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Human Breath-Hold Diving Ability and the Underlying Physiology

Humans freedive for recreation, food, and for records, displaying an ability superior to any other known terrestrial mammal. Harvest divers may spend up to 5 h daily submerged, and competitive deep divers may swim down to depths beyond 100 m – and up again – on one breath. This is paralleled only by aquatic and semi-aquatic mammals. In all air breathers, the ability to breath-hold dive is set by a number of physiological factors. Some of these have been extensively studied, like the 'diving response,' which diverts blood to the brain, heart and working muscles, while less sensitive organs can rely on anaerobic metabolism. The diving response is effectively triggered in trained human divers and may reduce the heart rate by 50% – similar to the response in semi-aquatic mammals, and it has been shown to conserve oxygen and prolong apneic duration. More recently, a spleen response during diving was described in humans resembling that found in seals. The spleen ejects its stored reserve supply of red blood cells into the circulation, elevating hematocrit, and thereby the oxygen carrying capacity, which also increases apneic duration. Other features not typical of terrestrial mammals, such as: naked skin with a continuous layer of subcutaneous fat; under water vision; effective locomotion in water; large flexible lungs; an ability to equalize ears and sinuses; efficient voluntary respiratory control and vocal communication; a long lifespan; and a large brain, are shared by many species with a semi-aquatic evolutionary history and are also shared by Man. This would seem to suggest a period of evolutionary pressure from life involving swimming and diving in human prehistory.

Introduction

Humans have a good natural diving ability, both in terms of the time that they can spend submerged and the depths that they can reach. This is despite the fact that there is no real requirement for most humans to even enter water. Breath-hold-, apnea- or freediving is practiced today, however, by several groups of people. People freedive for recreation as a natural part of bathing and swimming and discover that it is easy to dive to depths of a few meters (Figure 1a). Freediving is used to harvest food or other resources by several ethnic groups, whose daily lives involve repetitive diving to relatively shallow depths, spending a considerable part of their day in and under water. Two such groups of sea harvesters are the Japanese Ama divers (Figure 1b) and the Indonesian sea people. A third major group of modern breath-holders are competitive apnea divers, who train to reach greater depths and distances under water or to hold their breath for as long as pos-

sible (Figure 1c). The current depth record for swimming without fins: 101 m, is clearly remarkable for a land mammal.

A number of anatomical and physiological features combine to give humans this diving prowess which is not shared by our fellow terrestrial mammals. Anatomically, we have streamlined bodies, more similar in outline shape to that of marine mammals, which allow us to swim efficiently. The basic physiology that allows human apnea diving e.g., the human 'diving response' has been studied extensively for many years (Scholander et al., 1962; Rahn & Yokoyama, 1965) and it is evident that apnea training can increase an average healthy individual's underwater performance in a short time (Schagatay et al., 2000; Schagatay, 2010; Engan et al., 2013). Why do we differ in these abilities from other terrestrial mammals, including our closest relatives? Can the reason be a phase in human evolution when our ancestors underwent selective pressure from life in the littoral zone? The aim of this paper is to examine some features of human freediving capacity and the underlying physiological mechanisms that allow this activity.

Figure 1a) Recreational divers; b) Ama divers in Japan; c) Competitive divers during constant weight deep diving. Note that all divers dive in pairs for safety.

Harvest divers – extremes in daily dive times

A number of diving reliant communities exist in South East Asia, where they harvest the shallow sea beds. Two groups of divers, in particular, have been studied in the past: the Japanese Ama and Korean Hae Nyo (Rahn & Yokoyama, 1965; Holm et al., 1998); and the Sea Nomads who work in the warmer water of, e.g., Eastern Indonesia (Schagatay, 1996). These divers are not a modern phenomenon; Japanese historical records show evidence of such diving dating back to at least 2000 years ago, while the Sea Nomads of Southeast Asia have harvested their shallow archipelago at least since the 16th Century (Sather, 1997), and

probably much longer. Still, today marine harvesters dive repetitively for several hours a day with little or no equipment. In order to maximise their efficiency and catch, harvest divers strive to achieve the longest possible underwater working time per day.

Studies have examined the diving patterns of these repetitive divers and they have been reported to spend a great portion of their working day underwater (Hong et al., 1963; Hong et al., 1991; Mohri et al., 1995; Schagatay et al., 2011). In recent studies, we found that the Ama at Hegura island, during their 4 h working shifts, spent about 120 min a day underwater gathering sea molluscs by making serial dives with a mean dive duration of 38 s and mean surface interval duration of 38 s (Schagatay et al., 2011). Diving depths were 5-12 metres of sea water (msw) in that study, but Ama can reach 25 m. The daily 4 h in the water is stipulated by local fishing regulations; prior to this, divers worked shifts amounting to 6-8 h in the water per day, spaced by periods for warming up on the beach, as they were diving naked in relatively cold water (23-26 C). The Ama now dive while wearing a wetsuit, mask, fins, weight belt and cotton gloves, and the majority of the divers are female. We recently visited one such community at Hegura island in Japan. It was striking how so many of the still active divers were older than one might imagine for people dependent on physical work for a living – and that they appeared to be so healthy. One Ama diver, soon to become 97, said that she was retiring – although there was nothing physically wrong with her and the doctor had made no objections – the reason being that she had some older friends who had retired and she wanted to spend some time with them. Having started at the age of 16, she had been a professional diver for over 80 years.

While mainly women dive professionally among the Ama, both men and women dive for sea harvesting among the Sea Nomands in Indonesia and the Philippines, although the men do most of the spearfishing (see Abrahamsson & Schagatay, this issue). Many spearfishermen still submerge wearing only goggles and swimming trunks, and their mean dive duration was 28 s with a mean surface interval of 19 s, the latter being significantly shorter than the dive times (P < 0.001: Schagatay et al., 2011). Maximum diving depths were shallower than those of the Ama; 5-7 msw and diving amounted to 60 % of the total work period, which was anything between 2-9 h per day (Schagatay et al., 2011). The daily period of working time submerged – up to about 5 h – is to our knowledge the longest of any group of natural human breath-hold divers reported. A sixty percent dive-to-surface time is in line with the time spent underwater by various marine mammals, including the sea otter (Bodkin et al., 1993; see also Fahlman & Schagatay, this issue).

The Ama learned to swim and dive from their parents or siblings when a few years old, and often start working as Ama divers between the ages of 14-18, but the Sea Nomad children dive at a very early age, sometimes even before they can walk. According to local sources they were sometimes born in the sea, with beneficial effects for both the mother and child (Schagatay, discussions with Bajau, Indonesia, 1988). Human infants can swim spontaneously if exposed to water before 6 months of age, and have a reflex to breath-hold with immersion, and an effective bradycardic diving response (Goksor et al., 2002).

Adaptations allowing harvest diving

Repetitive diving, which is necessary to draw a subsistence living from the sea, requires several physiological adaptations by the air breather. Diving birds and mammals must all be able to control breathing voluntarily, have enhanced oxygen (O_2) and carbon dioxide (CO_2) storage capacity, limit their metabolic rate temporarily via the 'diving response', have a tolerance to low oxygen partial pressures (pO_2) and high carbon dioxide (pCO_2), and have the ability to recover efficiently from asphyxia–and the human diver's needs are similar (Elsner & Gooden, 1983). We also need to have adequate sensory functions and an ability to equalize the ears and to move efficiently under water.

All warm-blooded divers must also have a tolerance for the cold; the Ama of Japan and the Hae Nyo of Korea both dive in relatively cold water, which may have an influence on apneic duration and time spent in the water (Kang et al., 1965). Cold tolerance can be increased by acclimatization; even though these divers were described as the humans with the greatest cold tolerance when still diving naked, they lost most of this acclimatization with the introduction of wetsuits in the 1970s (Park et al., 1983). Now with wetsuits they can remain immersed in water throughout the whole 4 h dive shift.

Respiratory adaptations

Voluntary respiratory control is essential for all breath-hold divers, and an ability to voluntarily respiratory breathing is a prerequisite for advanced vocal communication – common among diving species. The ability to voluntarily breath-hold may, however, not be limited to diving species, and it seems to be present in our closest relatives; in recent observations a captive chimpanzee was seen to voluntarily immerse itself under water (Bender & Bender, 2013).

Being insensitive to asphyxia would not in itself be a solution for productive diving. For the harvest diver it is also essential to limit breath hold durations to avoid the excess accumulation of hypoxia biproducts which would require prolonged recovery times between dives; they should therefore be able to respond in time to the rising levels of CO_2 as well as hypoxia – a safeguard which appears to be well developed in diving mammals (Kooyman, 1989). Thus, while high tolerance to asphyxia before the brain shuts down is a good thing, in order to have a safety margin, removing sensory imput from increasing asphyxia alone, is not. It would seem, from registrations of diving durations in harvest divers, that these divers limit their dives to within the aerobic dive limit in order to recover quickly between dives.

Humans, like some shallow divers, e.g., sea otters, rely substantially on lung oxygen stores, as opposed to oxygen stores in blood and muscles. In comparison to matched controls, the Ama divers are known to have larger lungs (Ferretti & Costa, 2003) so they can increase oxygen storage and also regulate buoyancy. Before diving they usually inspire to only 85 % of their total capacity (Hong et al., 1963; Schagatay, 1996), probably to avoid problems of high buoyancy when descending to depths, which is inefficient in terms of metabolic cost. Another benefit may be that the human diving response (see

below) is improved at sub-maximal lung volumes (Andersson & Schagatay, 1998). Thus, although harvest diving is a straining activity, it does not seem to take the human diving potential to its limits. Our large lung volume may, however, assist with increasing the maximal breath hold period – as explored by competition divers (Schagatay et al., 2012).

An ability to rapidly equalize the air filled middle ears and sinuses with increasing hydrostatic pressure is also essential for diving in humans, without this the eardrums could rupture. In harvest divers 'hands free' equalization is normally used: the diver knows how to voluntarily open the Eustacian tubes, connecting the middle ear to the nasopharynx. With shallow depths, this method can be learned by most people with some training, otherwise air from the lungs can be expired against a closed nose as most people spontaneously do.

The diving response

The human diving response involves a number of physiological changes initiated at immersion, including the constriction of blood vessels to organs that can withstand hypoxia (Scholander et al., 1962; Irving, 1963). Blood is rerouted to the brain, heart (Andersen, 1966; Elsner & Gooden, 1983) and active muscles (Butler & Woakes, 1987), which together with a reduction in heart rate (HR) lowers the metabolism (Gooden 1994). The diving response has been shown to conserve oxygen efficiently and help to prolong apnea (Andersson & Schagatay, 1998; Schagatay & Andersson 1998). In humans, the diving response is triggered by apnea and by stimulation of thermo-receptors in the upper face which detect a chilling of the skin (Schuitema & Holm, 1988) as occurs during diving. Using apnea separately – and combined with facial chilling to induce a diving response of different magnitudes in Indonesian Sea nomads, we found that simultaneous apnea and facial immersion increased the magnitude of the HR reduction by 80% compared to apnea alone. This increased the apneic duration in these divers by 57% (Schagatay, 1996). Similar results were found in other groups of trained divers, but no difference in dive time resulted in non-divers, probably due to discomfort or stress caused by the face being under water in un-accustomed subjects (Schagatay & Andersson, 1998). The initiation by apnea and facial chilling means that the response is preventive since it develops well before hypoxia.

It is the relative temperature difference between the air and water that is important to the diving response, instead of water temperature *per se* (Schagatay & Holm, 1996; Schagatay, 2011a). This means the response is effectively triggered both in the Ama and in tropical divers like the Bajau, as long as the water temperature is lower than the surrounding air. Each time the diver submerges the face, the diving response constricts vessels to tissues tolerant to hypoxia, like the skin and resting muscles, while directing the blood to more oxygen craving organs like the heart and brain; thereby the oxygen supply lasts longer. The heart rate, at the same time, is reduced; adding to the oxygen conserving effect. The diving response is powerful in the Bajau (Schagatay, 1996) and in the young Ama (Holm et al., 1998) but it may not be a prerequisite for the short dives used in harvest diving; it was found that elderly Ama divers had a reduced diving response compared to young divers, even though they could continue their work as divers until an older age (Holm et al., 1998).

Spleen contraction

The spleen is used as an additional storage site for red blood cells in many mammals, and in humans, marine mammals, and some endurance runners, e.g. horses, and this supply can be recruited when enhanced oxygen transport is required (Stewart & McKenzie, 2002). The human spleen contraction response was first described in the Ama (Hurford et al., 1990) and it is triggered principally by hypoxia (Richardson et al., 2009) and enhanced by hypercapnia (Richardson, 2008). The response develops both during diving and at venues at high altitude – but to a greater degree during diving as a result of the co-occurring hypercapnia (Lodin-Sundström & Schagatay, 2010). In humans, apneic duration is known to increase during repetitive dives with short pauses in between. This is explained by the development of spleen-induced Hb increase over a series of three to five dives (Schagatay et al., 2005), with the response absent in individuals who have had the spleen removed (Schagatay et al., 2001). After a period of approximately 10 min without a dive, the red blood cells leave the circulation and are stored back in the spleen (Schagatay et al., 2005). Thus in the Ama harvest divers, whose rest periods were shorter than 10 min, after a few work up dives, diving may be made using this extra apneic capacity across an entire working period, which prolongs aerobic dive time and also promotes recovery. Recovery time after each dive is very important for the total time spent under water. Human harvest divers appear to keep dives short enough – within the aerobic dive limit – so that lactate and CO_2 do not build up excessively, necessitating longer recovery periods between dives. In a study on the Korean Ama, blood pH after a dive–reflecting lactate and CO_2 – decreased only slightly and recovery after normal short dives was completed within 20 s (Qvist et al., 1993). It appears that keeping dives short enough to avoid severe asphyxia, which would require longer recovery periods, is the most efficient way of budgeting time for these divers (Schagatay, 2011a). It should also be noted that a diver's ability to store CO_2 is estimated to be twice that of non-divers (Feretti, 2001), and other studies indicate that this is another trainable adaptation (Davis et al., 1987).

Underwater vision

Essential to the harvest diver is the ability to find the food. Vision is central in primates, and human vision underwater was considered to be poor – which appeared to present a good argument against a semi-aquatic phase in our evolutionary history. Semi-aquatic animals need adaptations to see well in both air and water – which is not easily achieved. However, observations of Sea Nomads diving without goggles suggested that they used their vision as the primary sense to find seafood (Schagatay, 1996). They often also swim at the surface with the face submerged apparently to see underwater, raising the head only for short breathing pauses (Personal observations). In a subsequent study on the Thai Sea Nomads, the Moken, it was found that children could see twice as well underwater as European children (Gislen et al., 2003). The main mechanisms for this superior underwater vision appeared to be pupil constriction, which is not typical among the strategies adopted by other semi-aquatic birds and

mammals. However, some seals (Sivak, 1978), dolphins (Herman et al., 1975) and sea snakes (Schaeffel, 1991) do appear to use this method and this may be an example of convergent evolution (Gislen et al., 2003). Also, the Moken children's eyes did not seem to be bothered by the salty sea water and they had normal corneas and excellent vision on land. Both Sea nomads and Ama divers lived from sea harvesting before the introduction of goggles or masks in the 19th century, and some sea nomads still dive successfully this way. Also they do not use a noseclip, even when diving to depths of 20-30 m; they obviously efficiently seal off the nose via the soft palate.

Competition divers – extremes in maximum performance of a single dive

Competitive breath-hold diving has most likely a much shorter history than sea harvesting. Although some records were set in the 1950s, with divers challenging each other for maximal depth, it is only in the last two decades that the sport has become formalised with regular world championships in maximal apnea duration, dive distance and depth, using self propelled dives. In 2010, William Trubridge reached the current depth record of 101 m without fins, while the present static apnea record by Stéphane Mifsud stands at 11 min 35 s since 2009 – representing clearly remarkable achievements for land mammals. Competitions are held in the six disciplines by the Association Internationale pour le Développement de l'Apnée (AIDA) – the recognised body for apnea competitions. Except fins, no technical aids are allowed for propulsion to reach the maximal distance or depth. These competition disciplines are: static apnea for maximal duration (1), horizontal distance swimming in a pool, with (2) and without fins (3), deep diving with (4) and without fins (5), and free immersion (6), where the diver descends and ascends by pulling along a rope. Table 1 shows the current records.

TABLE 1. The six disciplines in competitive apnea diving, with records, September 30, 2013.

Discipline	**Method**	**Record** Male/Female
1). Static apnea (STA)	Apnea at rest floating in pool	11:35/9:02
2). Dynamic apnea with fins (DYN)	Horizontal swimming with fins	281/234 m
3). Dynamic apnea without fins (DNF)	Horizontal swimming without fins	218/182 m
4). Constant weight with fins (CWT)	Vertical swimming with fins	1 28/101 m
5). Constant weight without fins (CNF)	Vertical swimming without fins	101/69 m
6). Free immersion (FIM)	Pulling down and up a rope	121/91 m

Comparisons of the figures for maximal dives in competition, and the depth and dive periods reported for the harvest divers, highlight the 'reserve capacity' inherently available to the human diver upon training to the limits. It also reveals the key difference between the two groups, with the harvest diver's focus on repetitive dives with minimized pauses, and the competition diver's focus on maximum performance in a single dive; recovery time does not matter to the latter. Remarkably, age does not seem to limit breath hold diving in the way that it does with other human physical activity, and this is as true for competitive apnea diving as it is for harvest diving. Many successful competition divers are in their forties or fifties.

Risk is limited in the self propelled disciplines, owing to the use of good safety measures, including safety divers ready to assist divers to the surface should a problem occur; hypoxic syncope does sometimes occur during maximum attempts, usually close to the surface, but with safety divers in place these are dealt with without complications. "Lung squeeze" is another problem emerging with increasing depths. The rules require divers to carry out a 'surface protocol' when surfacing; this involves a series of manoeuvres and the verbal statement "I am OK" in order to check that each diver is not severely hypoxic. Failure to do so leads to disqualification, and the rule thereby limits overambitious attempts. However, records do not seem to level off, and with more extreme depths the risks may increase substantially.

Where is the limit?

The assisted disciplines 'variable weight' and 'no limits' involve using weights for descent, and in 'no limits' also a lifting device for ascent, and no competitions are arranged for these types of diving, which are limited to a handful of record makers. The 100 m 'no limits' dive made by Jacques Mayol in 1976 surpassed physiologists' predictions on lung squeeze limitations; it had been predicted that human lungs would 'implode' and rupture by the pressure increase. The predictions also proved invalid when the 160 m record dive was set in the same discipline by Tanya Streeter in 2002, at that time, a world record for both men and women. In 2007, the current record was set when Herbert Nitsch made a dive to 214 m on one breath of air. To reach such depths using a weighted sled, and therefore being able to reach 'unphysiological' depths, obviously poses considerable risk of physical damage (Schagatay, 2011b). In an attempt in 2012 to beat his own record, Nitsch reached 250 m, but suffered severe injury during the very rapid ascent, probably caused by bubbles in his central nervous system. This could have resulted from decompression sickness (DCS) occurring if dissolved nitrogen forms bubbles or arterial gas embolism if lung air enters the bloodstream, both typical problems for SCUBA divers. Unfortunately, he may have surpassed the human freediving depth including with this dive, from which he is still recovering. Strikingly, also marine mammals, including deep diving whales, have been found to suffer from DCS probably caused by a too fast ascent (Hooker et al., 2009).

Adaptations allowing extended breath-hold diving

A number of features are involved in determining the maximal capacity of human divers for duration, distance or depth (reviewed in Schagatay, 2009, 2010, 2011b). The more gas storage is available in the body for the diver to use, the more the aerobic apneic duration can be extended. Several mechanisms are present for extending dives in humans and different methods are used by apnea divers to maximize their effects, including increasing the lung volume and the diving response. Increases of oxygen in the blood after dive training is due to both Hb elevation by spleen contraction, and long term effects elevating baseline Hb (de Bruijn et al., 2008).

Respiratory adaptations in elite divers

Voluntary breath control far beyond the comfort point and into the phase where the urge to breathe becomes severe, but without losing control and risking hypoxic syncope, is also essential to the performance of single maximum dives (see Schagatay, 2009). In order to prolong the comfortable phase of the dive, before an urge to breathe arises, a reduced ventilator response to rising pCO_2 can be productive, but the diver should benefit from a good ability to sense hypoxia, which may explain how they avoid syncope (Schagatay, 2009).

Although deep diving mammals generally do not have exceptionally large lungs, many shallow diving species diverge from equally-sized terrestrial mammals in this respect (Lenfant et al., 1970). In competition divers, where maximum oxygen storage is needed to give longer apneic periods, and a greater starting volume allows greater depths to be reached before lungs are compressed to residual volume, divers often overfill the lungs by means of buccal pumping, a type of breathing seen in amphibians (Örhagen et al., 1998). This involves packing air into the lungs using positive pressure created in the oral cavity, using the tongue as a piston (Örhagen et al., 1988). This method can also help divers to fill their lungs, despite being immersed to the neck, and be used to train to develop larger lungs. In an 11 week lung training study, we found a volume increase of 0.45 L of the Vital Capacity (Johansson & Schagatay, 2012). In another study investigating Vital Capacity in elite divers, lung volume was on average 1.8 litres larger than in non-diving control subjects, likely reflecting genetic differences as well as training effects (Schagatay, 2011a).

With diving beyond the depth where lungs are compressed to residual volume, lung air cannot be used for equalization of other air spaces. Equalization at depths beyond this point – occurring at an individual depth for each diver, but often between 25 and 40 m – requires extreme control of the pharynx, soft palate, epiglottis, and tongue. This is needed in order to separate the oral cavity after filling it with air and then using the mouthfill to repeatedly move air into the middle ears and sinuses during descent (see Schagatay, 2011b; Johansson & Schagatay, this issue). These techniques for deep equalization can also be learned by most freedivers, but require knowledge about how to per-

form the various steps – and practice. Unlike the Sea Nomad divers, competition divers normally use nose clips for deep diving, if they do not wear a mask; they do not seem to manage the soft palate well enough to close off the nose to avoid water from entering at the depths they reach.

The diving response in elite divers

Human diving adaptations thus include an oxygen conserving diving response to submersion (Gooden, 1994). The heart rate reduction is often monitored to give an indication of the magnitude of the diving response. Trained divers – including both harvest divers and competition apneists – have average heart rate reductions in the range of 45-50 %, and individuals among elite apnea divers may display a heart rate of less than 30 beats per minute during several minutes. Elite apnea divers' apneic heart rates during experimental apneas were found to be correlated to their competition results – the lower heart rate, the better they scored in a world championship (Schagatay, 2009).

Spleen contraction in elite divers

Although competition divers do not routinely dive repetitively with short pauses, spleen contraction is also seen during single deep dives (Lodin-Sundström et al., 2010). During warm up dives carried out before a competition, dive contestants may also recruite the spleen erythrocytes. The greatest splenic storage capacity among mammals is found in the deep diving Weddell seals and elephant seals (Castellini & Castellini, 1993), where the Hb may increase by over 50% after spleen contraction. Spleen contraction may increase Hb by up to 10% in the trained diver, an effect that depends on the size of the spleen. Competition divers have been found to have larger spleens than matched controls, which enhances gas storage capacity during dives and also allows faster recovery between dives (Schagatay, 2012). The spleen size among elite divers was found to correlate with their competition success (Schagatay et al., 2012). It is not clear if long term training can increase spleen volume, but studies of daily apnea training for two weeks in novice subjects did not show any changes (Engan et al., 2011). Long term exposure to hypoxia by either severe COPD or high altitude climbing may increase spleen volume and contractile function (Schagatay, unpublished observations) suggesting that the 2 week apnea training may have been too short to produce an effect.

Baseline erythrocyte increase

High amounts of erythrocytes are typical in extreme divers among mammals. When living at altitude, the human body is known to adapt to hypoxia by increasing the number of circulating erythrocytes. There is evidence that this response may also exist in elite divers; a study by de Bruijn et al. showed that baseline haemoglobin (Hb) levels were higher in elite divers than controls (de Bruijn, Richardson et al., 2004). Erythropoietin (EPO), a kidney hormone that promotes red cell formation, was found to be increased after an apnea series (de Bruijn et al., 2008), suggesting that the increased Hb is a response

to apnea training. A study of long term apnea training also supported the elevation of red cell formation (Engan et al., 2011). Interestingly, the high amount of red cells in the blood of some semi-aquatic mammals may also develop as a result of training (MacArthur et al., 2003).

The human diving response from a comparative perspective

Some features are shared by nearly all mammalian divers, such as an effective diving response, although the diving response may exist in all animal species to a greater or lesser degree (Lin, 1982). The extent of the bradycardia invoked is a reflection of the natural environment, with diving mammals showing a much greater heart rate reduction than terrestrial species (Elsner & Gooden, 1983; Kooyman,1989). Forced diving studies on inbred strains of rats have shown that an important part of their diving response is genetic and heritable, and is thereby able to respond to natural selection (Fahlman et al., 2011). In a comparative review, the heart rate responses observed during face-immersion apnea across a number of species were collated (Schagatay, 2011a). The greatest reductions in HR (70-90 %) were found in marine mammals, such as dolphins and seals, while the smallest (30-40 %) were observed in trained pigs, dogs and untrained humans. Interestingly, an intermediate group existed with approximately 50 % reduction of HR, and this contained beavers, muskrats, manatees and trained human divers (Schagatay, 2011a).

It was previously believed that the human diving response was not effective for conserving oxygen, since the response was small, and found to be most powerful only in very cold water – at a temperature where not many people would dive. However, the small response was found because at that time most experiments were carried out in laboratories on subjects who were inexperienced in diving, whereas more recent studies have clearly shown that this response is increased by apnea or dive training (Schagatay & Andersson, 1998; Schagatay et al., 2000; Engan et al, 2011), to levels found in semi-aquatic species. The need for very cold water to trigger such a response, was also a misconception: while a maximal response was found with facial immersions in 10 C water by cold acclimated people, the response was found to be just as powerful with facial immersions in 20 or even 30 C water by warm acclimated ones thus demonstrating the response is initiated by the change in temperature (Schagatay & Holm, 1996).

Human locomotion in water from a comparative perspective

The ability to swim well is naturally important for any aquatic or semi-aquatic animal. Human swimming ability is clearly superior to that of any of the great apes; trained swimmers have crossed the English Channel, and one individual the Berings strait.

There are a wide range of anatomical variations in swimming adaptations, reflecting the different evolutionary history of each species. Fully aquatic mammals, such as whales and dolphins (Cetacea), for example, swim much like fish, using a whole body movement and tail fluke propulsion, yet because of different basic anatomical features, having descended from terrestrial quadrupeds, they undulate the spine vertically. Seals and sea lions (Pinnipedia), on the other hand, while conducting a predominantly aquatic life, do, to some extent need to use their limbs on land, which is reflected in their swimming. Other semi-aquatic mammals, whose priority is efficient movement on land, have comparatively slow and inefficient aquatic abilities (Fish, 1993), much like humans. For a quadruped to be an efficient swimmer and reduce energy expenditure, drag needs to be reduced, by reducing the angles between the body and the extremities (Hardy, 1960). To this end, the human body is well designed, compared to other primates. The upright human anatomy with head, spine and legs in line, allows the body to move through water with a low drag. Humans are also unique because we do not have body fur; a naked body reduces drag to a level similar to eels (McNeil, 1977). Although humans cannot compete with the flippers of marine mammals for effective propulsion through water, large hands and feet make human divers more effective swimmers (Toussaint et al., 1991; Geladas et al., 2005). Augmenting the limbs with diving fins reduces the energy cost of crawl swimming by 40% (Zamparo et al., 2002). Despite this, the human diving depth record achieved with fins is only 27 m (21%) deeper than without fins. Although the Ama have used small fins for decades, initially they did not, and the Sea Nomads do dive efficiently without any, showing that the human anatomy is functional for marine foraging (Schagatay et al., 2011).

Does human diving ability support a period of littoral evolution?

Physiological adaptations, including a diving response occurring with every dive, a spleen response developing over a series of dives, and long term adaptations evident after training, like elevated hematocrit, large lungs and greater tolerance to asphyxia, show that the present day humans are fairly well adapted – certainly more so than most terrestrial mammals – for foraging in water. This is also supported by the fact that after training, most healthy humans can hold their breath for 3-4 min, swim 50 m underwater and reach depths of 20-30 m – feats unlikely in other terrestrial mammals (Schagatay, 2011a). In fact, these values are within the typical ranges of semi-aquatic mammals, such as sea otters (see also Fahlman & Schagatay, this issue). Interestingly, the diving patterns of the Ama and other harvest divers closely mimic the bimodal diving activity range of the foraging sea otter (Bodkin et al.,1993). The maximal human diving performance has likely not yet been reached, but the results of elite competition divers suggest that there is an untapped reserve capacity not explored by modern harvest divers. Also, the fact that many beginner divers discover a talent for diving to great depths, without much training,

seems to support evidence that our species has an inherent ability to dive (see Johansson & Schagatay, this issue).

Since more recent human evolution has most likely occurred on land, this suggests that our prehistoric ancestors may once have been more advanced divers than today's sea harvesters, in line with or even beyond the capabilities expressed by elite competition divers. The amazing and seemingly unique adaptability of humans to dive deeper and for longer periods than other terrestrial mammals, points to the conclusion that at some stage human ancestors were likely exposed to evolutionary pressures from swimming and diving (Hardy, 1960). This may also explain some of our other unique features among primates and terrestrial mammals, e.g., the lack of fur, a streamlined body, and a subcutaneous fat layer, which we share with most aquatic mammals. Moreover, our vocal communication and our adaptability to underwater vision, the fact that our babies can swim, a well-developed diving response, an efficient spleen response, long lifespan, and large brains, would also seem to indicate an aquatic past because such features are common in aquatic species, yet are less so in terrestrial ones. Furthermore, the great nutritional value of seafood – and the abundance of it within reach of littoral divers – makes it an appealing theory.

Conclusion

These facts regarding human diving ability, when put together, suggest that modern humans are well adapted for foraging in water to depths of 20-30 m by repeated short dives, with a reserve capacity for deeper and longer single dives. This inherent, trainable ability could well suggest that our ancestors were once under evolutionary pressure from living in the littoral zone, spending considerable time swimming and diving. If so, this might also explain some of our other unique features when compared to terrestrial mammals, particularly primates. Since more recent human evolution may not have involved diving activity, this could suggest that at some point in history our ancestors were even better adapted to diving than modern humans.

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