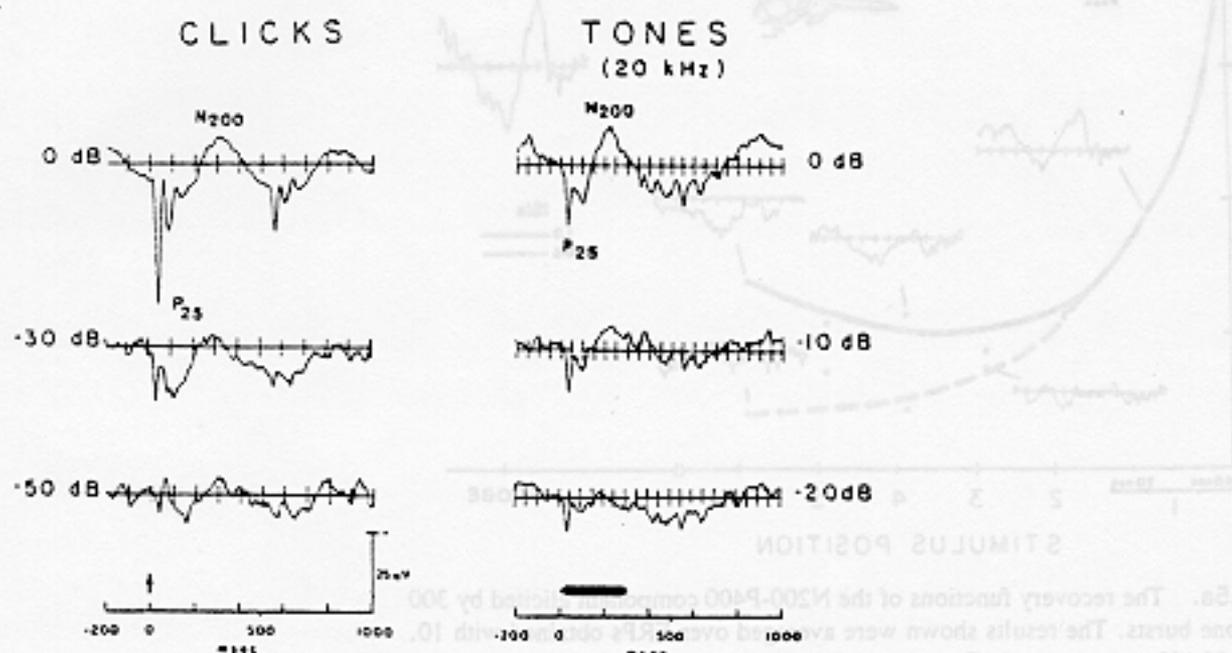


FIG. 3.4 Grand mean ERPs at different stimulus intensities elicited by brief broadband clicks (left) and 20 kHz tones (right). Long-latency components were elicited by both types of stimuli, but middle latency components were more prominent in response to the click stimuli. The ERPs shown were averaged over the different stimulus positions and trains used in Experiment III.

cy components with P25 amplitudes in excess of $40 \mu\text{V}$. As stimulus intensities were reduced amplitudes decreased for both middle- and long-latency components, with click ERPs showing a broader dynamic range than tone responses.

The recovery functions of peak-to-peak measures of the N200-P450 were comparable for the different tone frequencies and are shown in Fig. 3.5a (averaged over all tones). N200-P450 amplitudes declined markedly with stimulus repetition. In trains with tones separated by 1.0 sec ISIs, amplitudes declined to 30% of those recorded at the beginning of the train. In trains with 0.5 sec ISIs, amplitudes declined to 15% of control values. In response to click stimuli, the middle-latency components showed short refractory periods, and did not vary systematically with ISI in the range tested.

The refractory effects produced by stimulus repetition were highly specific to the conditioning stimulus. Probe tones had N200-P450 amplitudes more than 500% larger than conditioning tones in the same train position (Fig. 3.5a). Indeed, probe N200-P450s were larger than ERPs at train onset, suggesting that the refractory effects produced by the conditioning tones may have been specific to that stimulus.

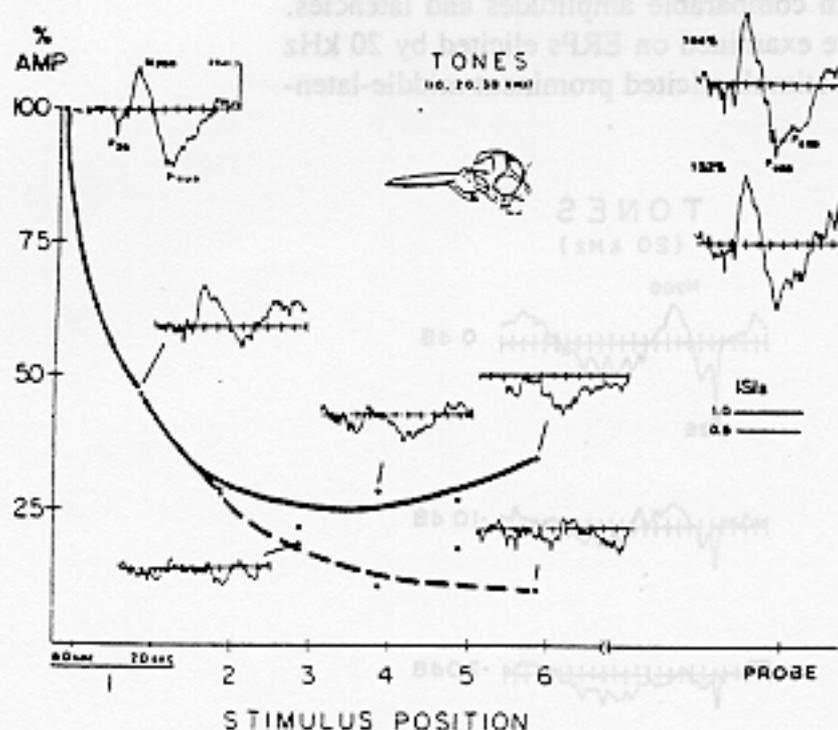


FIG. 3.5a. The recovery functions of the N200-P400 component elicited by 300 msec tone bursts. The results shown were averaged over ERPs obtained with 10, 20 and 30 kHz tone bursts in Experiment III. ERPs are shown for stimulus trains with 1.0 sec ISIs (top, solid line) and 0.5 sec ISIs (bottom, dashed line). ERPs to the probe stimuli are shown as inserts on the upper right, but data points for these traces are off-scale.

FIG. 3.4. Grand mean ERPs to broadband clicks (left) and 20 kHz tone bursts (right) elicited by both types of stimuli, but middle latency components were more prominent in response to the click stimuli. The ERPs shown were averaged over the different stimulus positions and trains used in Experiment III.

A late positive component (P550), seen as a shoulder on the P450 to baseline, was produced by probe stimuli and stimuli at train onset. Both the P550 and the P450 were reduced in amplitude during the conditioning train sequence. ERPs produced by FM-sweeps (not shown) also elicited enhanced and slightly prolonged P550 components, but because of the small numbers of trials in this category the ERPs were noisy and less consistent than those in other stimulus classes.

Several parallels were evident between the recovery cycles of human ERPs obtained in a similar paradigm (Fig. 3.5b) and dolphin responses. First, both the dolphin N200-P450 and the human N100-P200 were reduced in amplitude to asymptotic levels by the first several stimuli in a train. Second, in both species the ERPs were largest at the longest ISI.

However, several differences were also observed. First, the degree of refractoriness was greater for dolphin than human ERPs. For example, amplitudes in

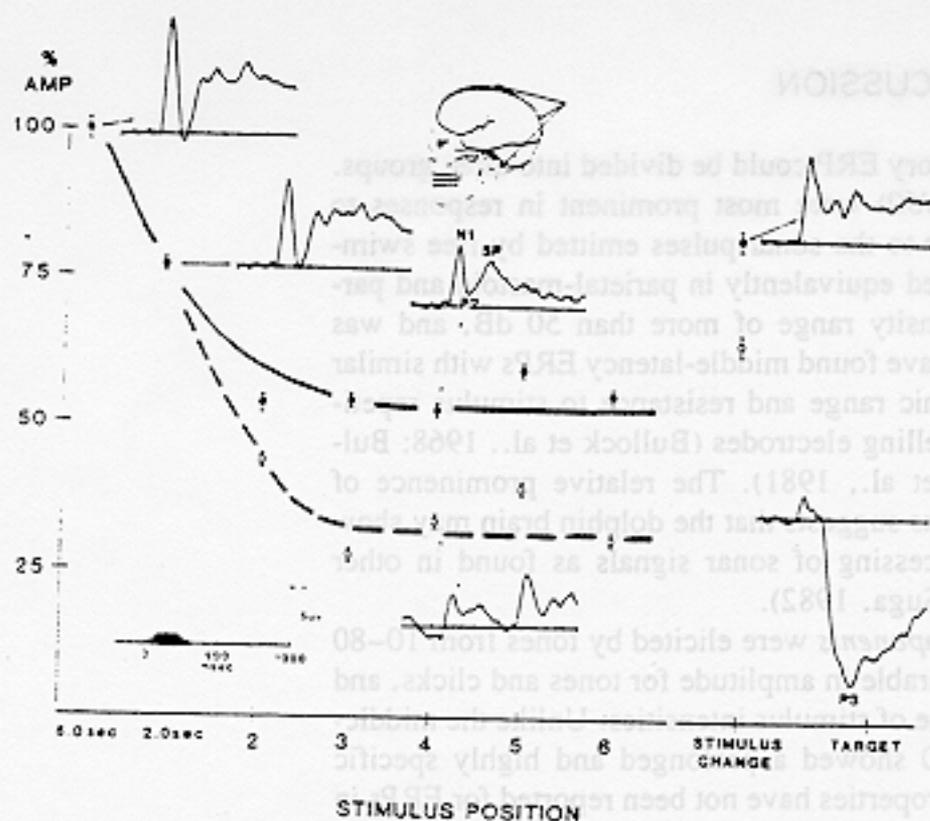


FIG. 3.5b. The recovery functions of the N100 component of the human ERP in a group of 12 human subjects in a paradigm similar to that of Experiment III. Grand mean ERPs are averaged over subjects and different evoking stimuli, including pure and complex tones, vowels and consonant-vowel-consonant syllables. ERPs are shown for stimulus trains with 1.0 sec ISIs (top, solid line) and 0.5 sec ISIs (bottom, dashed line). ERPs to deviant nontarget stimuli are shown on the top right. ERPs to target stimuli (requiring a button press response) are shown on the bottom right. Note the occurrence of a large P300 to the target stimuli.

the 0.5 sec ISI trains were reduced to about 15% of initial amplitudes in the dolphin vs. about 30% in humans. Second, a larger difference was observed between ERPs following 6.0 and 2.0 sec intertrain intervals for the dolphin than for humans, suggesting that the refractory period may have been more prolonged in the dolphin. Third, the refractory process was more specific in the dolphin. In humans, tone pips of one pitch reduce N100-P200 amplitudes to tone pips separated by several octaves. In the dolphin no such reduction was evident: probe N200-P450 amplitudes were larger than those at train onset.

The probe tones also produced additional late positivity in man (P300) and dolphin (P550). In humans, when stimulus order is counterbalanced across subjects, probe P300 amplitudes are seen to be reduced over successive stimulus blocks (Woods & Elmasian, 1985). In the dolphin, we were unable to determine if similar amplitude reductions of the P550 occurred, or otherwise operationally dissociate it from the P450. However, the P550 elicited by the frequency-shifted tones appeared to be relatively larger than to tones with similar P450 amplitudes at train onset.

DISCUSSION

The components of the dolphin auditory ERP could be divided into three groups. *Middle-latency components (P25, N60)* were most prominent in responses to ultrasonic, broad-band clicks similar to the sonar pulses emitted by free swimming dolphins. The P25 was recorded equivalently in parietal-mastoid and parietal-snout placements over an intensity range of more than 50 dB, and was resistant to stimulus repetition. We have found middle-latency ERPs with similar properties, including a broad dynamic range and resistance to stimulus repetition, in previous studies using indwelling electrodes (Bullock et al., 1968; Bullock & Ridgway, 1972; Ridgway et al., 1981). The relative prominence of middle latency ERPs evoked by clicks suggests that the dolphin brain may show a similar specialization for the processing of sonar signals as found in other echolocating mammals (O'Neill & Suga, 1982).

Long-latency N200 and P450 components were elicited by tones from 10–80 kHz. These components were comparable in amplitude for tones and clicks, and could be recorded over a limited range of stimulus intensities. Unlike the middle-latency components, the N200-P450 showed a prolonged and highly specific refractory period. These refractory properties have not been reported for ERPs in the cat (Buchwald, Hinman, Norman, Huang, & Brown, 1981; Wilder et al., 1981) or monkey (Arthur & Starr, 1984), but are similar to those of human long-latency N100-P200 components (Picton et al., 1977; Woods & Elmasian, 1985).

In humans, the refractory period of the N100-P200 has been suggested to reflect the degree of memory excitation required by a stimulus (Picton, Campbell, Baribeau-Braun, & Proulx, 1978). When a stimulus has been presented its

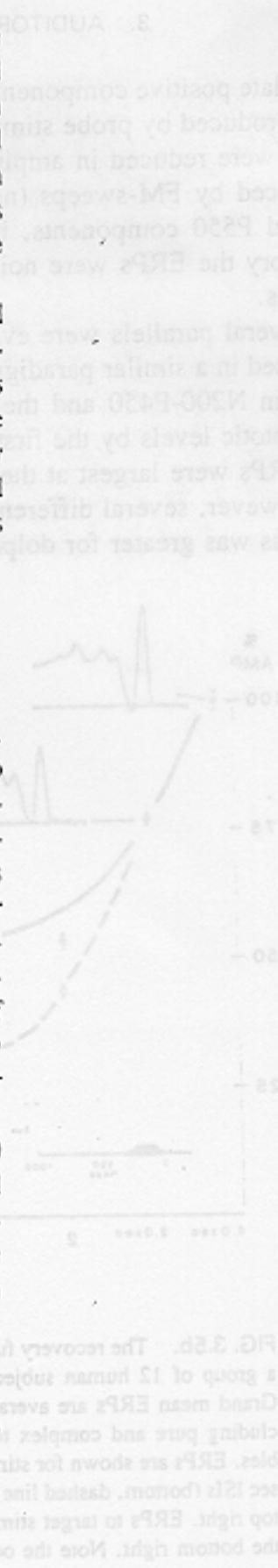


FIG. 3. Grand mean ERP waveforms for dolphin (left) and human (right) subjects. The top right shows ERPs to target stimuli (N200-P450) and the bottom right shows ERPs to a large P300 stimulus. The dashed line indicates the 100 ms ISI between stimuli. The recovery time course of the N200-P450 component is shown by the solid line in the bottom right. The recovery time course of the N100-P200 component is shown by the solid line in the top right. The recovery time course of the P300 component is shown by the solid line in the bottom right. The recovery time course of the P550 component is shown by the solid line in the top right.

representation in memory is primed so that its repetition produces only a small additional N100-P200. With increasing ISIs the memory representation decays so that N100-P200 amplitudes are enhanced. When a tone follows another of a different pitch, portions of its representation will have been excited so that its N100-P200 amplitude will be only partially recovered. Following this line of reasoning the discreteness of the neuronal representation of a sound in memory would be reflected in the degree of specificity of the refractory process. If so, the mnemonic representation of tones would appear to be more discrete in the dolphin than in man, since the ERP recovery functions are more specific.

A second difference between dolphin and human acoustic memory is also suggested by the data. In humans, ERPs show large increases in amplitude as ISIs are extended up to several seconds, and then smaller increases as intervals are lengthened further. For example, in humans only small differences in N100-P200 amplitude are observed between 2.0 and 6.0 sec. In the dolphin marked differences were observed in the N200-P450 at these intervals. This suggests that in the dolphin the neural excitation may still have been in the rapidly changing phase (similar to that observed in humans at shorter intervals) at 2.0-6.0 sec ISI. In any case, these characteristics of the ERP are consistent with a precise and persistent representation of acoustic features in the memory of the dolphin (Herman, 1980).

In the dolphin a *long-latency positive component (P550)* was elicited in all three experiments by infrequent or task-relevant stimuli. It was difficult to distinguish this component operationally from the P450 since both were enhanced by the low probability of stimulus delivery. For example in experiment III both P450 and P550 activity were enhanced following deviant stimuli. In humans the same relationship is observed between the P300 (emitted in response to deviant stimuli) and the P200 (enhanced to infrequent stimuli because of the specificity of the refractory process discussed above). However, the P550/P450 ratio appeared higher to deviant stimuli than to other stimuli in the train, as would be expected if the P550 were correlated with the processing of startling or deviant stimuli.

The relatively small amplitude of the P550 components recorded in experiment II, which most closely resembled human P300 paradigms, may have been related to several factors. First, the harmonic structure of the stimuli may have made them confusing to the dolphin because of echoes and distortion in the restraining tank. Second, the animal had never been presented with the stimuli while restrained and half submerged, and may have experienced difficulty in generalizing across different conditioning and test environments. Indeed, in the absence of an overt motor response we could not be certain that the animal was differentially responding to the target tone.

The small amplitude of the P550 in experiments I and III may be due to other factors. First, unless infrequent stimuli cue responses, the P300 components that they elicit are reduced in amplitude with repeated presentations in humans

(Courchesne, 1978) and monkeys (Arthur & Starr, 1984). Habituation may have similarly reduced P550 amplitudes in the dolphin. Second, in P300 experiments requiring auditory discriminations, humans with perfect pitch have small P300s (Klein, Coles, & Donchin, 1984). The small P550s in the dolphin may similarly reflect a highly evolved capacity for pitch discrimination.

The latency of the P550 component also deserves comment. In humans, P300 latencies are related to the time required to recognize (McCarthy & Donchin, 1981), and respond to stimuli (Woods, Courchesne, Hillyard, & Galambos, 1980). Insofar as the latency of the P300-equivalent is indicative of the time required for processing auditory stimuli in different species, the dolphin would at first glance appear to process at least some auditory stimuli more slowly than humans, cats (Wilder et al., 1981), or monkeys (Arthur & Starr, 1984). However, several other factors may also have contributed to the prolonged latencies of the P550 component which we observed. First, reflections and resonances in the small restraining tank may have made acoustic discriminations more difficult. In humans P300 latencies in difficult tasks may exceed 600 msec (Pritchard, 1981). Second, human P300 latencies are longer than those of equivalent potentials in animals with smaller brains. Thus, there may be a relationship between the time of transmission between certain neuroanatomical structures and the latency of the P300-like component. The prolonged latency of the P550 in the bottlenosed dolphin is consistent with the large brain size (1500 grams) of this species, and suggests that the P300 pathways may have increased in length in comparison with terrestrial mammals. Third, different species may vary in the extent to which stimuli are used for "context updating" (Donchin, 1981). A deeper and more thorough updating may be associated with longer latency P300s. If so, the long latency of the P300 equivalent in dolphin would be consistent with a thorough analysis of acoustic inputs. Fourth, P300 latencies in man increase (by up to 120 msec) with aging (Goodin, Squires, Henderson, & Starr, 1978). If a similar relationship holds in dolphins the relatively advanced age of our animal (22 years) may have contributed to the prolonged latencies of the P300-like potentials that we observed.

SUMMARY

We recorded event-related potentials (ERPs) from the skull surface of a bottlenose dolphin (*Tursiops truncatus*) in response to a variety of auditory stimuli including pure and complex tones, FM sweeps, clicks, and dolphin calls. The effects of stimulus repetition and probability on ERPs were examined in three experiments. In each experiment, infrequent, deviant sounds (such as dolphin calls mixed with trains of tones) or task-relevant stimuli (associated with rein-

forcement) were presented at low probabilities in an effort to elicit endogenous potentials similar to those which occur in humans following the presentation of infrequent or surprising stimuli.

Three classes of responses were recorded. *Middle-latency components* (P25-N60) showed short refractory periods and were maximal in amplitude to brief click stimuli similar to echolocation pulses. *Long-latency components* (N200-P450) showed comparable amplitudes for click and tone stimuli. When stimuli were repeated, the N200-P450 was markedly reduced in amplitude at all intervals tested (up to 6.0 sec). This refractory process was specific to the stimulus because conditioning tones of one frequency did not reduce N200-P450 amplitudes to probe tones of another frequency. The dolphin N200-P450 showed more marked and specific refractory effects than the human N100-P200 recorded in a comparable paradigm. The differences may reflect a more precise representation of auditory stimuli in dolphin short-term acoustic memory.

Deviant stimuli produced an enhanced *long-latency positive component* (P550) in the dolphin, similar in some respects to the "decision-related" P300 wave in humans.

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