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Signature whistle variations in a bottlenosed dolphin, *Tursiops truncatus*

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Abstract To examine whether context-specific information is superimposed upon the individual cues present in the whistling of the bottlenosed dolphin, *Tursiops truncatus*, parameter variations within the two most frequently emitted whistle types of a captive individual were investigated in three different behavioural contexts. The study concentrated on comparing signal features of spontaneously occurring vocalizations in two possible phases following the performance of a trained discrimination task and those occurring during isolation. Phases of the discrimination task differed according to whether the animal showed "correct" (reward given) or "incorrect" performance (no reward). Signature whistles were most common in isolation, but also represented just over half of the whistles following a choice task. Of 14 signature whistle frequency and time parameters measured 9 differed significantly between isolation and at least one of the phases following a choice task (Table 1). Three parameters also varied according to whether performance was correct or incorrect. In contrast, only one out of four parameters (start frequency) measured from the second most frequent whistle type varied significantly between contexts (isolation vs. phase following correct choice). The results indicate that not only identity but also context-related information is available in the whistles of a bottlenosed dolphin.

Key words Signature whistle · Vocal communication
Forced choice procedure · *Tursiops truncatus*

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Introduction

Bottlenosed dolphins (*Tursiops truncatus*) are well-known for their impressive abilities in both producing and perceiving sounds. Their sound repertoire comprises whistles, burst-pulsed sounds and clicks (Popper 1980). Although the last of these are mainly used for echolocation, all of these signal categories seem to play a role in social interactions (review in Herman and Tavolga 1980). However, whistles have been the most commonly studied vocalizations in bottlenosed dolphins so far.

The whistle repertoire of a bottlenosed dolphin is especially characterized by its individually specific signature whistle (Caldwell and Caldwell 1965, 1968). Each individual has its own distinctive whistle contour, which is highly stereotyped and can remain stable for up to at least 12 years (Sayigh et al. 1990). It is reported to be the most frequently emitted whistle type of captive individuals (Caldwell et al. 1990) as well as of temporarily captured, free-ranging ones (Sayigh et al. 1990). In a detailed isolation study, only 4 out of 114 individuals of at least 1 year of age showed a signature whistle level below 80% of all whistles (Caldwell et al. 1990). However, in more varied contexts it accounts for lower percentages (Lang and Smith 1965; Bastian 1967; Tyack 1986; Janik and Todt 1992). Tyack (1986), for example, found signature whistle percentages of 67% and 48%, respectively, in two captive, but freely swimming and interacting individuals.

Caldwell and Caldwell (1968) hypothesized that the main function of signature whistles is to signal the individual identity of the whistler to members of its social group. In this context the high percentages of signature whistles even in close-contact interactions raise the question of whether this whistle category broadcasts information in addition to the individual cues it provides. Superimposing additional information would be possible in different ways. Timing and use of accompanying signals, or of the signature whistle itself, as well as whistle rates, could bear additional cues indicating, for example, a signaler's state. Alternatively, the dolphin might alter single signal parameters of a whistle without affecting the general shape of its contour.

In this paper variation in a range of acoustic parameters of signature and other whistles was investigated in order to test for the significance of systematic variation with behavioural context. For this, it was best if the contexts were as standardized as possible. Contexts such as socializing or feeding include many different behavioural alternatives for the dolphin. Even in a group of apparently resting animals individuals can take different roles. To handle this difficulty of assessing behavioural situations this study concentrated on behaviour in an artificial context, in which the dolphin was either rewarded during a visual discrimination task or not, depending on whether it made a correct or incorrect choice. Acoustic parameters were measured from whistles which occurred spontaneously in phases following a choice, and were investigated in relation to the two alternatives "reward" or "no reward". Additionally, the resulting variations were compared with data from an isolation context, since this has been a standard situation used in earlier studies on signature whistles (Caldwell et al. 1970, 1990).

Methods

The study was conducted at the "Delphinarium Münster", Germany. The subject was an approximately 7-year-old female bottlenosed dolphin (*Tursiops truncatus* Montague) named Nynke. Data sampling covered a continuous period of 12 weeks from June to August 1990. All recordings were made with the animal in the main pool (10 × 20 × 4 m), separated from its poolmates (two other adult females) in the resting pool by a lattice. The animals were accustomed to this situation and to the procedure of separation. They did not show any physical interactions during experiments, although the lattice did not prevent bodily or acoustic contact.

Contexts

Recordings were made during both choice experiments and an isolation context (ISO), when no humans were present. During isolation trials the animal was isolated in the main pool. The mean duration of an ISO trial was 256.3 s (SD 106.3).

For the choice contexts the dolphin had been trained to choose one of two objects presented simultaneously in air (a two-alternative forced-choice procedure). When the animal reached a criterion of 18 correct choices in a session of 20 trials, the relation between the positive stimulus (S+) and the negative stimulus (S–) was reversed. This means that the previously unrewarded object was rewarded and the previously rewarded object was unrewarded in the next experimental session. This procedure was continued with the object values reversed each time the dolphin reached the criterion (successive reversal problems, see Beach and Herman 1972).

Each trial consisted of two successive phases, one preceding the choice and one following it. In the phase preceding the choice the animal stationed itself 2 m in front of the test board while pushing its rostrum towards a starting point (a red float, as used for supporting nets) situated 50 cm above the water surface. A stimulus presentation was started by lifting a covering shield from the test board, so that the dolphin could see the stimuli. After approximately 4 s a release tone was given, whereupon the animal left the starting point, and chose one of the objects by removing it from the board. In cases when the correct choice was made an acoustic, secondary reinforcer (bridge) was given immediately after the removal. In cases of incorrect choice no such signal was given. In the phase following the choice (PFC) the animal swam to the experimenter, who was now visible to the dolphin, to deliver the object. In correct choice contexts (PFCcorrect) it received a fish reward, following incorrect choice (PFCincorrect) no reward was given. Then, the animal returned to the starting point and stationed itself there until the next trial was started. Sound analysis was concentrated exclusively on the phase following the choice. The mean durations of PFC contexts were 32.2 s (SD 10.3) for PFCcorrect and 34.7 s (SD 8.7) for PFCincorrect.

Recordings and analysis

A Nagra IV-SJ tape recorder was used to record vocalizations underwater (B&K 8103 hydrophone and B&K 2010 preamplifier) and in air (B&K 4135 microphone and B&K 2619 preamplifier). This system had a frequency response from 25 to 35000 Hz ± 1dB. Additionally, a Uher 4200 Report Monitor tape recorder with a B&K 8103 hydrophone and a B&K 2625 preamplifier (frequency response: 25–25000 Hz ± 3 dB) was used to monitor whistles of conspecifics in the resting pools. The two hydrophones were 24 m apart. Thus, a comparison of amplitudes between the two tapes allowed identification of whether the dolphin producing a recorded sound was in the main or resting pool.

Sound analysis used SIGNAL software (Beeman 1989). Spectrograms of whistles at half-speed were prepared [fast fourier transform (FFT), FFT size: 1024, DT: 20.5 ms, DF: 49 Hz, time step size: 10 ms, weighting function: hanning window] and categorized by visual inspection into six types. Any whistle that did not clearly match any of the six categories, or was too short to be reliably assigned, was classed as "remainder". Successive whistles were always separated by silent intervals even if they were emitted in a series. Since every whistle type appeared singly as well, whistles in a series were regarded as separate units.

The parameter analysis was focused on the two most frequent whistle types, the signature whistle and the "rise" whistle. Differences in duration and frequency were measured between the start, major inflection points (occurring only in the signature whistle), and the end for whistles of both types (Fig. 1). Thus, start frequency, end frequency, frequency range and duration was measured for both types. The frequency and time of the local maximum [inflection 1 and T(inflection 1)] and the local minimum [inflection 2 and T(inflection 2)], as well as differences in time and frequency be-

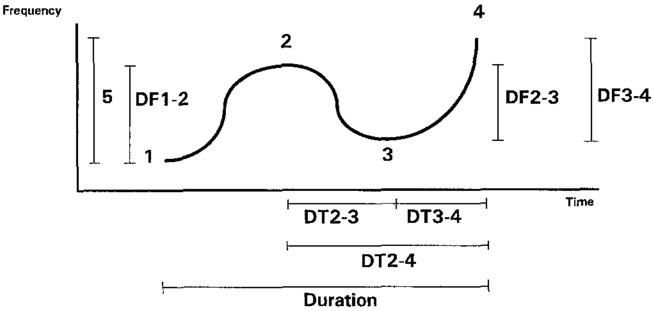


Fig. 1 Schematic spectrogram of a signature whistle showing the parameters analysed (*1* start frequency, *2* frequency and time of inflection 1, *3* frequency and time of inflection 2, *4* end frequency, *5* frequency range, *DF1–2* frequency difference between 1 and 2, *DF2–3* frequency difference between 2 and 3, *DF3–4* frequency difference between 3 and 4, *DT2–3* time difference between 2 and 3, *DT3–4* time difference between 3 and 4, *DT2–4* time difference between 2 and 4, *duration*)

tween start, local maximum, local minimum and the end (DF1–2, DF2–3, DT3–4, DT2–3, DT3–4, DT2–4) were measured for the signature whistle only. These measurements were taken automatically with specially written software (Janik 1992) on a digital line spectrogram of the fundamental. The line spectrogram is a reduction of the original produced by a peak function, which gives only the peak frequency in every FFT column. Nevertheless, every whistle spectrogram was visually compared with its peak contour plot as there were many signals in which the peak lay partly on one harmonic or on simultaneously emitted clicks. In those cases it was set back manually to the fundamental.

The contour of the signature whistle of the study animal had two major inflection points – first a local maximum, followed by a local minimum. These two inflections were localized automatically in each whistle by an algorithm that found the maximum difference in frequency between all occurring maxima and minima in the fundamental contour plot of a single whistle (Janik 1992). The comparison of all differences avoided incorrect determinations which could occur due to additional, minor inflections within the main contour.

Each whistle in a sequence was analyzed separately. By using an analysis of variance to test the influence of context on signal parameters we avoided the problem of inflating the sample size due to the fact that a whistle is not independent of the preceding one (Kramer and Schmidhammer 1992). Since data were not normally distributed (Kolmogorov-Smirnov test, $P<0.05$) a non-parametric Kruskal-Wallis (KW) ANOVA was used. A Bonferroni procedure for dependent data was applied to interpret the ANOVA at a level of significance equal or lower than 0.05 for all rejected H_0s (Cross and Chaffin 1982). This was necessary because several parameters were measured and tested on the same set of whistles. The Bonferroni procedure adjusts the α level to avoid the rejection of true null hypotheses in such cases. To determine which pairs of contexts were different in a significant K-W ANOVA the method of multiple comparisons of contexts was used (Siegel and Castellan 1988). As far as possible SPSS/PC+ routines were used for the statistical analysis.

Results

The animal emitted 1743 whistles in 221 choice trials and 18 isolation trials. Out of this sample 637 whistles occurred in 76.9 min of isolation trials, 809 whistles during 96.6 min of PFCcorrect (180 trials), and 297 whistles during 23.7 min of PFCincorrect (41 trials). Mean whistle rates were 8.1 whistles/min (SD 3.1) in isolation, 8.4 whistles/min (SD 5.5) in PFCcorrect and 12.7 whistles/min (SD 7.3) in PFCincorrect. Whistle rates of PFCcorrect and PFCincorrect differed significantly (K-W ANOVA with multiple comparisons, $P<0.05$).

Figure 2 shows sound spectrograms of each whistle type that occurred in this study. Signature whistles showed the highest degree of stereotypy. However, truncated versions, consisting only of the first hump of the contour, occurred as well. According to their contour structures the other whistle types were named “rise”, “flat”, “down”, “sine” and “hole” whistles. The first four of these had parallel definitions to Tyack (1986). The fifth type did not occur in Tyack’s study. All other whistles were pooled in a “remainder” class. Signature whistles of poolmates are not discussed in this paper. In five cases a whistle with the same contour as the signature whistle of a poolmate was emitted by the experimental animal. However, one of the poolmates did not vocalize at all when it was isolated (four ISO sessions, 25 min total duration), so that its signature contour could not be determined.

The distribution of whistle types across contexts is presented in Fig. 3. While the signature whistle accounted for 80.2% of all whistles in ISO, its relative frequency was reduced by more than 25% in PFCcorrect and PFCincorrect. The relative frequency of all other whistle types was higher in PFC contexts as compared to isolation. Frequency distributions hardly differed at all between PFCcorrect and PFCincorrect. The same proportions were found by comparing absolute whistle rates for each whistle type. Thus, changes of general whistle rate did not affect the composition of the performance.

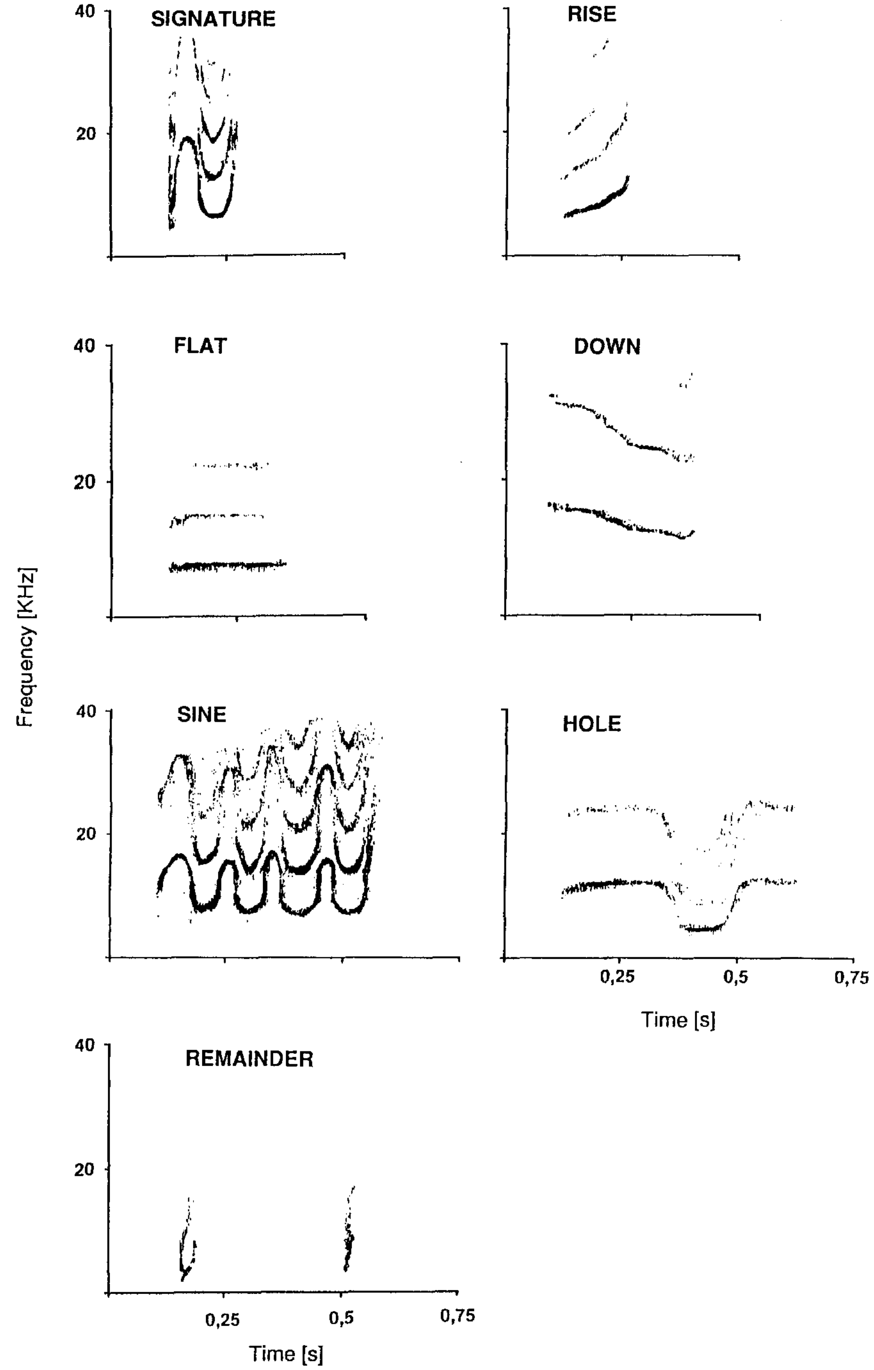
A total of 523 signature whistles (ISO: 117, PFCcorrect: 292, PFCincorrect: 114) and 282 rise whistles (ISO: 51, PFCcorrect: 175, PFCincorrect: 56) had a high enough signal-to-noise ratio for parameter measurements to be made. Table 1 presents medians, first and third quartiles and test results for each parameter of both whistle types in all contexts. For the signature whistle a K-W ANOVA revealed significant differences ($P<0.05$) in start frequency, end frequency, frequency range, DF1–2, DF3–4, duration, T(inflection2), DT2–3 and DT2–4. Multiple comparison tests showed that these parameters differed mainly between ISO and PFC contexts. Signature whistles in PFCcorrect and PFCincorrect differed significantly only in frequency range, DF1–2 and DT2–3. To summarize these results, the signature whistles emitted in ISO compared to those in PFC contexts had a 1.1–1.5 KHz lower median start frequency, a 1–1.9 KHz higher median end frequency, and a 5–15 ms shorter median duration in the last two-thirds. In line with these differences, there was a vertical stretching of the contour in its first and last part and a shorter duration in ISO compared to the PFC contexts. The vertical range in the first part was even smaller in PFCincorrect compared to PFCcorrect, while the temporal expansion in the last third was greater in PFCincorrect (all results $P<0.05$).

Of the four rise whistle parameters only the start frequency differed: it was significantly lower (by 1.1–1.5 KHz) in ISO compared to PFCcorrect (K-W ANOVA with multiple comparisons, $P<0.05$). Rise whistles emitted in PFCcorrect and PFCincorrect showed no significant differences on any measure.

Discussion

The results demonstrated clearly that different aspects of context are related to different characteristics of signaling behaviour in the bottlenosed dolphin. Both signature whistle percentage and whistle rate in the isolation context were consistent with earlier experiments (Caldwell and Caldwell 1965; Caldwell et al. 1970, 1990). A much lower proportion of signature whistles appeared in all phases of the discrimination task. But while signature whistle percentage was not affected by

Fig. 2 Sound spectrograms of whistle types produced by the experimental animal



whether or not the response was correct, whistle rate increased only in phases following an incorrect choice (no reward). The high proportion of rise whistles suggests that it plays an important role in this context. However, the rise contour could have been an imitation of the signature whistle of the oldest pool member from which a signature whistle could not be recorded. Such cases of mimicry were reported by Tyack (1986). It occurred also between the two younger animals in this study.

The results of the parameter analysis are the first report that a bottlenosed dolphin varies parameters of its whistle types in relation to context. The differences in the signature whistle, in both the frequency and the time domain, were more marked between isolation and the discrimination task than between the two alternative phases following a choice. Rise whistles showed no systematic variation in PFC in relation to whether the choice was correct or incorrect. They differed in only one parameter in the comparison between isolation and the discrimination task. Various authors have suggested that parameter variation plays an important role in bottlenosed dolphin communication (Herman and Tavolga 1980; Caldwell et al. 1990). In Odontoceti, changes of signal parameters within single types of whistles or burst-pulsed sounds in relation to context have been

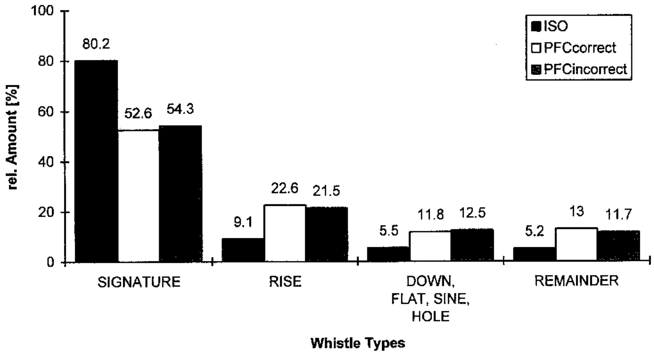


Fig. 3 Percentages of whistle types in contexts. Data for down, flat, sine and hole whistles were pooled due to their rare occurrence (*ISO* isolation, *PFCcorrect* phases following correct choices, *PFCincorrect* phases following incorrect choices)

reported only for *Globicephala melaena* (Taruski 1979) and *Orcinus orca* (Ford 1989). However, these studies were not able to identify the sender of a signal. Thus, different variations could have been produced by different individuals.

Variations of whistle types might either be motivational signals caused by changes in physiological parameters or more referential ones communicating information on external referenda (Marler et al. 1992). Bottlenosed dolphins can be trained to alter signal parameters within single signal types as shown in psychophysical (Moore and Pawloski 1990) and mimicry studies (Richards et al. 1984). Signature whistles varied much more between contexts than rise whistles. This seems to support a referential interpretation because changes of motivational parameters should have a similar effect on all types of vocalization (Jürgens 1979; Morton 1982). However, such changes could occur on a much shorter time scale than we investigated here. If they also affect whistle type distribution a short-term change of the motivational state could be connected with a decrease in the proportion of rise whistles. Rise whistles may even not be produced at all during particular motivational states of the dolphin. In this case signature whistle variations could have been caused by changes in motivational parameters, we just would not have been able to record the corresponding rise whistle variations.

Looking at the receiver we have to ask whether the variations found in whistle structure are perceivable at all. Bottlenosed dolphins are able to perceive frequency differences such as those found here if stimuli are presented for a duration of at least one second (Herman and Arbeit 1972; Jacobs 1972; Thompson and Herman 1975, review in Ralston and Herman 1989). However, the critical points where frequency differences were found only occur for very short durations in the natural dolphin whistle. A study by Yunker and Herman (1974)

Table 1 Parameter differences of the two most frequent whistle types in relation to context (*ISO* isolation, *PFCc* = PFCcorrect: phases following correct choices, *PFCi* = PFCincorrect: phases following incorrect choices, *KW* Kruskal-Wallis)

Parameter	PFC correct			PFC incorrect			ISO			KW-ANOVA *P*	Significance of Multiple comparison test (*P*<0.05)		
	1.Quartile	Median	*3.Quartile*	*1.Quartile*	Median	*3.Quartile*	*1.Quartile*	Median	*3.Quartile*		PFCc-PFCi	PFCc-ISO	PFCi-ISO
Signature Whistle													
Frequency (Hz)													
Start Frequency	*4960*	6073	*7348*	*5643*	6478	*7490*	*4503*	4969	*5694*	0.0000		*	*
End Frequency	*8097*	9109	*11032*	*7864*	8957	*10810*	*9472*	10145	*11387*	0.0000		*	*
Frequency Range	*9413*	10729	*12551*	*8780*	10162	*11564*	*9834*	11698	*12836*	0.0001	*		*
Inflection 1	*15081*	16093	*17384*	*14879*	15946	*17120*	*14855*	16563	*17784*	0.1662			
Inflection 2	*6073*	6781	*7231*	*6174*	6680	*7211*	*6418*	6855	*7246*	0.1481			
DF1-2	*7895*	10121	*11715*	*7262*	9160	*10830*	*9472*	11388	*12733*	0.0000	*	*	*
DF2-3	*8097*	9535	*10805*	*7981*	9272	*10323*	*8127*	9524	*10955*	0.3787			
DF3-4	*1442*	2328	*4049*	*1215*	2047	*3770*	*2677*	3416	*4555*	0.0000		*	*
Time (ms)													
Duration	*140*	160	*175*	*140*	160	*180*	*135*	145	*162*	0.0039		*	*
T (inflection 1)	*60*	75	*85*	*60*	70	*85*	*65*	75	*85*	0.5377			
T (inflection 2)	*110*	120	*140*	*115*	125	*145*	*100*	110	*125*	0.0000		*	*
DT2-3	*40*	50	*55*	*45*	55	*60*	*35*	40	*45*	0.0000	*	*	*
DT3-4	*20*	30	*45*	*20*	30	*45*	*30*	35	*40*	0.0829			
DT2-4	*70*	80	*95*	*75*	85	*100*	*65*	75	*85*	0.0000		*	*
RISE Whistle													
Frequency (Hz)													
Start frequency	*4960*	6275	*7692*	*4959*	6640	*7920*	*4037*	5176	*6004*	0.0030		*	
End frequency	*11943*	14980	*17206*	*11210*	13968	*17206*	*10766*	12940	*17391*	0.3270			
Frequency range	*4960*	7773	*10223*	*4884*	7085	*9767*	*5280*	7971	*10663*	0.8499			
Duration (ms)	*60*	125	*210*	*76*	132	*221*	*65*	95	*140*	0.1615			

suggests that the temporal differences found in this study are not perceivable. On the other hand it is quite clear that such small differences in both the frequency and the time domain have to be perceived for echolocation (Au and Pawloski 1992). Unfortunately, we still do not know whether in this species the same auditory mechanisms underlie the perception of echolocation sounds and that of whistles (Moore 1988). Bullock and Ridgway (1972) showed that click sounds evoke short latency, short duration potentials in the midbrain of a listening bottlenosed dolphin while whistle-like sounds evoked long latency, long duration potentials mainly in the posterior lateral temporal cortex. Further studies are clearly needed to assess the role of whistle variations in the communication system of bottlenosed dolphins. These must emphasize particularly the influence, if any, that these have on the receiver.

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References

Au WWL, Pawloski DA (1992) Cylinder wall thickness difference discrimination by an echolocating Atlantic bottlenose dolphin. J Comp Physiol A 170:41–47

Bastian J (1967) The transmission of arbitrary environmental information between bottlenose dolphins. In: Busnel RG (ed) Animal sonar systems, vol II. Laboratoire de Physiologie Acoustique, Jouy-en-Josas, pp 803–873

Beach FA, Herman LM (1972) Preliminary studies of auditory problem-solving and intertask transfer by the bottlenosed dolphin. Psychol Rec 22:49–62

Beeman K (1989) 'SIGNAL' Software Manual. Engineering Design, Belmont

Bullock TH, Ridgway SH (1972) Evoked potentials in the central auditory system of alert porpoises to their own and artificial sounds. J Neurobiol 3:79–99

Caldwell MC, Caldwell DK (1965) Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). Nature 207:434–435

Caldwell MC, Caldwell DK (1968) Vocalization of naive captive dolphins in small groups. Science 159:1121–1123

Caldwell MC, Caldwell DK, Turner RH (1970) Statistical analysis of the signature whistle of an Atlantic bottlenosed dolphin with correlations between vocal changes and levels of arousal. (Technical Report No. 8). Los Angeles County Museum of Natural History Foundation, Los Angeles

Caldwell MC, Caldwell DK, Tyack PL (1990) A review of the signature-whistle-hypothesis for the Atlantic bottlenose dolphin. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 199–234

Cross EM, Chaffin WW (1982) Use of the binomial theorem in interpreting results of multiple tests of significance. Educ Psychol Meas 42:25–34

Ford JKB (1989) Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Can J Zool 67:727–745

Herman LM, Arbeit WR (1972) Frequency difference limens in the bottlenose dolphin: 1–70 KCs. J Aud Res 12:109–120

Herman LM, Tavolga WN (1980) The communication systems of cetaceans. In: Herman LM (ed) Cetacean behavior: mechanisms and functions. Wiley, New York, pp 149–209

Jacobs DW (1972) Auditory frequency discrimination in the Atlantic bottlenose dolphin, *Tursiops truncatus* Montague: a preliminary report. J Acoust Soc Am 52:696–698

Janik VM (1992) Zum Einsatz von Pfifftypen und Pfifftypvariationen beim Großen Tümmler, *Tursiops truncatus*, in visuellen Diskriminationstests. Diploma Thesis, Freie Universität Berlin

Janik VM, Todt D (1992) Context related parameter variations of signature whistles in the bottlenosed dolphin. In: Elsner N, Richter DW (eds) Rhythmogenesis in neurons and networks: proceedings of the 20th Göttingen neurobiology conference. Thieme, Stuttgart, p 245

Jürgens U (1979) Vocalization as an emotional indicator: a neuroethological study in the squirrel monkey. Behavior 69:88–117

Kramer M, Schmidhammer J (1992) The chi-squared statistic in ethology: use and misuse. Anim Behav 44:833–841

Lang TG, Smith HAP (1965) Communication between dolphins in separate tanks by way of an acoustic link. Science 150:1839–1843

Marler P, Evans CS, Hauser MD (1992) Animal signals: motivational, referential, or both? In: Papousek H, Jürgens U, Papousek M (eds) Nonverbal vocal communication: comparative and developmental approaches. Cambridge University Press, Cambridge, pp 66–86

Moore PWB (1988) Dolphin echolocation and audition. In: Nachtigall PE, Moore PWB (eds) Animal sonar: processes and performance. Plenum, New York, pp 161–168

Moore PWB, Pawloski DA (1990) Investigations on the control of echolocation pulses in the dolphin (*Tursiops truncatus*). In: Thomas J, Kastelein RA (eds) Sensory abilities of cetaceans. Plenum, New York, pp 305–316

Morton ES (1982) Grading, discretness, redundancy, and motivation-structural rules. In: Kroodsma DE, Miller EH, Ouellet H (eds) Acoustic communication in birds, vol 1: production, perception, and design features of sounds. Academic Press, New York, pp 183–212

Popper AN (1980) Sound emission and detection by delphinids. In: Herman LM (ed) Cetacean behavior: mechanisms and functions. Wiley, New York, pp 1–52

Ralston JV, Herman LM (1989) Dolphin auditory perception. In: Dooling RJ, Hulse SH (eds) The comparative psychology of audition: perceiving complex sounds. Lawrence Erlbaum, Hillsdale, pp 295–328

Richards DG, Wolz JP, Herman LM (1984) Vocal mimicry of computer-generated sounds and vocal labelling of objects by a bottlenosed dolphin, *Tursiops truncatus*. J Comp Psychol 87:10–28

Sayigh LS, Tyack PL, Wells RS, Scott MD (1990) Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. Behav Ecol Sociobiol 26:247–260

Siegel S, Castellan NJ Jr (1988) Nonparametric statistics for the behavioral sciences, second edition. McGraw-Hill, New York

Taruski AG (1979) The whistle repertoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. In: Winn HE, Olla BL (eds) Behavior of marine animals, vol 3, Cetaceans. Plenum, New York, pp 345–368

Thompson RKR, Herman LM (1975) Underwater frequency discrimination in the bottlenosed dolphin (1–140 KHz). J Acoust Soc Am 57:943–948

Tyack P (1986) Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? Behav Ecol Sociobiol 18:251–257

Yunker MP, Herman LM (1974) Discrimination of auditory temporal differences in the bottlenosed dolphin and by the human. J Acoust Soc Am 56:1870–1875