In-air and underwater hearing sensitivity of a northern elephant seal (*Mirounga angustirostris*)

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Abstract: In-air and underwater sound detection thresholds were obtained for a female northern elephant seal (*Mirounga angustirostris*). Hearing sensitivity in air was generally poor, but was best for frequencies between 3.2 and 15 kHz, and showed greatest sensitivity at 6.3 kHz (43 dB re: 20 μPa). The upper frequency limit in air was approximately 20 kHz. The underwater audiogram is similar to those obtained from other phocids in that sensitivity was best between 3.2 and 45 kHz, with greatest sensitivity at 6.4 kHz (58 dB re: 1 μPa) and an upper frequency cutoff of approximately 55 kHz. The elephant seal was more sensitive to low frequencies (<1 kHz) than other pinnipeds tested. Thresholds obtained in water were lower than those obtained in air (19 dB in terms of sound pressure, 52 dB in terms of sound intensity), indicating that the elephant seal is adapted for underwater hearing. The outer and middle ears of the elephant seal are modified relative to those of other phocids. These modifications are probably needed to cope with extreme static pressures related to deep diving, and are likely to confer relatively good auditory sensitivity under water.

Résumé : Les seuils de détection des sons ont été évalués dans l’air et sous l’eau chez une femelle de l’Éléphant-de-mer boréal (*Mirounga angustirostris*). La sensibilité auditive à l’air est généralement médiocre et elle est plus grande aux fréquences situées entre 3,2 et 15 kHz, et c’est à la fréquence de 6,3 kHz (43 dB re : 20 μPa) qu’elle s’est avérée maximale. La limite supérieure de détection du son à l’air a été évaluée à 20 kHz. L’audiogramme sous l’eau est semblable à ceux obtenus chez d’autres phoques : la sensibilité est plus grande entre 3,2 et 45 kHz, maximale à 6,4 kHz (58 dB re : 1 μPa) et la limite supérieure de détection des sons a été évaluée à 55 kHz. Ce phoque est plus sensible aux basses fréquences (<1 kHz) que tous les autres pinnipèdes testés. Les seuils obtenus sous l’eau sont plus bas que ceux obtenus en milieu aérien (19 dB (pression du son), 52 dB (intensité du son)), ce qui indique que l’Éléphant-de-mer boréal est adapté à l’audition sous l’eau. L’oreille externe et l’oreille moyenne de l’animal sont modifiées par rapport à celles des autres phocidés. Ces modifications sont probablement nécessaires pour supporter les pressions statiques extrêmes qui sont reliées aux plongées en profondeur et sont aptes à procurer à l’animal une sensibilité auditive relativement élevée sous l’eau.

[Intaduit par la Rédaction]

Introduction

The pinnipeds are amphibious carnivores comprising three families, the Phocidae (true or “earless” seals), the Otariidae (“eared seals,” or the sea lions and fur seals), and the Odobenidae (walrus). All pinnipeds forage under water, but must occasionally return to land, where parturition and lactation occur. As a result, they are adapted for an amphibious existence, in terms of both overall morphology and sensory function. As a result, they are adapted for an amphibious existence, in terms of both overall morphology and sensory function. The reproductive behavior and diving physiology of the northern elephant seal have been studied in detail for the past three decades (reviewed in Le Boeuf and Laws 1994); however, except for recent studies on visual sensitivity (Levenson and Schusterman 1997) and low-frequency hearing (Kastak and Schusterman 1998), still relatively little is known about its sensory systems. Accordingly, the elephant seal has become a species of special interest with respect to its auditory capabilities, primarily because its deep-diving habits potentially place it at risk from the effects of anthropogenic noise propagated great distances through the deep sound channel. This is an oceanic region of minimum sound speed (800–1200 m depth at low and mid latitudes) that facilitates exceptionally long-distance propagation of sound (Urick 1983; Richardson et al. 1995). Such noise could affect communication, navigation, predator detection, or foraging in deep water, provided that one or more of these life-history aspects depends on acoustic cues.
Underwater audiograms, and some in-air audiograms, have previously been constructed from sound-detection thresholds obtained for two otariid species, the California sea lion (*Zalophus californianus*, Schusterman et al. 1972; Schusterman 1974) and northern fur seal (*Callorhinus ursinus*, Moore and Schusterman 1987; Babushina et al. 1991). Auditory threshold data have also been published for several phocid species, including the harbor seal (*Phoca vitulina*, Møhl 1968; Turnbull and Terhune 1990; Terhune 1991), ringed seal (*Phoca hispida*, Terhune and Ronald 1975), harp seal (*Phoca groenlandica*, Terhune and Ronald 1971, 1972) and Hawaiian monk seal (*Monachus schauinslandi*, Thomas et al. 1990). In general, the phocids have a greater range of sensitivity as well as a higher upper frequency cutoff under water, while the otarids show better sensitivity in air. The exception to this trend is a single monk seal tested only under water (Thomas et al. 1990). This individual showed relatively poor sensitivity as well as a narrow range of best sensitivity and a relatively low upper frequency limit. It is unclear whether the dissimilarities between the audiograms of the monk seal and those of other phocids indicate interspecific variation or merely inter-individual variability. If the monk seal data reflect true species differences in auditory sensitivity, it is reasonable to expect that the elephant seal, related to the monk seal at the subfamilial level (Monachinae), will show similar auditory characteristics.

The elephant seal’s essentially aquatic life-style suggests that it might possess relatively poor in-air hearing sensitivity. Indeed, acoustic signals produced by this animal in air are loud and repetitious and are sometimes accompanied by exaggerated visual displays (Bartholomew and Collias 1962). Additionally, it has been suggested that seismic cues, produced by displaying males slamming their forequarters on the ground, are important in intra-individual signaling (Shipley et al. 1992). These communicative properties could be considered characteristic of a species that has evolved a reliance on modes of in-air signaling constrained by limited aerial hearing sensitivity.

In-air hearing sensitivity might also be constrained by deep diving, in that auditory anatomy has been altered over time to withstand depth-related changes in static pressure. Increased pressure on air spaces bordered in part by soft tissue (e.g., the middle-ear space and external auditory meatus) can easily cause damage to anatomical structures such as the tympanic membrane. The external auditory meatus and middle ear space of pinnipeds are wholly or partially lined with distensible cavernous tissue (Odend’hal and Poulter 1966; Møhl 1967; Repenning 1972). This tissue is highly vascularized and contains sinuses that are thought to fill with blood when the ear is exposed to increasing static pressure. As the cavernous tissue expands, the volume of the auditory air spaces decreases, relieving pressure-induced stress on the tympanic membrane. In addition to cavernous tissue, the elephant seal also possesses an unusually narrow external auditory meatus, the opening of which is barely visible as a pinhole behind the eye (compare with the more obvious external ear openings of the harbor seal and California sea lion shown in Fig. 1). It is unlikely that the aerial sound conduction pathway common to terrestrial mammals (the open lumen of the external auditory meatus) exists in the northern elephant seal, presumably because of the need to eliminate air-filled cavities or reduce their volume while diving. Thus, it would appear from an anatomical standpoint that the elephant seal is specialized for underwater sound detection at the expense of in-air hearing sensitivity.

In light of the apparent adaptations of the elephant seal’s ear, we predicted that this species should be more aquatically adapted than the pinnipeds tested thus far with respect to hearing sensitivity (Kastak and Schusterman 1998). That is, sensitivity under water should be better than that of other pinnipeds (i.e., lower underwater thresholds), while sensitivity in air should be poorer (i.e., higher in-air thresholds). Additionally, we hypothesized that when thresholds obtained in both media were compared, this animal would show better hearing sensitivity under water than in air. To assess the auditory capabilities of the northern elephant seal relative to other pinnipeds, we trained a juvenile female elephant seal to participate in an acoustic signal detection task in air and under water. The data reported in this study represent the first complete in-air and underwater audiograms for this
species; the low-frequency data (6.4 kHz and lower) included herein have previously been reported (Kastak and Schusterman 1998).

Materials and methods

Subject

The subject for this study was Burnyce, a female northern elephant seal. This animal was obtained from Sea World in San Diego, California, where she was rehabilitated after stranding as a yearling. The study began when she was approximately 2 years old and was completed when she was 4 years old. She was housed at Long Marine Laboratory in Santa Cruz, California, in free-flow salt-water tanks and adjacent haulout space. She received a diet of 4–12 kg of freshly thawed capelin (Mallotus villosus) and herring (Clupea spp.) each day. Approximately 15–25% of this diet was consumed during experimental sessions. The seal was cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care and the Chancellor's Animal Research Committee of the University of California at Santa Cruz. Experimental sessions (one per day, 4–5 days per week) were conducted between 09:00 and 12:00. Session lengths ranged from 25 to 70 trials. For approximately 30 days in the late spring and early summer of each year of testing, the subject exhibited decreased appetite and motivation while molting. During these periods, tests were not conducted.

Apparatus

The apparatus for threshold testing in air was a PVC frame on which a chin station, a moveable door, and a response paddle were mounted. The apparatus for underwater testing was similar to the in-air apparatus but was modified to be mounted along the side of a 7.5 m diameter, 2.5 m deep test tank using flexible support brackets. The chin station was positioned approximately 1.5 m from the wall of the tank and approximately 1 m below the water surface.

Experimental set-up

Pure tones (500 ms duration) were generated by a Stanford Research Systems DS345 function generator and shaped with rise/fall times of 40 ms to eliminate switching transients. The signal was manually triggered and fed through an HP 350C stepwise attenuator and a Krohn–Hite 3550 band-pass filter. For testing in air, the signal was presented through Telephonic TDH-39 earphones fitted in a neoprene harness positioned on the animal’s head. For underwater testing, the signal was amplified (Realistic MPA-20) and projected through either a J-11 underwater transducer (for testing at 0.075 kHz), a J-9 transducer (for testing at 0.1–18 kHz), or a B&K 8104 hydrophone (for testing at 4 and >18 kHz). The underwater transducers were situated approximately 5 m away from and in the same horizontal plane as the subject’s head. In air, signal and ambient-noise measurements were made under the earphones at the opening of the external auditory meatus using an Etymotic ER-7C probe microphone. Under water, signal and noise measurements were made with a calibrated type H-56 hydrophone. In both cases the incoming signal was fed to an oscilloscope (Hitachi V202) and PC-based real-time spectrum analyzer (Spectra Plus, Pioneer Hill Software) for analysis. Under water, reflections from the water surface as well as the tank bottom and walls resulted in spatial variability in signal amplitude, especially at frequencies above 6 kHz. For this reason the sound field was precisely mapped and the subject’s head was required to remain motionless in an area where a constant-amplitude signal occurred (variability no more than ±3 dB).

Procedure

Standard behavioral psychophysical techniques (Stebbins 1970) were used to estimate sound-detection thresholds. The task was a go/no-go procedure in which the subject responded to the presence of a tone by pressing a response paddle. In air, a session began when an assistant called the subject out of the pool and positioned the headphones, ensuring placement of the earpieces directly over the meatal openings. To begin a trial the subject was cued to position on the chin station and another assistant raised the door separating the chin station and response paddle. The door remained open for 4–6 s, during which time the probability of signal presentation was 0.5. On signal trials, a paddle-press response was reinforced with a piece of fish. Failure to respond was followed by closure of the door and a brief pause before the next trial. On signal absent, or catch trials, the subject was given a piece of fish for not responding. If a paddle press occurred during a catch trial, a false alarm was scored and the seal was restationed without reward to begin the next trial. Under water, sessions were conducted in the same way, except that the subject was signaled by an assistant to swim down to the chin station to begin a trial. Correct responses were reinforced with fish. Following all incorrect responses the door was closed and the subject was recalled to the side of the pool then restationed after a momentary pause. The experiments were conducted in double-blind fashion, in that neither the assistant nor the subject could predict the occurrence of a particular trial type. Additionally, the experimenter viewed each trial on a video monitor and so had no direct access to the subject or the assistant. Following each trial the assistant signaled the subject’s response to the experimenter, who then indicated to the assistant (via microphone and loudspeaker) whether to reinforce the subject’s response. Thresholds were determined using two psychophysical methods. The first was a method of constant stimuli, in which five or six discrete signal levels were presented randomly in a series of experimental sessions. The method of constants was run until the subject’s pooled data resulted in a threshold with 95% confidence limits within ±3 dB, determined by probit analysis (Finney 1971). This method was used for threshold determination for frequencies of 0.075–6.4 kHz. For reasons of efficiency, a second procedure (up-down, or staircase) was used to determine thresholds at frequencies above 6.4 kHz. In this procedure the signal amplitude was attenuated in 4-dB steps following a correct detection (hit). After the first failure to detect (miss), the attenuation step size was changed to 2 dB; the signal level was increased by 1 step following each subsequent miss and decreased by 1 step following each subsequent hit. Thresholds were estimated as the signal level corresponding to 50% correct detections using the method outlined in Dixon and Mood (1948) and based on a minimum of 6 reversals. Although the confidence-limit method was not applied to data obtained in this fashion, standard deviations of staircase threshold estimates did not exceed 3 dB.

Results

False alarm rates for all frequencies were below 12% and averaged 4% for in-air and underwater testing combined. The in-air audiogram is plotted in Fig. 2, in addition to audiograms from a phocid, the harbor seal (Møhl, 1968; Turnbull and Terhune 1990; Terhune 1991; Kastak and Schusterman 1998), and an otarid, the northern fur seal (Moore and Schusterman 1987; Babushina et al. 1991). Although the general shapes of the three audiograms are similar, the elephant seal is less sensitive than the other phocid by about 10–30 dB across the entire audible range. The upper frequency limit for the elephant seal in air is about 20 kHz, which is similar to that for the harbor seal but lower than...
those of the northern fur seal (shown in the figure) and another otariid, the California sea lion (Schusterman et al. 1972).

The underwater audiogram is shown in Fig. 3, along with those for the fur seal and harbor seal. A comparison indicates that the elephant seal’s best sensitivity is about the same as that of other pinnipeds (about 60 dB re: 1 µPa). In general appearance, the audiogram is similar to that of the harbor seal, as well as other phocids (except the one Hawaiian monk seal tested; Thomas et al. 1990). Like the harbor seal, the elephant seal has a higher upper frequency cutoff (about 55 kHz) than the fur seal, and an extended, relatively flat range of best sensitivity. The elephant seal’s low frequency sensitivity is better than that of the harbor seal and fur seal.

Comparisons between in-air and underwater thresholds were made in two ways. The first comparison was made with respect to sound-pressure thresholds, correcting in-air thresholds for differences in reference level (1 vs. 20 µPa), under the assumption that pressure is the relevant mechanical stimulus for auditory sensation (Kastak and Schusterman 1998). The second comparison was of sound-intensity thresholds, using estimates of sound intensity calculated from measured pressure levels. This calculation corrects for reference levels, as well as the differences in acoustic properties of the two media, to provide an indication of the acoustic energy flow in the sound-field at threshold. This conceptualization allows for comparisons without regard to the mechanical stimulus likely to be transduced by the ear. Figure 4 is a combination plot of pressure and intensity thresholds for the three species listed previously. The right and left ordinates of each plot indicate acoustic intensity and pressure, respectively. The axes are shifted so that the in-air curves coincide (i.e., pressure and intensity are matched for airborne sound). The elephant seal’s underwater thresholds average 19 dB lower than corresponding in-air thresholds when compared in terms of pressure, and 52 dB lower when compared in terms of intensity.

Discussion

Apart from the Hawaiian monk seal, the northern elephant seal is the only monachine seal for which auditory data have
Fig. 4. In-air and underwater sound detection thresholds for an otariid, the northern fur seal (A), and two phocids, the harbor seal (B) and northern elephant seal (C). The axes have been normalized for airborne sound so that the pressure and intensity audiograms for air overlap (thick line). Underwater audiograms are referenced with respect to pressure (solid thin line) and intensity (broken line). A curve above the thick line indicates poorer sensitivity in water relative to air, while a curve below the thick line indicates better sensitivity in water relative to air. The elephant seal is unique in that it is more sensitive in water regardless of the manner in which the thresholds are compared. Data for the other species are from studies listed in Figs. 2 and 3.

been obtained. However, the two species show relatively little similarity in underwater hearing ability; the monk seal hears relatively poorly compared with the elephant seal with respect to overall sensitivity and upper frequency limit. There are several possible reasons for these differences: (i) they are related to differences in ecology; (ii) the monk seal is
primitive with respect to auditory functioning, and therefore is not well adapted to hear under water; or (iii) either the monk seal or the elephant seal data were obtained from individual animals not representative of the species. Statement i is plausible, given the differences in the ecology of the two species (i.e., the elephant seal is a deep diver, whereas the monk seal is not). However, the monk seal data differ dramatically from those obtained from other shallow-diving phocids, while the elephant seal audiogram is similar to those from other phocids. Although the monk seal is often considered primitive (King 1983), as is suggested in statement ii, there is little anatomical reason to suspect a lack of adaptation for aquatic hearing (Repenning 1972). Finally, with respect to statement iii, it is unlikely that the elephant seal data are aberrant, primarily because of the similarity of the audiogram to those of other phocids, but also because the animal’s best sensitivity, around 60 dB re: 1 \mu Pa, is similar to that of most of the other pinnipeds tested. Further testing of the monk seal is necessary to determine whether this close relative of the northern elephant seal has auditory characteristics similar to those of the latter animal or other phocids.

Despite the similarities in the underwater hearing abilities of phocids and otariids, i.e., maximum sensitivity is about the same at approximately 60 dB re: 1 \mu Pa in the frequency range of about 4 to 20 kHz, there are some striking differences between the two groups. The phocids have lower thresholds at both low (<4 kHz) and high (>20 kHz) frequencies. Additionally, in most phocids, underwater pressure thresholds are similar to the corresponding in-air thresholds (e.g., those shown in Fig. 4), while in otariids, underwater thresholds are higher than in-air thresholds, which suggests that phocids are amphibiously adapted while otariids have remained essentially air-adapted (Kastak and Schusterman 1998). In light of the extent of otariids’ terrestrial interactions, many of which involve some sort of vocalization, this is hardly surprising. Phocids, conversely, vocalize a great deal under water but must also detect important acoustic signals in air (e.g., pup calls; Renouf 1984), so they must rely to a greater extent on amphibious hearing.

Because of acoustic-impedance differences, the hearing thresholds of an “ideal” amphibious ear will be higher in air than that of an ideal terrestrial ear, and higher in water than that of a completely aquatic ear (Mohl 1968). Perhaps the primary reason for the diminished in-air sensitivity of the pinniped ear is the modified anatomy of the external meatus, which is long, twisted, collapsible, and lined with hair and wax. These, and modifications to the middle ear, are likely to be adaptations related to the increased static pressures associated with deep diving.

The external meatus of the elephant seal is an extreme example of this type of modification, and it is almost certain that airborne sound must pass through an air-flesh interface before reaching the middle ear. In other words, in-air hearing in the elephant seal must take place via bone conduction, and this mode of hearing is reflected in the seal’s poor sensitivity to airborne sound relative to other pinnipeds tested. The cost of deep diving (a decrease in hearing sensitivity in air resulting from modifications of the ear) may have countered the natural selection pressures that acted to maintain in-air hearing sensitivity in other pinnipeds. In the elephant seal, pressures to maintain effective vocal signaling in air appear to have acted on the production end of the communication channel rather than on the reception end. The result was the development of extremely high-amplitude, low-frequency vocal signals that propagate great distances, instead of the well-developed airborne auditory sensitivity common to other pinniped species. The development of such signals, in turn, relaxed pressures on the auditory system to function well in air, thus allowing the ear to become even further modified for deep diving. The terrestrial social repertoire of the elephant seal also comprises seismic communication and conspicuous visual cues (Bartholomew and Collias 1962; Sandegren 1976; Shipley et al. 1992), presumably to compensate for poor sensitivity to airborne sounds.

Although the primarily low frequency vocal displays of adult elephant seals have become exaggerated to accommodate poor hearing sensitivity in air, the harmonic structure of vocalizations such as pup calls, which appear to be important in individual recognition, extends into the frequency range of better airborne sensitivity (i.e., above 2–3 kHz; Petrinovich 1974). Selection on vocal traits in elephant seals thus appears to have followed two paths: the first resulted in high-amplitude, low-frequency (and thus long-range) calls important in aggressive interactions and dominance relations and the second resulted in less intense, complex, generally higher frequency and shorter range calls, which are probably important in mother–pup recognition.

An indication of the extent to which pinniped ears are adapted for amphibious functioning can be seen in Fig. 4. In water, the elephant seal’s hearing is more sensitive than in air, regardless of whether pressure or intensity thresholds are compared. This animal’s ear is better adapted to function in water, not only in terms of energy efficiency (reflected in the lower intensity thresholds under water), but also in terms of receiving and transducing the relevant mechanical stimulus (reflected in the lower pressure thresholds under water). In contrast to those of the elephant seal, the ears of the other phocids and of otariids function better in water in terms of overall energy efficiency (lower intensity thresholds under water), but function better in air in terms of pressure detection (lower pressure thresholds in air). Whether pressure or intensity should be used as a means of comparing in-air and underwater hearing is debatable; for a detailed discussion see Kastak and Schusterman (1998).

In-air hearing is extremely poor in the elephant seal relative to other pinnipeds, and it is likely that adaptations for deep diving (e.g., reduction of the lumen of the external meatus) are responsible for the severe hearing decrement in air. This decrement plays a significant role in explaining the aquatic nature of the elephant seal’s hearing. Indeed, in terms of lowest absolute thresholds, the elephant seal’s auditory functioning under water is not extraordinary, except at low frequencies, where it is more sensitive than other pinnipeds. Further, the lowest thresholds of the elephant seal are still some 20 dB higher than the lowest thresholds of the wholly aquatic odontocete cetaceans for which data exist (for review see Richardson et al. 1995). The superiority of underwater hearing relative to in-air hearing in the elephant seal could be explained by selective pressures on hearing (such as the acoustic detection of predators) or by constraints imposed by diving to great depths, or both. Evidence for underwater sound production by the elephant seal is scant, and
this species appears to be relatively nonsocial outside of the breeding season. Thus, it is possible, though unlikely, that underwater sensitivity evolved to enhance intraspecific communication under water. Further analysis of recordings from migrating seals should shed light on the importance of underwater vocalization for communication, navigation, or foraging.

Deep diving, on the other hand, imposes problems related to the presence of air spaces in the middle and outer ear. The reduction of the external meatus and presence of cavernous tissue in the ear are likely to be morphological adaptations that minimize both water penetration into the ear canal and the size of the middle-ear space. Such reductions in the volume of the outer and middle ear air space could secondarily enhance underwater sound detection by matching the acoustic impedance of the ear with that of water (Repenning 1972). If impedance matching occurs, then conventional (i.e., tympanic-ossicular) sound conduction could take place under water as well as in air, which may help to explain the better than expected auditory sensitivity of these animals in water (Møhl 1968; Repenning 1972; Moore and Schusterman 1987; Terhune 1989); Given the extremes of static pressure with which the elephant seal must cope, the theoretical impedance match at depth might be more complete than in other pinnipeds, simply because of the greater reduction (or elimination) of air spaces in the ear. This impedance match would greatly reduce the acoustic energy loss at the middle ear, thereby increasing auditory sensitivity. Although the elephant seal appears to be poorly adapted to hear in air, it may be better adapted than other pinnipeds to hear under water, simply by virtue of mechanical changes related to deep diving. Consequently, adaptations related to diving led to the solution of problems related to extremes of static pressure, as well as to underwater acoustics.

Elephant seals are considered to be a species of special concern with respect to the adverse effects of anthropogenic noise on marine mammals because they routinely dive to depths as great as or greater than the deep sound channel. The propagating characteristics of the channel result in longer ranges of audibility for the elephant seal compared with other pinnipeds, solely on the basis of each species’ typical dive depths. In addition, elephant seals could be particularly vulnerable to anthropogenic noise because of their sensitive low-frequency underwater hearing. Since most anthropogenic noise is low frequency in nature, noise exposure limits in noise on marine mammals because they routinely dive to lower levels of behavioral response to airborne anthropogenic noise than do harbor seals or California sea lions (Stewart 1993), a finding consistent with the elephant seal’s poor airborne hearing sensitivity.

The elephant seal is unique among pinnipeds in its behavior, and evidently in its auditory capacities as well. The paucity of auditory data on monachine seals, especially other relatively deep divers such as the Weddell seal (Leptonychotes weddellii), must be rectified before firm conclusions can be drawn regarding the adaptive significance of the structure and function of the pinniped ear.

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References


King, J.E. 1983. Seals of the world. 2nd ed. British Museum (Natural History), London.


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