Behav Ecol Sociobiol (1983) 13:49–55

Behavioral Ecology and Sociobiology

Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds

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Received November 18, 1982 / Accepted March 30, 1983

Summary. Playback experiments were performed with wild humpback whales, *Megaptera novaeangliae*, during their breeding and calving season off the island of Maui, Hawaii. Singing whales usually stopped singing upon playback of either songs recorded from lone whales or social sounds recorded from groups of five to eight humpback whales in which males were fighting, probably for access to a female in the group. Three out of four lone singers and six of the eight groups of one or two adults exposed to social sounds charged the playback boat, but the two cows with calves and two groups of three of more adults exposed to social sounds moved away.

Of the 16 groups of whales exposed to playback of song, 14 groups moved away. These responses are very similar to those evoked by singing whales or the large active groups from which the social sounds were recorded. The playback experiments thus support the conclusion that the songs and social sounds of humpback whales mediate the responses of approach or avoidance that these whales make to singing whales or large groups in which aggressive behavior is occurring.

Introduction

Humpback whales, *Megaptera novaeangliae*, congregate during their winter breeding and calving season in shallow (<100 m of depth) protected waters approximately 20° of latitude (Dawbin 1966). At this time, lone adult humpbacks sing complex songs (Payne and McVay 1971) that repeat every 5 to 30 min in bouts that can last for as long as 22 h (Winn and Winn 1978). Approximately 20 singing whales whose sex has been determined (Winn et al. 1973; Glockner-Ferrari and Ferrari 1981; James Darling, personal communication) have been males (with one possible exception, Tyack 1982). When singing whales join with other whales, they stop singing. While singers approach whales nearby, most whales in Hawaiian waters avoid singers that are less than approximately one kilometer away (Tyack 1981).

Humpbacks on the breeding grounds also produce sounds that are not repeated in long complex patterns. A whale will often repeat any one of these sounds several times producing a series lasting approximately 2–20 s, but seldom is any other pattern obvious (Silber 1982; Tyack 1982). Since these sounds tend to be produced by whales in groups, these sounds have been called social sounds in contrast to song which is almost always produced by lone whales.

More than half of humpback cows with young calves in Hawaiian waters are accompanied by an adult male called an escort (Herman and Antinoja 1977; Glockner-Ferrari and Ferrari 1981). Social sounds are only rarely heard from groups of one or two adults or from cows and calves with or without an escort. They are produced primarily in groups of 3 or more adults, in which males are fighting, apparently for proximity to a female in the group (Tyack and Whitehead 1983). Whales that are fighting in these groups have been observed to strike each other (Darling et al., in press) and produce loud sounds in this way in addition to vocal sounds.

Singing whales, nonsinging lone whales, or groups of two adults frequently swim straight and rapidly towards these large groups and join them, coming from distances as great as 9 km away (Tyack and Whitehead 1983). The only statistically significant deviation from the general tendency for all groups of whales to avoid one another is the direct approach of singers towards these large groups (Tyack 1982).

It is unlikely that humpbacks could use any but acoustic cues to locate and respond to groups several kilometers away. Humpback song, social sounds, and the sounds of impact produced by whales fighting in large groups have been recorded in Hawaiian waters from whales known to be several km away. These sounds are probably audible to whales at ranges of up to 9 km, the maximum range at which whales have been observed to respond unequivocally to another group with direct and rapid approach.

But it is clearly important to test the hypothesis that humpback whales respond specifically to the sounds produced by singers or large groups. During the spring of 1981, I conducted a series of experiments in which I observed the responses of different kinds of humpback social groups to playback of recordings of humpback song or social sounds.

Two previous reports have demonstrated responses of whales to sound playback. Cummings and Thompson (1971) found that gray whales, *Eschrichtius robustus*, fled from playback of recordings of the killer whale, *Orcinus orca*, a known gray whale predator. Clark and Clark (1980) reported that southern right whales, *Eubalaena australis*, approached an underwater loudspeaker playing back right whale sounds or human imitations of right whale sounds, and right whales increased their own rate of vocalization during such a playback. Right whales tended to move away during playback of water noise, 200 Hz tones, or humpback song. But neither of these papers investigate the effects of differences in the vocalizations of one species.

This paper is the first to demonstrate a differential response of a baleen whale to playback of two different categories of sound produced by conspecifics.

Materials and methods

Experimental procedure. To start a playback experiment I approached a whale or group of whales, called the target group, in a 5 or 6 m boat, shut off the engine and drifted quietly during the playbacks. If the target group was moving on a steady course, I attempted to position the playback boat so that the group would be moving neither directly toward nor away from the boat at the start of a playback experiment. The average distance between a group of whales and the playback boat at the start of playback was about 900 m (range: 80–2,980 m).

Several other boats usually worked with the playback boat during an experiment to monitor the vocalizations of target groups and to photograph distinctive natural markings of whales in the area. The positions of boats and whales were recorded by observers on land using a theodolite (a technique described in Tyack 1981). This allowed me to calculate the distance between each target group and the playback boat as well as to determine the approach or avoidance of target groups. Only groups of whales that were less than 3 km from the playback boat at the start of a playback experiment were included in the results.

Paired playback experiments. At the start of this series of playback experiments, I varied playback duration in a search for an optimal duration (range of playback duration = 10–59 min; mean = 26 min). It proved difficult to compare individual playbacks of song and social sounds given the difficulty of controlling the varying conditions of playback such as distance, time of day, etc. Both for this reason and to determine how the same whale or group of whales would respond to both playback stimuli, I performed a series of paired playbacks. In these paired playbacks, I would first play one stimulus, wait for an interval of 1 to 5 min (mean = 2 min), and then play the other stimulus for as close as possible to the same duration as that of the first. The mismatch in durations of the two stimuli in each of the eight paired playbacks were <1, <1, <1, 1, 1, 2, 3, and 11 min. The 11 min mismatch occurred during the first paired playback. In this case, after a 15 min playback of song, a social sound playback was started. At 11 min and 14 min into this playback, two groups of whales started to charge the boat; I did not stop the playback at 15 min duration but continued until three min after the last charging whale passed the boat. In order to play both stimuli to the same group of whales, the durations of paired playbacks (range = 10–30 min; mean = 21 min) were shorter than those of the other playbacks (range = 24–59 min; mean = 37 min).

Description of sounds used as stimuli. The two kinds of sounds used as stimuli in these playback experiments were humpback song, recorded from lone adults off Maui, and social sounds, recorded from groups of five or more adult humpbacks engaged in aggressive behavior.

Since the songs of humpbacks within one population change even during one singing season (Payne et al., in press), playback of one song stimulus tape throughout the season might evoke different responses as the current song diverged more and more from the song used in playback. I therefore used two different song playback tapes to test whether slightly outdated songs might evoke a different response from contemporary ones. I noticed no obvious difference in response to either of the two song tapes, one from 29 January 1981 and the other from 7 March 1981, including an experiment in which we played back a song recorded from a singer on 7 March 1981 to the same singer the same day.

The playback tapes of social sounds contained both vocalizations and sounds produced when whales struck one another. It has not been reported that humpback social sounds change from year to year as humpback song does. But it was impossible to record social sounds without including a faint background chorus of song. This led me to use a recent tape when possible in case outdated song in the background might affect response to the playback. I started the social sound playbacks with a tape recorded on 20 February 1980 from a group of six whales in which I observed violent contact between fighting whales as they circled our boat. After 11 March 1981, I used a tape recorded on 17 February 1981 by G. Silber in which the background songs were more recent. It was difficult to obtain long recordings of social sounds since the large active groups which produced them at the highest rate moved rapidly. Both of the above tapes were short enough that for playbacks of more than

10 min, I had to rewind the tape (a process which took less than 1 min) and start over. By 15 March 1981, I had enough recordings of social sounds to combine several recordings sequentially from 17 February 1981, 2 March 1981, 9 March 1981, and 20 February 1980. This produced a tape of 30 min duration with no repetition and with a lower intensity of songs in the intervals between social sounds. There was no obvious difference in response of whales to these three tapes of social sounds.

Equipment used for sound playbacks. The equipment used for sound playback appeared closely to approximate the natural stimuli. A Nakamichi 550 cassette tape recorder was used both to record the sounds used in the playback tapes and to play them back. A Crown IC-150 preamplifier and a Crown DC-300A power amplifier powered by a storage battery and inverter were used to amplify the signal, which was projected underwater with a J-11 transducer at a depth of approximately 10 m. This system had a frequency response of ± 5 dB from 40 Hz to 10 kHz and a maximum projection level at 2 kHz of ca. 155 dB re 1 μPa at 1 m. These measurements were made with a calibrated Bruel and Kjaer model 8100 hydrophone in an acoustic test tank using pulses of sound short enough that one could measure the source level of sound following the direct path before reverberation. This maximum projector level compares well with the published source levels for humpback song of Levenson (1972), who reported a mean broad band source level of 155 dB re 1 μPa calculated for a range of 1 m by correcting for transmission loss the source level of a singing humpback that was 2.5 km away. Tests of our playback apparatus near singers indicated that source levels of our playbacks were only slightly lower than those of humpback song. These field tests of relative intensity were only approximate. Soon after one member of our research team (G. Silber) had recorded a singing whale approximately 200 m away, I played back song to him at roughly the same distance as the singer. The level of the playback appeared to be less than 5 dB below that of the singing whale.

The playback signal was clearly audible with our listening apparatus at a range of more than 3 km over the chorus of humpback song heard off Maui in the spring. I presume that the whales could hear this signal from a greater distance, since the sensitivity of whale hearing is likely to be at least as good as that of our hydrophone, since a free floating whale does not encounter the noise produced by water flow past a suspended hydrophone or by cable vibration, and since a whale may use binaural cues.

Results

Responses of whales to playbacks

The most dramatic of the responses of whales to these playbacks was for a whale to charge the playback boat. In 4 years of studying humpbacks off Maui, involving over 2,000 h of observing whales from boats and from a shore lookout, I have never seen a whale charge a boat except during these playbacks. Whales have been seen to charge in a similar fashion toward large active groups of humpbacks like those from which the social sounds were recorded, but it is more impressive to an observer in a 5 m boat when a 15 m whale charges the boat. Charging whales came straight at the boat at high speed (up to 12 km/h), often remaining at the surface and producing a visible surface wake and bow wave. But at more than 15 m from the boat, they dove and then passed under the playback boat at a depth of 5 to 10 m, usually swimming within 5 m of the underwater sound projector. Some whales approached the boat below the surface and did not leave a wake. Since they too came within 5 m of the speaker, I called this response charging also. A charging whale then usually swam around the boat in ever widening circles, occasionally making another pass under it. Although charging whales came as close as 2 m to the speaker, they never touched it.

The other clear-cut response of whales to these playbacks was that all but one of the six singing whales that were target groups appeared to stop singing when either social sounds or song was played back to them (although in two cases they may have rapidly moved out of range of the monitoring boat). Two of the three singers first exposed to playback of song stopped singing after 3 or 8 min of playback. Two of the three other singers first exposed to playback of social sounds stopped after 2 or 11 min of playback. The one singer (marked for footnote e in Table 2) that did not stop singing when first exposed to playback of song, did stop singing after one min of the subsequent playback of social sounds.

If a humpback group did not charge in response to playback, a simple measure similar to the swimming score developed by Clark and Clark (1980) was used to describe the approach or avoidance of the group toward or away from the source of sound playback. A group was scored as moving toward the boat if the total distance it swam toward the boat during the playback was greater than the total distance it swam away from the boat. The motion of a whale was scored as away if the total distance it swam away from the boat during playback was greater than the total distance it swam towards the boat.

Differential response to song and social sounds

There was a highly significant difference in the charging response of whales exposed to social sounds vs song (Table 1). None of the 16 groups exposed to song charged the boat while nine of the 16 groups exposed to social sound playback charged the boat ($P<0.0004$; Fisher exact probability test, Siegel 1956; however, since some whales were exposed to more than one playback, not all

Table 1. Patterns of response of different humpback groups to playbacks of song or social sounds. Responses scored were charging the playback boat, or if the group did not charge, whether it moved toward or away from the playback boat. Since some whales were exposed to more than one playback, not all responses were necessarily independent. However, if one assumes independent responses, the probability that the difference in the number of charges in response to social sounds versus song is significant at the $P<0.0004$ level (Fisher exact probability test; Siegel 1956)

Playback stimulus	Kind of group	Response			Total
		Charge	No charge		
			Movement		
			Toward	Away	
Song	Singer	–	1	3	4
	1–2 adults + calf	–	–	5	5
	1–2 adults	–	1	5	6
	3–4 adults	–	–	1	1
Total		0	2	14	16
Social sounds	Singer	3	–	1	4
	1–2 adults + calf	–	–	2	2
	1–2 adults	6	–	2	8
	3–4 adults	–	–	2	2
Total		9	0	7	16

of the responses were necessarily independent). This difference in response to playback of social sounds compared with playback of song was due only to responses of singing whales, lone nonsinging adults, and groups of two adults. Of these groups, nine of the twelve exposed to social sounds charged the boat, while none of the ten of these groups exposed to song charged during the song playback. None of the cow and calf groups (with or without an excorting adult), nor any of the groups of three or four adults charged the boat during playback of either song or social sounds.

If a whale or group of whales did not charge the boat, then its movement was scored in Table 1 as either toward or away from the playback boat. While the sample sizes are small, it is clear that most whales moved away from the playback boat during playback of song. The two cows with calves and the two groups of three or four adults exposed to social sounds also moved away from the playback boat. The only pronounced differential response to these two stimuli was the charging response of singers, lone nonsinging adults and groups of two adults. Because the movement patterns of whales are complex, the apparent avoidance of whales to playback of song is difficult to interpret in the absence of a control stimulus such as water noise.

Table 2 lists a detailed summary of all playback experiments performed off Maui during 1981. A total of 23 playbacks, 12 of song and 11 of social sounds were performed from 7 to 26 March 1981. Two groups were monitored simultaneously during four song playbacks and during three social sound playbacks; three groups were followed during one social sound playback. Thus a total of 16 groups were followed for each playback stimulus.

Humpbacks charged the boat during none of the 12 playbacks of song, but they charged during six of the eleven social sound playbacks. This difference in response measured using each stimulus presentation as the unit of analysis rather than responses of each group of whales was significant to the $P<0.005$ level (Fisher exact probability test, Siegel 1956). However, since some whales were exposed to more than one playback, not all of the responses evoked in different playbacks were necessarily independent. During four of the social sound playbacks, whales swam at the surface approaching to less than 5 m from the speaker. During the other two, whales came within 5 m of the speaker without being seen charging at the surface.

Eight paired playbacks of song and social sounds were performed as described in the Methods section. These paired playbacks are indicated by brackets in Table 2. Whales charged the boat during three of the eight paired playbacks, and in all three cases the charges occurred during playback of social sounds. Two whales charged during the first paired playback, so a total of four whales or groups of whales charged during the social sound portions of paired playbacks while none charged during song portions. There was no obvious effect of playback order during paired playbacks. Whales charged during the social sound portion in two of the five paired playbacks when song was played first and during one of the three playbacks when social sounds were played first.

The only target groups that charged the playback boat during any of the playback experiments were whales that were singing just before playback. Three of the four singers exposed to social sounds responded by charging the boat. The five other lone whales or groups of whales that charged the boat during playback of social sounds had not been closely followed before the playback. Two of these were pairs of adults; three were lone adults. We could not determine if any of these had been singing before the playback.

The social sound playbacks ranged in duration

Table 2. Chronological list of all playback experiments performed to humpback whales off Maui in 1981. The playback stimulus called 'Soc' in the stimulus column is social sounds. Under the heading 'Kind of target group', Table 2 lists the number of *A* for adult whales, *C* for a calf or 'Singer' if the whale was singing. The distance between the playback boat and a target group was linearly interpolated from transit readings if the whales were not sighted with the transit at the start or stop of a playback. Distances marked ± or > were estimated from the playback boat when the whale surfaced. Distances marked with a < were estimated from the playback boat when the whale was so close that it was visible below the boat. Responses scored in the 'Response' column were charging the playback boat, or if the group did not charge, whether it moved towards or away from the playback boat. The number in the 'Singer stops?' column indicates when the singer stopped in minutes after the start of playback. Paired playbacks of song and social sounds are connected by a bracket next to the date

Date 1981	Stimulus	Duration (min)	Kind of target group	Distance at start (m)	Minimum distance (m)	Distance at stop (m)	Response	Latency of song stop (min)
7 March	Song	29	2A+C	310	310	3,400	Away	–
			Singer	1,720	1,720	2,760	Away	3
7 March	Song	26	Singer	350	350	700	Away	8
8 March	Song	30	2A+C	320	320	1,270	Away	–
10 March	Soc	40	2A[a]	340	<5	±100	Charge	–
11 March	Soc	59	Singer?[b]	1,450	<5	470	Charge	11
			1A[b]	?	<5	470	Charge	–
11 March	Song	15	2A[b]	±200	±200	1,410	Away	–
11 March	Soc	26	2A[b]	1,630	1,630	2,730	Away	–
			2A	1,410	±100	690	Charge	–
			1A	1,310	<5	230	Charge	–
11 March	Song	10	2A[c]	700	700	1,630	Away	–
			1A[c]	280	280	1,630	Away	–
11 March	Soc	12	3A[c]	1,640	1,640	2,540	Away	–
12 March	Song	21	2A+C	±100	±100	±200	Away	–
12 March	Soc	21	2A+C	±200	±200	±400	Away	–
13 March	Soc	52	Singer[d]	420	<5	420	Charge	2
			1A[d]	?	<5	420	Charge	–
19 March	Song	24	2A+C	80	80	120	Away	–
21 March	Soc	16	4A	750	750	2,240	Away	–
21 March	Song	13	4A	2,530	2,530	3,720	Away	–
21 March	Soc	30	Singer	230	230	860	Away	–
21 March	Song	30	Singer	860	860	1,000	Away	–
			Singer[e]	1,720	1,440	1,440	To	–
21 March	Soc	26	Singer[e]	270	<5	560	Charge	1
21 March	Song	27	1A[e]	680	680	3,790	Away	–
26 March	Song	21	1A+C	360	360	>850	Away	–
			2A	2,980	±1,000	±1,000	To	–
26 March	Soc	20	1A+C	>850	>850	>1,000	Away	–
			2A	830	<2	70	Charge	–
26 March	Song	20	2A	160	160	990	Away	–
26 March	Soc	20	2A	990	990	1,180	Away	–

[a] A singer stopped singing and joined a lone adult two min before the start of playback to form this group of two adults

[b] The singer followed at the start of the 59 min social sound playback was probably one of the two whales that charged the boat, but it was not identified after charging. The two whales that charged joined after charging the playback boat to form a group of two adults

[c] A group of two adults joined a lone adult 5 min into the playback to form a group of three adults

[d] These two lone adults join to form a group of two adults for 6 min after charging the playback boat

[e] This singer started to sing approximately 10 min before the end of the previous 30 min social sound playback when it was 1,920 m from the playback boat

from 12 to 59 min. The longer the playback, the more likely whales were to charge (Spearman rank correlation coefficient = 0.68, $P < 0.05$). Of the three playbacks in which two different groups of one or two whales charged, two were the longest playbacks of social sounds. Of the four social sound playbacks in which no whale charged, three had the shortest durations.

Three lone whales or groups of whales were exposed twice to social sounds (the whales marked for footnote c on 11 March and the singer marked for footnote e on 21 March listed in Table 2). One

whale that did not charge the boat during the first playback of social sounds, charged during the second one. On the other hand, two groups of whales that had already charged the playback boat, moved away during song playback and also during the second playback of social sounds. These three cases suggest that once whales charge the boat during social sound playback, they may be less likely to respond to a second such playback.

Discussion

The rapid approach of right whales to playback of right whale sounds reported by Clark and Clark (1980) appears to be similar to the charging response described in this paper. This is of particular interest because the right whale sounds used as a playback stimulus by Clark and Clark were recorded from a large active group of right whales similar to the large active humpback groups from which social sounds were recorded (Clark, in press). These large active groups in both species move rapidly, vocalize frequently, and produce frequent displays at the water surface. In both species, males in such groups have been seen to compete for proximity to a female (humpbacks: Tyack and Whitehead 1983; right whales: Payne and Dorsey, in press).

The responses of different social groups of humpback whales to playback of song or social sounds are very similar to their responses to singing whales or the large active groups from which the social sounds were recorded (see Tyack 1982 for a comprehensive analysis of approach and avoidance of different humpback groups). Most whales seem to avoid lone adults that are singing; few whales approached the source of song playback. While most whales seem to avoid singers, I have observed some interactions off Maui in which a whale stopped singing and approached another singer (e.g., Fig. 3 in Tyack 1981) or in which a cow and calf or nonsinging lone adult approached and joined a slowly moving singer (e.g., Fig. 7 in Tyack 1981). A larger sample size of song playbacks might evoke responses similar to these infrequent interactions.

Cows and calves and large active groups tend to avoid large active groups (Tyack 1982). The two cows and calves and two large active groups to which social sounds were played also avoided the playback boat. But many lone adult whales, especially singing whales, and some pairs of adult whales appear to be highly motivated to join such large active groups. When such a group forms, they often display a dramatic change in behavior, swimming at high speed directly toward the large active group, often staying near the water surface until they join with the group (e.g., Fig. 6 of Tyack and Whitehead 1983). Not only is this response very similar to that observed when a whale charges a boat during playback of social sounds, but the same kinds of humpback groups perform both responses.

Statistical analysis of these playbacks was complicated since the experiments were a mixture of paired playbacks of both stimuli to the same group and individual playbacks of one stimulus to a group. Furthermore, it was not possible to identify and follow all groups that were within acoustic range of the playback stimulus, and that might thus respond to it. As mentioned in the Methods section, in order to perform two playbacks to the same group of whales, the paired playbacks had to be shorter than the single playbacks. Since whales were less likely to charge during short playbacks of social sounds, the paired playbacks did not prove optimal for evoking the charge response. For all statistical analyses reported in the results I thus compared responses during all playbacks of social sounds to responses during all playbacks of song. This analysis presumes that the responses evoked by each playback were independent. Playback responses were not necessarily independent, however, for individual whales or groups of whales were known to be exposed to more than one playback during paired playbacks. The only indication of an effect from previous exposure to playback came from the three cases where a whale or group of whales were exposed twice to social sounds. These cases indicated that once a whale has charged in response to playback of social sounds it may be less likely to charge a second time, but this would only act to reduce the effective sample size of the social sound playbacks.

It is often difficult to discriminate between functions, or attributes of a signal that confer a selective advantage upon a signaller, from incidental effects of a signal. Otte (1974), for example, points out that while every signal has legitimate receivers, other animals – predators, parasites, or competitors – can exploit the signal to obtain information to the disadvantage of the signaller.

The responses of singing humpbacks to social sounds may be such an incidental effect. Social sounds are produced primarily by large groups of humpbacks (Silber 1982; Tyack 1982) in which males are competing for access to a female (Tyack and Whitehead 1983), and these sounds broadcast the location of such a group to whales nearby. Singing whales and some other groups of one or

two adults respond to such sounds by approaching the source, and they often join such large groups. Only under unusual conditions would males in a large group gain from this attraction of additional rivals. Instead, social sounds may function to affect interactions within the group. The problems of discriminating between functions and effects are even more apparent when one considers that a female in groups of three or more adults might stand to gain a more fit escort the more males are competing for access to her. A female might produce sounds in a large group that do function to attract singers and other whales in the area.

In spite of complexities in interpreting the function of humpback song or social sounds, these playback experiments clearly do support the conclusion that the songs and social sounds of humpback whales mediate the responses of approach or avoidance which these whales make to singing whales or large groups in which aggressive behavior is occurring.

Acknowledgements. I would like to thank Roger Payne and Donald R. Griffin for help throughout this project. I thank J. and M. Bird, J. Darling, S. Earle, G. and L. Ellis, S. and D. Ford, R. Geissler, G. Hawkes, J. Lee, J. Luckey, B. Mathews, K. Miller, F. Nicklin, M. Rice, G. Silber, and C. Zabriskie whose cooperation in the complicated field operation was essential for the success of the playback experiments. Thanks to Charles Malme of Bolt Beranek and Newman for help calibrating the playback apparatus. Thanks to Donald R. Griffin, Christopher Clark, and William Watkins for comments on a draft of this paper, and to Jane Peterson for entering the manuscript into a word processor. This research was funded by grants from the National Geographic Society; the Clifford E. Lee Foundation; the World Wildlife Fund, US; the World Wildlife Fund, Canada; the Atherton Foundation; and the Maui Whalewatchers. This research was conducted under permit No. 184 issued to Roger Payne by the US National Marine Fisheries Service.

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