



Evolution of the thirst mechanism in *Homo*: The need and limitations of thirst and hydration

Frank E. Marino

School of Rural Medicine, Charles Sturt University, Leeds Parade, Orange, NSW 2800, Australia

ARTICLE INFO

Edited by: Michael Hedrick

Keywords:

Drinking
Evolution
Fluid balance
Homo
Hydration
Osmolality
Performance
Thirst

ABSTRACT

There is a view that the perception of thirst and actual body fluid balance may affect cognitive and exercise performance. The evolutionary evidence suggests that our survival was dependent on our ability to sweat profusely when hunting during the heat of the day (*persistence hunting*), so if water deficits were not tolerated, consequently the thirst mechanism would limit our persistence hunting capability. This also means that hunting and searching for water was undertaken with some extent of water deficit, and in turn suggests that performance; physical and cognitive, was conducted with a degree of dehydration. Given the current views on the maintenance of body water for performance, there is a need to evaluate the evidence relating to tolerance limits for water deficits with respect to both physical and cognitive performance. This review considers the thirst mechanism and the conditions and selective pressures under which this might have evolved. Consideration will be given to how the thirst mechanism influences our physical and cognitive performance. The review suggests that *Homo* developed appropriate tolerances for water deficits and thirst perception, with a safety margin that prevented detrimental declines in physical and cognitive performance to the point of inhibiting corrective action. This would have offered a selective advantage, enabling the search for water and functioning adequately during periods of water scarcity.

1. Introduction

There are several seminal texts describing the human need for drinking and the biology of thirst (Wolf, 1958; Fitzsimons, 1972; Fitzsimons, 1979; Rolls and Rolls, 1982) which underscore the relative importance placed on human water balance and its effects on health and survival. As for the need to drink and its relationship to human performance, there is little debate about the benefit of appropriate hydration necessary to either maintain or enhance performance under a range of conditions (Adolph, 1938; Adolph and Dill, 1938; Adolph, 1947; Périard et al., 2021). This has also extended to the effect of water balance and physical performance in animals (Schmidt-Nielsen, 1979). Historically, water availability and deficits are thought to be responsible for catastrophic outcomes on the battlefield (Hubbard et al., 1982), in athletic competition (Kenefick and Sawka, 2007) and for the deterioration in cognitive performance (Adan, 2012). An additional concern is the potential effects of climate change on access to water resources for our increasing population and the negative impact on health and liveability, making water security an imperative (Vorosmarty et al., 2000; Kummu et al., 2010; Frederick and Major, 1997; Vineis et al., 2011). Given what

we already understand about hydration, water balance and human performance, it may be questionable as to whether an additional review or even an opinion is necessary. However, there is a dearth in the literature with respect to the evolutionary antecedents about how thirst, drinking and the need for water might influence human physical and mental performance.

There is broad consensus that human performance, particularly in the heat, is influenced by fluid balance and the level of hydration (Sawka et al., 2007), and although this view has been challenged (Noakes, 2010; Noakes, 2012b; Cotter et al., 2014; Wall et al., 2015; Hoffman et al., 2018) the evidence that thermoregulation during exercise is compromised as a water deficit ensues, has a long history and is not easily dismissed (Cheuvront et al., 2010). Tied to the intricate relationship between hydration, water deficit, performance and thermoregulation is the perception of thirst. Although fundamental to our need to consume fluids, thirst perception and its origins are usually considered superficially by describing it as a potential effect on the performance outcome (Armstrong et al., 2014). Nevertheless, others have suggested that the perception of thirst and actual hydration status may have different effects on human performance (Adams et al., 2018). For example,

E-mail address: fmarino@csu.edu.au.

<https://doi.org/10.1016/j.cbpa.2024.111745>

Received 24 May 2024; Received in revised form 29 August 2024; Accepted 16 September 2024

Available online 19 September 2024

1095-6433/© 2024 The Author. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

cognitive performance may be preserved if dehydration is a consequence of exercise (Serwah and Marino, 2006), but this may not be the case if dehydration is passively induced (Goodman and Marino, 2021).

Nevertheless, it does seem counterintuitive and paradoxical that a body water deficit and the accompanying thirst sensation should be so dire that it hinders the capability to correct the situation by degrading human cognitive and physical performance. To that end, the evolutionary evidence suggests that our survival was highly dependent on our ability to sweat profusely while hunting and chasing animals in the heat of the day (Lieberman, 2015; Halsey and Bryce, 2020). If this was the case, and water deficits could not be tolerated, then thirst would have been an ineffective mechanism because it would hamper our ability to correct the deficit. Seeking water sources was likely achieved when there was already a body water deficit that could not be avoided, and this in turn means that performance; physical and cognitive, must have been conducted under a degree of dehydration. Added to this is the likelihood that our chances for survival were dependent on our ability to search for highly dispersed water sources (Finlayson, 2013; Finlayson, 2014). How we achieved this is still debated but it appears that we may have used several methods to find and access water.

The purpose of this review is to consider the thirst mechanism within an evolutionary context and the conditions under which it likely developed. The review will also consider how the thirst mechanism influences the cognitive domains and physical performance under conditions in which hydration is thought to be a key factor. Finally, consideration will be given to how the development of a body water deficit to a certain level may not necessarily be detrimental in certain situations since *Homo* evolved resilience to water deficits.

2. Searching for, and finding water

The initial thoughts and intuition about how humans or other animals might go about finding water would be inextricably linked to the need to quench thirst. However, this need alone would not be sufficient to detect water sources. No doubt thirst can be motivation to seek water, but the detection of water sources must have required other inputs. It would, therefore, be most desirable for there to be additional avenues beyond the need to satisfy thirst that would assist in the search for water sources. Current evidence suggests that the sensation of wetness, observation of fauna and detection of specific humid odour are likely to be the most salient possibilities for the detection of water.

The sensation of wetness can act as feedback signalling changes in the immediate environmental conditions or even the individual's changing physical state. As such, this can alter behaviour and can assist in maintaining homeostasis by either seeking shelter, increasing fluid intake, or reducing physical activity. It has been shown that beyond the sensations generated by changes in either core (T_c) or skin (T_{sk}) temperatures, wetness is a critical element for human behaviour and comfort and has a significant influence on thermal behaviour (Vargas et al., 2018).

By comparing T_c and T_{sk} temperature responses against the perception of skin wetness during and post exercise in moderate ambient conditions (27 °C, ~22 % relative humidity; rh), it was evident that the perception of skin wetness persisted well into post-exercise recovery even when T_c and T_{sk} were declining (Fig. 1A). The more salient finding was that the contribution for the desire to receive neck cooling was 52 % from the perception of skin wetness and less from either T_c (22 %) or T_{sk} (26 %) (Fig. 1B).

These findings indicate that humans have an innate awareness of the environmental conditions such that skin wetness, which might be a direct response to body heating and then cooling by evaporation of sweat, will instigate behaviour to either dampen these responses or avoid such conditions. In this sense, skin wetness would signal that there is likely to be water loss from the system which would heighten the need to replenish the current or impending water deficit, thereby increasing the motivation to search for water sources. Although some species such

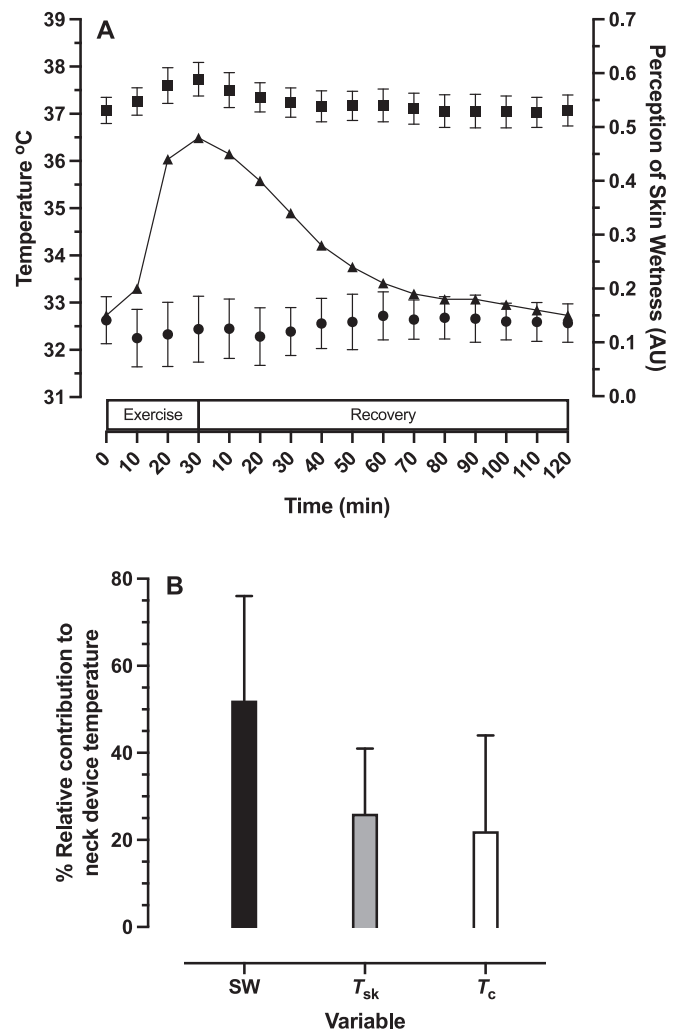


Fig. 1. A: The core (squares) and skin (circles) temperature response during exercise (left ordinate) and the perception of skin wetness (triangles; right ordinate) during exercise (0–30 min) and in recovery (0–120 min). B: The % relative contribution to the neck cooling device temperature over the time period shown in A for skin wetness (SW), skin (T_{sk}) and core (T_c) temperatures. Data are mean \pm SD (error bars removed from SW for clarity). Data in A redrawn from combined data in Fig. 1A-C and data in B redrawn from Fig. 4 from Vargas et al. (2018).

as insects are endowed with specific organs (hygroreceptors) to sense humidity and wetness, humans have no such specific receptor despite the skin being the largest organ; therefore, the perception of skin wetness must be derived from other sensory inputs (Filingeri, 2015). It is not apparently obvious why humans did not evolve hygroreceptors, but it might be a reasonable assumption that the need to live in a wide range of environments, from very humid to very dry negated the need for specialised hygroreceptors; since they would be redundant in dry environments. Rather, *Homo* developed other physiological and behavioural adaptations to manage humidity and hydration in a range of environments.

It appears that in humans, integration of the differences between pressure and friction from mechanoreceptors coupled with the sensation from evaporative cooling from thermoreceptors provide the necessary input for sensing skin wetness (Filingeri et al., 2014). As the evaporative capacity of sweat is dependent on the difference in the water vapour pressure between ambient air and the skin, wetness can be perceived as discomfort. If this perception of wetness is prolonged, the eventual outcome could lead to water deficits since this could be interpreted as a reduced need for water consumption. Therefore, searching for water

sources in a range of conditions must have been a significant survival strategy that forms part of our evolutionary history (Finlayson, 2013; Finlayson, 2014; Rosinger, 2021).

An additional consideration is how our evolutionary history shaped our strategies to meet our water needs, especially for access to water (Rosinger, 2021). A basic strategy would have been to follow animals to water holes with knowledge of their transience perhaps passed on through generations. Although plausible, dry periods on the savanna would have presented a very different challenge compared to that of a forest. A forested area contains very different water sources such as streams, rivers and vines which can be harvested for drinking as observed in chimps (Matusaka et al., 2006). In contrast, a savanna habitat is likely to have dispersed water holes altering in availability due to climatic and seasonal changes (Smit et al., 2007). Living in a habitat where water availability can change from season to season and for extended periods, presents a challenge which would require a strategy other than just sighting a water source. Animals can provide humans with a range of possible water harvesting techniques and can lead us to water because they utilise a range of alternative methods to access water. Gurera and Bhushan (2020) in their systematic review on water harvesting in nature, note the techniques used across various animal and plant species. For example, plants can harvest water through deposition of water droplets, channelling *via* grooves, coalescing and gravity driven collection. Animals on the other hand will manipulate their surroundings to collect water so that a turtle might dig a small ditch for catching rainwater, snakes will coil up in the open during rain to collect water in the shallow loops they form. There are numerous water harvesting methods utilized by a myriad of animals which also include body surface structures that assist in channelling water. A reasonable assumption is that *Homo* would have learned to manage and harvest water by observing animals within their habitat. However, the possibility that *Homo* mirrored water harvesting techniques of other animals is speculative given that there does not appear to be documented evidence to support this. Thus, the question as to how *Homo* located sources to harvest water remains unresolved.

A defining activity of *Homo* is the capability to hunt which is thought to have originated some two million years ago (Liebenberg, 2013). However, it is now recognised that running and chasing an animal until it overheats and drops from hyperthermia represents a transition from predation to hunting (Liebenberg, 2006; Bramble and Lieberman, 2004). Since it has been observed that tracking and hunting takes place during the warmest part of the day, it has been termed *persistence hunting* which has been posited as an evolutionary advantage for *Homo* (Carrier, 1984; Liebenberg, 2006). As such, one possibility is that with the need to have a high sweat rate to keep cool during persistence hunting (Lieberman, 2015), the likelihood is that this activity was conducted within the range of available water sources for drinking. In accordance with this view, it has been suggested that with the development of a large brain, *Homo*'s ability to retain information about the location of water sources was enhanced (Eckhardt, 1987).

Beyond simply sighting a body of water, the origins for the human ability to search for and find water sources is difficult to pin-point, although there must have been environmental cues for this to occur, especially during dry periods. One of the earliest mentions of a possible environmental cue was in 1891 (Phipson, 1891a; Phipson, 1891b) which described an odour emitted by soils and sedimentary strata following a heavy shower of rain. It was suggested that this odour was due in large part from the release of organic substances deposited by the local flora penetrating the pores of the surrounding earth during dry periods and then eventually displaced by heavy rain. This odour was subsequently 'coined' petrichor (Bear and Thomas, 1964) replacing the term argillaceous odour. These authors described how the odour is related to plant oils which are released into the air along with bacterial by-products known as *geosim*, when soil becomes wet. This provides the distinct smell that is apparent in the atmosphere when rain falls following a long dry period. It appears that the human sensitivity to *geosim* is likely to be

as low as 9.5 parts per trillion (Polak and Provasi, 1992) suggesting that *Homo* at some point in our evolutionary past was highly sensitive to wetness based on odour. However, it is not known from what distance petrichor can be detected by humans. Generally, detection of odour is highly dependent on a number of factors at any one time, including the concentration of the odorant, the prevailing environmental conditions such as air movement and humidity. Although there is a general assumption that human olfactory capability is less well developed compared with other animals, current data suggests otherwise (McGann, 2017). That is, it is apparent that humans can possibly discriminate over a trillion odours (Bushdid et al., 2014), making us potentially more sensitive to some odours compared with dogs and rodents (McGann, 2017). Moreover, there is now compelling evidence that humans can, with a sampling of a single unique odour be able to identify a location and then return to that location using only the olfactory information to inform their positioning (Jacobs et al., 2015). A key point these authors make is that if humans are indeed specialised for walking and running long distances (Bramble and Lieberman, 2004; Liebenberg, 2006; Hora et al., 2020) then it would make intuitive sense to employ olfaction in navigation, especially if sourcing water was a key survival strategy. Although speculative to suggest that humans might have used petrichor as a strategy to search for and find water, this environmental cue, and our olfactory sensitivity for it could have been one method our ancestors used to sense rain and find water sources to enhance their survival.

In summary, since *Homo* is not endowed with specific hygroreceptors to sense wetness, coupled with our capacity for profuse sweating, the need to search for and find water sources in a range of environments was very likely a selective advantage. However, this advantage must have been shaped by several capabilities leading to sensing wetness, utilizing a range of water harvesting methods and cues from a range of animals within the habitat.

3. Evolutionary basis of thirst, hydration, and performance

The backdrop for the need to adequately hydrate and mitigate the thirst sensation is the popular message that we need to drink at least eight glasses of water a day for which there is no particular evidence (Valtin, 2002). Although the meaning of thirst is generally understood by the public at large, thirst is a complex phenomenon which is developed and then instigated by a series of physiological and behavioural responses. Basically, thirst is associated with the desire to drink with the goal being to satiate the discomfort that arises from that sensation. In the study of exercise and human performance, the thirst sensation is typically recommended as a method to maximise fluid replacement before, during and after exercise (Sawka et al., 2007). However, this recommendation is based on the need to avoid either a fluid deficit (dehydration) or overload (hyponatremia) so that exercise performance and health is not compromised; for it follows that if a body water deficit can be avoided, then the thirst sensation may not reach the threshold required to initiate the behaviour for sourcing water. Considering thirst in this binary way might be useful to mitigate becoming either dehydrated or overhydrated, but it does not relate to the underlying factors which might either initiate, reinforce, or terminate drinking, each of which may have individual or combined effects for the thirst response. For instance, depletion of either the intracellular or extracellular fluid compartments can stimulate thirst, whereas taste may reinforce drinking and termination can be brought about by gastric distention (Rolls and Rolls, 1981). Thus, to understand the evolution of the thirst mechanism consideration needs to be given to each of these responses.

3.1. Fluid compartments

In considering thirst and the drive to drink, the inter-relationships and limitations of the body's fluid compartments are key. These are well described as extracellular fluid which accounts for about 20 % of body mass (plasma is ~5 %, interstitial fluid is ~15 %) and intracellular

fluid which makes up ~40 % of body mass (Guyton and Hall, 2006). A loss in total body water, clinically defined as dehydration (Thomas et al., 2008) can be the result from either a water deficit or from both salt and water losses. For instance, during exercise of sufficient duration, and relative to the ambient conditions (Nielsen, 1996), the sweating response can be in the order of 1.8 l/h, equating to a body mass loss of 5.2 kg (6.9 % of body mass) although higher rates of 2.79 l/h have been documented (Armstrong et al., 1986). In his classic text, Adolph (1947) reports that dehydration in a harsh desert environment can be up to 11 % of body mass. Thus, if total body water is 60 % of body mass for a 75 kg man, total body water will be 45 kg. If dehydration of 11 % of body mass occurred for this individual (8.25 kg) this could constitute up to 18 % ($8.25/45 \times 100$) of total body water loss. In fact, a loss of a mere 2 % body mass for the same individual would translate to over 3 % loss of total body water.

The magnitude of the change in total body water should not be underestimated with respect to its significance for thirst. Adolph (1947) reported on the qualitative signs and symptoms of dehydration, describing that at 2 % mass loss, “thirst is noticeable very early” but that from 6 to 8 % mass losses, “Vague discomfort...gradually becomes defined in the flushing of the skin, heat oppression, weariness, sleepiness, impatience, anorexia, and dizziness. At about the time that the walking pace can no longer be maintained, dyspnea, tingling, and cyanosis as well as a suggestion of tetany appear. Still later, a man cannot stand alone, either because of impaired coordination or fainting” (p.p. 228). Notably, the effects of any mass losses above 10 % were anecdotal reports from men accidentally lost or stranded in a desert for some days. In addition, it was not certain whether a lethal water deficit was closer to 15 or 25 % of mass loss (Adolph, 1947) (or 25–41 % total body water for a 75 kg man).

The historical context for our understanding of the relationship between body water deficits and thirst are relevant as it can help explain in part our continued obsession with water consumption for both health and human performance (Valtin, 2002; Noakes et al., 2004; Noakes, 2012a). However, since Adolph’s observations on body water deficits and thirst, the evidence from both laboratory and field studies in which water deficits beyond 2 % and up to 7 % of mass losses were recorded, runners seem to perform successfully and without medical complication in warm conditions over consecutive days (Chlíbková et al., 2018; Tan et al., 2021).

The key concern with respect to body water deficits is how this relates to initiating the thirst sensation. It is not known whether there are specific thresholds in the changes of the different fluid compartments; cellular *versus* extracellular which will instigate the thirst sensation. An early consideration was that as dehydration ensues body cells act as osmometers so that differences in cellular water and total body water would signal a change equating to a threshold that would initiate the thirst sensation; estimated to be 0.861 % (where water content is 70 % of body mass) (Wolf, 1958). However, it is important to note that it is not an either/or mechanism and that changes in both ICF and ECF compartments influence the initiation of thirst and drinking. This is thought to be controlled by neurons known as osmoreceptors located centrally within three small, interconnected forebrain nuclei known as the lamina terminalis (Leib et al., 2017). These osmoreceptors have an intrinsic ability to alter their rate of action potential firing in response to increases in the $[Na^+]$ in the ECF (Bourque, 2008; Gizowski and Bourque, 2018). Although ECF hypertonicity can cause cellular dehydration or cell shrinkage activating stretch receptors in the osmoreceptor walls, this response is inhibited by hypo-osmolality (Rowland, 2022).

The threshold for driving the thirst sensation is likely a key factor since it would dictate whether drinking should initiate and continue because it is thought that cognitive and physical performance is to some degree dependent on body water deficits. However, the advice to athletes and industry workers has varied considerably over many years. For athletes, early advice was to drink frequently during exercise (ACSM, 1975). This was superseded with the advice to avoid feeling thirsty since

it was thought that at this point it was too late to replace all the fluids lost (Greenleaf, 1992). This was then altered to encourage athletes to ingest a volume of fluid equivalent to the loss in body mass due to sweating (Convertino et al., 1996), and following this it was drinking to avoid excessive dehydration (>2 % body mass loss) (Sawka et al., 2007). The reasons for the change in advice for fluid replacement are varied but one key issue for the change was that excessive drinking in some cases led to the development of life threatening hyponatremic encephalopathy (Rosner, 2008). Later advice advocated that drinking for exercise performance should be according to the dictates of the thirst sensation (Noakes, 2010), although even this has been challenged on the basis that this strategy will not necessarily achieve appropriate water balance (Adams et al., 2019). This latter view was based on two key observations. First, during recovery from 180 min of exercise in the heat (35.2 °C) thirst perception was significantly greater for the hypohydrated who received no fluid compared with euhydrated (Fig. 2). Second, *ad libitum* consumption of fluid post exercise when hypohydrated (>2 % body mass loss), negated differences in the perception of thirst between euhydrated and the hypohydrated (Fig. 2). The authors concluded that the utility of thirst in guiding hydration practices has limited value.

Although the findings and conclusions by Adams et al. (2019) seem appropriate given that thirst sensation was not suppressed when fluids were restricted in a hypohydrated state, an alternative conclusion would be that thirst sensation as a drive for drinking is quite precise. That is, when hypohydrated and permitted *ad libitum* fluids, the thirst sensation was similar to being euhydrated during recovery (Fig. 2). In fact, the consumption within the first 10 min of recovery was over 1 l when hypohydrated with *ad libitum* replacement. This volume represented about 55 % of the total body mass loss, however, was not further replaced because of protocol limitations. It is unknown whether total losses would have been replaced if the opportunity to continue drinking was available. This conclusion needs to be considered against the well-known response that simply replacing body water following exercise with just plain water has shown the potential for large falls in serum osmolality and diuresis which compromised positive fluid balance (Costill and Sparks, 1973). This has led to the understanding that replacing fluid without electrolytes may not in of itself result in body water balance (Nose et al., 1988; Maughan et al., 1994). Subsequent studies also confirmed that fluid replacement is more likely to be more effective if consumed with food, thereby, assisting in the replacement of electrolytes (Maughan et al., 1996). This suggests that the thirst mechanism likely co-evolved with the need to consume other nutrients from foodstuffs to maintain body water balance.

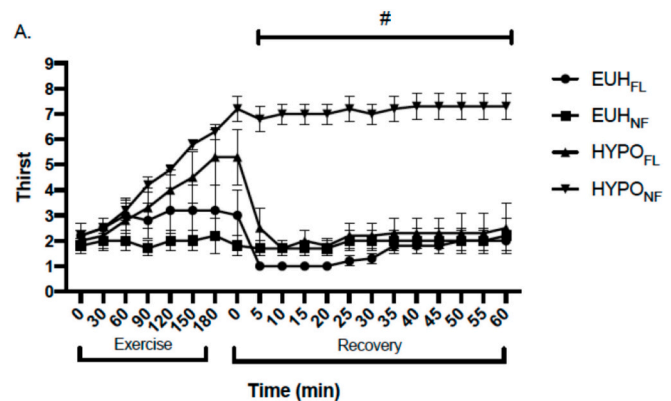


Fig. 2. Thirst perception measured during exercise in the heat (35.2 °C) and recovery under four different hydration conditions (EUH is euhydration, HYPO is hypohydration) either with *ad libitum* fluid (FL) or without fluid (NF) replacement. #*P* < 0.05 between HYPO_{NF} and all other conditions. Figure reproduced from Adams et al. (2019) with permission from MDPI Creative Commons license.

3.2. Palatability and termination of drinking

The evolving and meandering advice for fluid replacement indicates that the thirst sensation as a mechanism for preserving body water volume and physical performance, is somewhat limited. It is also evident that the biological evolution of thirst as a sensory signal is seldom considered even though there is good evidence which indicates that deviations in blood volume and osmolality are detected by specialised neurons within the subfornical organs in the brain (Lind et al., 1984). It also appears that drinking behaviour is instigated well before significant changes in blood volume and osmolality occur so that fluid intake is thought to be anticipatory (Stricker and Hoffmann, 2007). In fact, recent evidence indicates that there are well established neural mechanisms that modulate drinking in anticipation of fluid loss, including drinking during meals, rapid satiation of thirst and that oral cooling alone can quench thirst (Zimmerman et al., 2016). It has also been shown that pleasantness from drinking is associated with activation of the cingulate and orbitofrontal cortices (processing of emotions and decision making, respectively) (Lavin et al., 2013) whereas, over-drinking activates the midcingulate cortex, insula and amygdala (nocifensive behaviour) (Vogt, 2016). In essence, the anticipatory nature of drinking behaviour with the potential for rapid quenching of thirst by either cooling, or by ingested volume, is indicative of a highly evolved corrective mechanism which permits the relatively fast restoration of water balance. Notably, cooling and volume are only two of several variables which may modulate fluid intake. Gastric distension can also cause a reduction in the rate of drinking (Sobocińska, 1978; Camps et al., 2018) which has also been shown to activate vagal afferents in cortical and subcortical activity thought to control fluid intake (Wang et al., 2008). It has also been suggested that the intensity of thirst is reduced with each gulp by neural feedback conveying information to the brain about the status of dry mouth, taste, volume swallowed and gastric distention. All of these inputs provide a survival advantage by reducing the time needed to spend at a water source to correct the water deficit, minimising exposure to predators (Saker et al., 2014).

3.3. Body mass loss

Although there is sufficient biological and behavioural evidence which indicates that thirst is a highly evolved corrective mechanism, much of this understanding comes from animal studies. In humans, particularly with respect to athletic competition, a body mass loss of ~2 % is reported to be enough to hamper exercise performance (Cheuvront et al., 2003; Sawka et al., 2007) and similarly with respect to cognitive performance (Adan, 2012). Notably, the relationship between thirst sensation and losses in body mass remains unclear, even though it has been suggested that "At 2 per cent weight loss, thirst may be violent, but does not seem to increase much in intensity as the water deficit increases." (p. 14) (Schmidt-Nielsen, 1979). This is a curious phenomenon for which there is scant evidence and seems counterintuitive as a survival mechanism. For if escalating water deficits did not promote appropriate behavioural and motivational changes to seek and find water, then the thirst mechanism would have limited reproductive value.

Nevertheless, the meagre amount of evidence that is available does indeed show that the intensity of the thirst sensation grows as a consequence of increasing hypohydration based on body mass losses. Fig. 3 shows data collated from two separately published studies by the same group and seemingly collected on the same participants (Sawka et al., 1985; Engell et al., 1987). The redrawing of these data show that as hypohydration develops up to a body mass loss of 7 %, so too does the subjective assessment of thirst intensity and, importantly this is also confirmed by rising osmolality. This latter association was also corroborated by Thompson et al. (1986) who showed that as plasma osmolality increased by infusion of hypertonic saline, so did the intensity of thirst. Given these data, the notion that thirst intensity does not intensify any

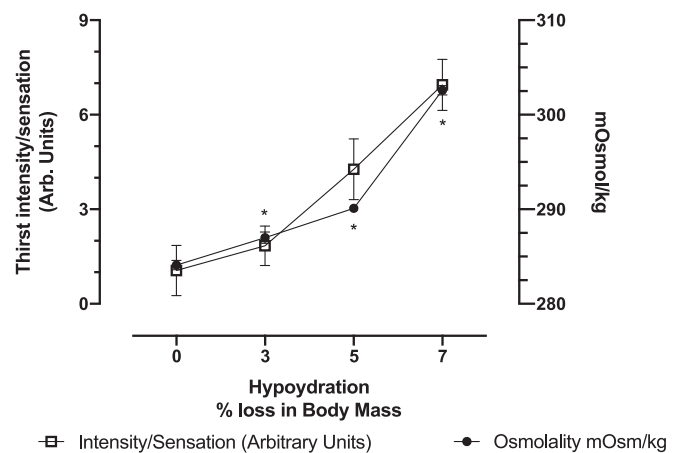


Fig. 3. Shows the subjective assessment of thirst intensity/sensation from a category scale as arbitrary units (*right ordinate*; where 0 is not at all and 9 is severe) and osmolality (*left ordinate*) as hypohydration increases from 0 to 7 % loss in body mass. Data related to thirst sensation are redrawn from Engell et al. (1987) and data related to osmolality are redrawn from Sawka et al. (1985). Data are mean \pm SE. Statistical significance was not reported for thirst intensity/sensation; * $P < 0.01$ each point in time for osmolality.

further beyond 2 % body mass loss is questionable. This is a key point if the thirst mechanism is at least to be of inherent value as a mechanism to alter behaviour for the purpose of satiation and survival. This would make evolutionary sense as the drive to drink would be much more critical as osmolality rises. Of course, these data need to be confirmed and extended by further experimentation, although any experiment requiring participants to hypohydrate beyond 7 % losses in body mass would no doubt present an ethical issue.

Notwithstanding the ethical considerations, in competition settings it is not unusual for reported body mass losses to be in the range of 5–10.7 % (mean \pm SD 6.2 ± 1.1 %) for long duration events such as a triathlon (224 km) with no evidence for a greater number of medical complications or higher rectal temperatures although higher serum sodium concentrations have been reported (Sharwood et al., 2004). Perhaps the key observation in that study was the tendency for athletes who lost the most body mass achieved the fastest run times. As such, these contrasting data bring into sharp focus the historical view that dehydration beyond 2 % body mass loss may not be a significant hindrance to either health or performance, at least in healthy people and during athletic competition.

4. Homeostasis, thirst and fluid loss

As already discussed in section 3.1, changes in the fluid compartments which lead to reductions in body water can initiate drinking, typically known as a *homeostatic* response; the aim of drinking being to ameliorate the compartmental fluid shifts (Gizowski and Bourque, 2018). There are also *non-homeostatic* instigators of drinking which do not necessarily alter the status of the fluid compartments. These can include palatability of the fluid, the need for lubrication during eating, dry-mouth, and polydipsia (Rolls and Rolls, 1982). The distinction between *homeostatic* and *non-homeostatic* stimuli for thirst and eventual drinking is key, as biologically the need to seek water and increase its intake can be for entirely different reasons and may not always be driven by the apparent survival needs *per se*. Nevertheless, non-homeostatic mechanisms for fluid intake can be of significant survival value. From an evolutionary perspective, living in dry or unpredictable environments would necessitate drinking without being thirsty which would ensure adequate body water content ahead of periods of water lack or when travelling long distances. This is especially the case if most drinking occurs rapidly and well before it can be detected by

osmoreceptors in the brain (Stricker and Hoffmann, 2007). The evidence for this in humans is scarce but there are animal models which show that pre-emptive fluid intake may be a behaviour that anticipates body water deficit before it arises (Gizowski and Bourque, 2018; Zimmerman et al., 2016). This anticipatory drinking behaviour would have also benefited physical performance by delaying dehydration in long distance tracking of prey and by maintaining cognitive acuity (Goodman and Marino, 2021).

In relation to human cognitive and physical performance, however, advocating for fluid intake is essentially based on the need to reduce the homeostatic imbalance of the fluid compartments. For the purpose of this review, the emphasis is on thirst as a consequence of homeostatic imbalances.

A key component in understanding how thirst might have evolved as a mechanism mitigating homeostatic fluid imbalance, is that multiple processes are available to stimulate the search for water and initiate drinking. Although water moves freely among the body compartments, we must rely entirely on the water contained within these fluid compartments at any given time, which presents a survival challenge. Early data on the possibility of preloading with water prior to walking in the desert suggests that ~1 l of additional water can be ingested with ~85 % used in the formation of sweat, and only ~15 % lost through urine (Brown, 1947). Although this seems a favourable option it does come with feelings of discomfort from gastric fullness and additional mass to be carried if exercise performance is the goal. Besides the potential for limited value (Marino et al., 2003), a potential complication from preloading with water before exercise and continuing to do so during exercise, is the risk of developing exercise associated hyponatremia (Hew-Butler et al., 2015).

In extant primates, 2 d of water deprivation resulted in a 10 % loss in body mass and 12.5 % loss of total body water, but interestingly hematocrit and hemoglobin concentration and blood viscosity were not significantly affected by this magnitude of dehydration (Zurovsky et al., 1984). This study showed that these primates were able to maintain their plasma volume at the expense of losses from other body fluid compartments. This suggests that there may be a level of redundancy which avoids circulatory distress when there is a large loss of fluid from the extracellular compartment. These authors suggest that this redundancy is brought about from the baboon's ability to retain and increase blood albumin levels which is responsible for maintaining blood colloid oncotic pressure (Belinskaia et al., 2021).

Thus, the notion that animals and *Homo* could have possibly moved relatively unrestricted away from water sources without dire consequences has merit in the fact that large body water losses can be sustained for long periods. This has been recently modelled based on persistence hunting in the Kalahari which compared adult body size extrapolations of *H. erectus* fossils from previously published studies (see citations in Hora et al., 2020) to a recent Kalahari hunter over nine persistence hunts in high ambient temperatures (31–45 °C and 23–71 % rh) (Hora et al., 2020). These researchers predetermined that the limit of 10 % of body mass loss and the ability to hunt without drinking for at least 5 h was a threshold that could limit persistence hunting, since this was apparently the longest duration reported for a successful persistence hunt of large prey. Their findings indicate that dehydration would not limit persistence hunting in *H. erectus* for up to 5 h and 40 min with no drinking required before reaching the dehydration limit. This highlights two key points with respect to thirst. First, there is no doubt that over a period of 5 h of persistence hunting, changes in osmolality with rising thirst sensation would have developed consistent with Fig. 3. As such, there is no evidence that thirst stifled the chase. Second, the desire to initiate drinking can be overridden even with high levels of dehydration with accompanying homeostatic challenge from compartmental fluid shifts, at least for the time of the hunt. Although it may seem confounding to equate the context of a hunt with a competitive athletic event, in reality these are similar albeit with different high stakes. Not least of which a hunt would require skill and pacing while in pursuit of a

larger animal so as to not give up ground for fear of losing a well-earned meal.

4.1. The tight regulation of fluid compartments and hormonal action

As already discussed, physiological responses which initiate thirst, and which lead to drinking are reasonably well described and are dependent on which fluid compartment is altered (McKinley and Johnson, 2004). A key physiological measure is that the normal range of circulating anti-diuretic hormone (ADH; vasopressin) is very small at 0–3 p-grams/ml (~ 3×10^{-12} M), (Bankir et al., 2017) signifying the potency of ADH and the level of defence for keeping fluid compartments stable. In fact, when the extracellular sodium concentration rises by as little as ~2 mEq/l over the normal value, thirst is signalled. When we consider this miniscule change in the extracellular osmolality and the potency of ADH in response, it would not be unreasonable to posit that the thirst mechanism evolved as an advanced warning system. For if the opposite were the case where a higher threshold for the thirst sensation to initiate drinking was required, a significant fluid deficit would ensue and water seeking might be delayed with a potential catastrophic outcome. There is good evidence, albeit mainly from animal models, that thirst is a feedforward and adaptive response that precedes physiological challenges. These challenges can be the result of rises in core body temperature (Barney and Folkerts, 1995) or even food intake which has also been reported to be a potent stimulus for drinking within minutes of consumption, especially when the food is likely to lead to hypertonic plasma (Mandelblat-Cerf et al., 2017).

An additional process to maintain water balance is instigated by the kidney itself, acting as an endocrine organ and secreting the hormone renin when there is a need to conserve water or sodium (Maebashi and Yoshinaga, 1967; Sladek et al., 1981). In response to a reduction in blood volume, renin is secreted which forms angiotensin-I in plasma which when enzymatically converted to angiotensin-II, stimulates thirst and appetite for sodium (Robinson et al., 1999). The fact that the kidney is also involved in stimulating fluid intake suggests that the kidney is not just an organ that filters plasma and forms urine. The renin-angiotensin response by the kidney itself presents an additional line of defence in the conservation of osmolality.

In summary, since there is limited capacity for either a water reserve or preloading with the body constantly mitigating changes in body fluid, it is desirable that *Homo* developed more than one mechanism to maintain and preserve fluid balance as a critical aspect of physiological control. These multiple systems and their inherently very low thresholds for stimulating the thirst sensation provides a useful margin of time for locating a drinking source rather than being a signal for a desperate need to drink. Notably, there is a high tolerance of up to 10 % body mass loss before a life threatening situation arises in both *Homo* (Adolph, 1947; Beis et al., 2012; Zouhal et al., 2011) and possibly extant primates (Zurovsky et al., 1984). This is consistent with the evidence that tri-athletes and ultra-endurance runners in the field can experience between 5 and 12.6 % body mass loss with no serious consequences (Sharwood et al., 2004; Speedy et al., 1999).

5. Thirst, cognitive and athletic performance

5.1. Thirst, hydration, and cognition

The effects of body water deficits on cognitive function can be potentially confounded by the superimposed exercise. For example, regardless of exercise mode or intensity there is potential for a positive effect on cognitive function during and up to 20 min post exercise (Chang et al., 2012) with an inverted-U relationship evident during exercise induced hyperthermia (Schmit et al., 2017). It has also been shown that choice reaction time is improved during exercise in the heat with and without complete fluid replacement (Serwah and Marino, 2006). Nevertheless, it is desirable in exercise contexts that cognitive

function is preserved since decision making could be an advantage in competitive settings. To this end, there are studies which have evaluated the effect of exercise induced hypohydration on executive function, memory and attention tests (Cian et al., 2001; Cian et al., 2000; Gopinathan et al., 1988; Ganio et al., 2011). Collectively these studies conclude that there is a negative relationship between exercise induced dehydration and cognitive function. Although the general advice is that a body mass loss of 2 % might hamper cognitive performance (Sawka et al., 2007) others report no changes in cognitive performance with up to 4 % of body mass loss (Ely et al., 2013). Given the state of the literature at present, it is not possible to conclusively state that hydration at a given level will hamper cognitive performance. The only conclusion that can be drawn is that hydration during exercise will not likely hamper cognitive performance.

Nevertheless, the effect of hydration on cognitive performance might be dependent on whether consumption is based on the perception of thirst. For example, in a study by Rogers et al. (2001) participants were able to drink cool water in a graded fashion (none - 120 - 330 ml) after their thirst perception was measured, then subsequently completing cognitive tests, showed that if thirst perception was low the impact of drinking was detrimental rather than either beneficial or neutral for cognitive performance. Conversely, cognitive performance was improved if thirst sensation was high when drinking was proportional to the level of thirst. This pattern was also confirmed in a subsequent study which showed that water consumption can have contrasting effects on different cognitive processes based on subjective thirst; water consumption appeared to have a corrective effect on response times in thirsty individuals (Edmonds et al., 2013).

If we accept that a water deficit resulting in at least a 2 % loss in body mass is sufficient to induce the thirst sensation (Schmidt-Nielsen, 1979), its effect on cognition may be of practical significance. For example, it has been hypothesised that water consumption alone could free up attentional resource that might be occupied because of processing the sensations of thirst rather than a particular task at hand (Cohen, 1983). This possibility was examined in a novel study which compared drinking to the dictates of thirst with restricted fluids while thirst was induced by saltwater mouth rinsing during 60 min of cycling in normothermic conditions (Goodman and Marino, 2021). Mental fatigue was then induced with a 60 min Stroop task while prefrontal cortex (PFC) haemodynamics were monitored. Although the body mass loss was minimal (<1 %) for the thirst condition, this resulted in fewer iterations of the Stroop task being completed (Fig. 4A) while PFC oxyhemoglobin (O₂Hb) was elevated in advance compared to the sated condition (Fig. 4B). The advanced elevations in PFC O₂Hb with the higher ratings for perception of thirst during the mentally fatiguing task is a key observation as this is thought to be representative of increased neural recruitment in the PFC (Tam and Zouridakis, 2015). The suggestion was that this reflected a compensatory neurophysiological response since additional PFC O₂Hb was elicited, possibly to supplement behavioural performance (Wang et al., 2016). However, the realignment of the PFC O₂Hb to match that of the sated condition after 15 min suggests that the compensatory response is unable to continue as sustained neural recruitment (Goodman and Marino, 2021). In fact, it was clear from the results of the Stroop task that the scores between thirst and sated conditions were similar for up to 40 min, after which they began to diverge until the last 10 min when the scores were again similar (Fig. 4B).

The evolutionary significance of a pre-emptive compensatory neurophysiological response is not entirely clear. However, thirst can elicit neural activity that rapidly spreads throughout the brain (Allen et al., 2019) whereby neural networks allow for adaptability, plasticity and information storage (Armstrong and Kavouras, 2019). The additional PFC neuronal activation when thirsty could signify cognitive adaptation during the task. Therefore, rather than have a significant reduction in performance on the actual task when thirsty, the additional neuronal activation might provide the capacity to process the needs of the task with reductions in performance only lasting for a short time (10

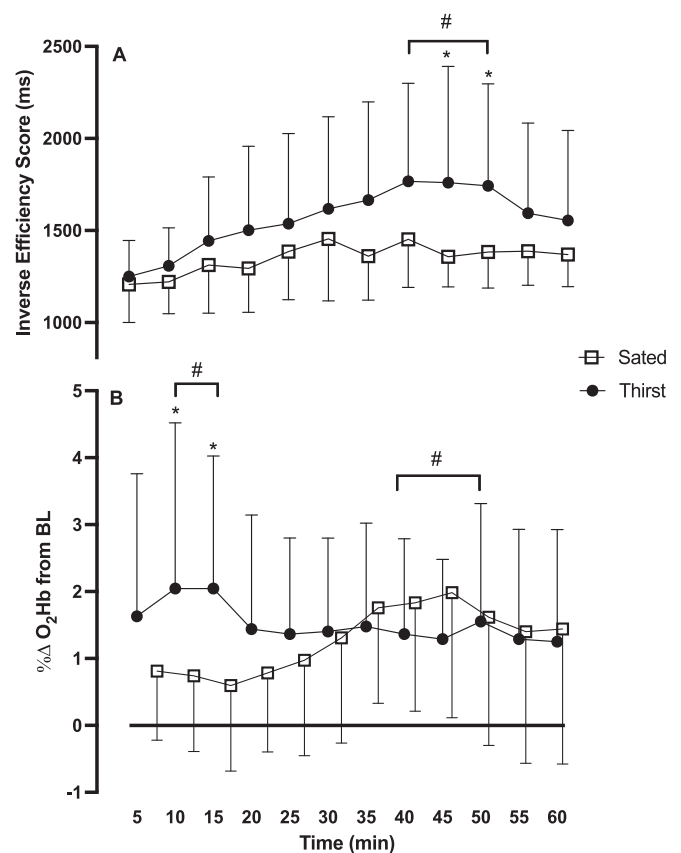


Fig. 4. Inverse efficiency score (IES) for performance on the Stroop test (A) and % change in of the prefrontal cortex oxygenated hemoglobin (% Δ O₂Hb) from base line measures (B) during sated and thirst conditions. Note the advanced increased % Δ O₂Hb in thirst at 10–15 min (B) ahead of the increase in IES at 40–50 min (A). * $P \leq 0.05$ different from all other time points in the thirst condition while significant *post hoc* analyses for condition at each time are represented by # ($P \leq 0.05$). A lower IES score indicates superior performance. Data are mean \pm SD. Figures redrawn from Goodman and Marino (2021) with kind permission from Elsevier.

of the total 60 min). Thus, the deterioration on task was not long lasting with O₂Hb returning to sated values at about the mid-point. This suggests that the thirst sensation can be managed by additional neuronal activation during a cognitively demanding task which could mitigate a significant reduction in cognitive capability. A compensatory neurophysiological response is an enticing hypothesis which might help explain the relationship between the thirst sensation and cognitive performance since the difference in body water deficit was minor (<1 %).

Finally, the potential effect that needs to be considered is whether cognition is affected by the actual awareness of thirst by virtue of knowing the body fluid status. This does not seem to have been studied with respect to cognition, but it does warrant consideration since under exercise conditions the drive to drink when knowing the extent of body fluid loss *versus* not knowing appears to make no difference to water intake, suggesting that being aware of a fluid deficit does not override the actual thirst sensation (Capitán-Jiménez and Aragón-Vargas, 2021). This would make evolutionary sense since if the opposite were the case so that knowledge of the fluid deficit was a requirement for initiating drinking, then fluid replacement or even venturing too far from a water source would be restrictive. From a cognition point of view, the possibility that the brain might mitigate the sensation of thirst regardless of actual water deficit by pre-emptively increasing neural recruitment provides a safeguard for cognition to continue, albeit with some deficiency.

5.2. Thirst and exercise performance

The number of published reports examining the effects of varying levels of hydration on exercise performance are voluminous and span a multitude of contexts including high performance sport, recreational, industrial, clinical, social, normothermic and heat stress conditions. The early view was that replacing water lost by sweating would be the best way to maintain physical performance, especially in the heat (Pitts et al., 1944). As already outlined, advice regarding the adequate level of hydration for athletic performance has varied and altered over time (ACSM, 1975; Greenleaf, 1992; Convertino et al., 1996; Sawka et al., 2007). However, the effect of dipsogenic drive on athletic performance, independent of water deficit has been relatively under investigated. This may be because it is difficult to blind participants to fluid ingestion and that separating the thirst sensation from body water loss is non-invasively difficult. An additional difficulty in evaluating this is that the thirst sensation can be quickly extinguished by drinking *via* stimulation of oropharyngeal receptors and/or gastric stimulation (Geelen et al., 1984).

Although invasive, blinding the level of hydration has been achieved by saline infusion when participants were dehydrated by 3 % body mass loss following 2 h of submaximal exercise in the heat (Wall et al., 2015). In this study saline infusion replaced either 100 %, 33 % or 0 % of fluid losses while the strength of thirst perception was measured pre and post dehydration and then pre and post a 25 km time trial (TT). These authors found that the subsequent 25 km TT in the heat was not different when the starting hydration status was maintained by infusing saline at a rate equal to sweat rate. Fig. 5 shows the rating of perceived thirst at the measurement times with saline infusion.

These data indicate that thirst perception did not affect the performance of the 25 km TT given that the ratings were almost identical across the measurement periods regardless of the hydration status. Notably, there was no oral hydration or mouth rinse available during the TT which may have hidden any differences in dipsogenic drive for each condition. That is, it is not possible to evaluate how strong the psychological effect of thirst perception might have been if fluids were made available for consumption. All that can be concluded with respect to

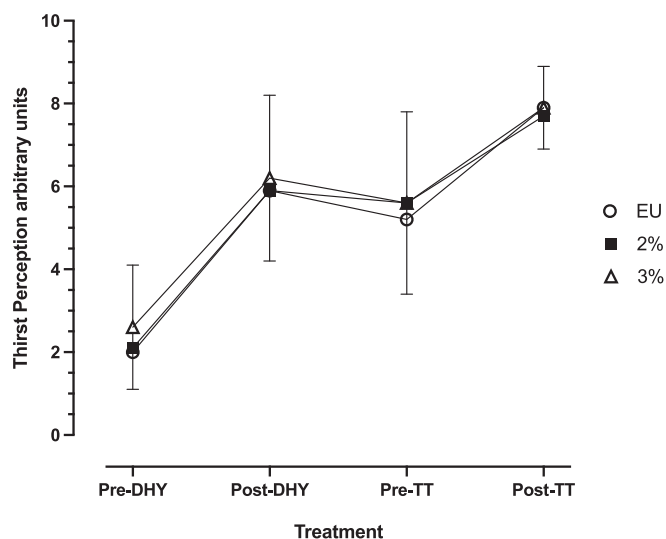


Fig. 5. The rating of thirst perception at the four phases of the trial for euhydration (Euh), and dehydration (DHY) at 2 and 3 % body mass loss. Ratings were taken pre and post DHY of a 2 h exercise heat stress test followed by a 25 km time trial (TT) each in 33 °C and 50 % relative humidity. Rehydration was undertaken by intravenous saline infusion commencing Post-DHY and then continuing through pre and post TT. There were no differences between conditions over the measurement periods. Data redrawn from Table 2 in Wall et al. (2015).

thirst perception is that it was similar across conditions and that it did not influence TT performance. However, the possible psychological effect of thirst perception on a 20 km TT in which participants were either thirsty or not thirsty was examined using either sham or saline infusion (Cheung et al., 2015). After being dehydrated by exercise in the heat, sham or saline infusion was used to maintain either a euhydrated or dehydrated (>3 % body mass loss) state. The key difference was that *ad libitum* mouth rinsing with water was available when thirsty during euhydrated and dehydrated trials *versus* when not thirsty. Fig. 6 shows the rating of thirst perception under the four different conditions. The perception of thirst increased from baseline when participants were thirsty in both a euhydrated and dehydrated state. These authors concluded that the presence or absence of *ad libitum* water mouth rinse, to bypass the conscious awareness of hydration status and to alter thirst sensation during exercise in the heat, did not influence TT performance.

The findings from the limited blinded hydration studies (Wall et al., 2015; Cheung et al., 2015) indicate that thirst perception escalates whether euhydrated or dehydrated (Figs. 5 & 6), but more so when participants are dehydrated (Fig. 6). From an evolutionary perspective, these findings fit with the hypothesis that if water deficits, and by extension thirst perception, could not be tolerated then thirst would be overwhelmingly limiting and hamper our ability to correct the water deficit and impinge on our survival. For if thirst was a limiting factor, then performance should also be hampered, at least within the parameters of the time trials in these blinded studies (20 and 25 km). These findings support the notion that water deficits and thirst sensation are difficult to avoid and, therefore, physical performance must be undertaken under their “influence”.

6. Summary and conclusions

The purpose of this review was to consider the development of the thirst mechanism with an evolutionary perspective and the conditions under which it likely evolved. A major consideration was the human sensitivity to changes in body water with respect to losses and the sensation of wetness. The literature in this area suggests that *Homo* adapted to environmental challenges to search for highly dispersed water sources using senses other than sighting a body of water (e.g., argillaceous odour, tracking animals). It is also evident that *Homo* can tolerate up to 11 % body mass losses with no immediate physiological

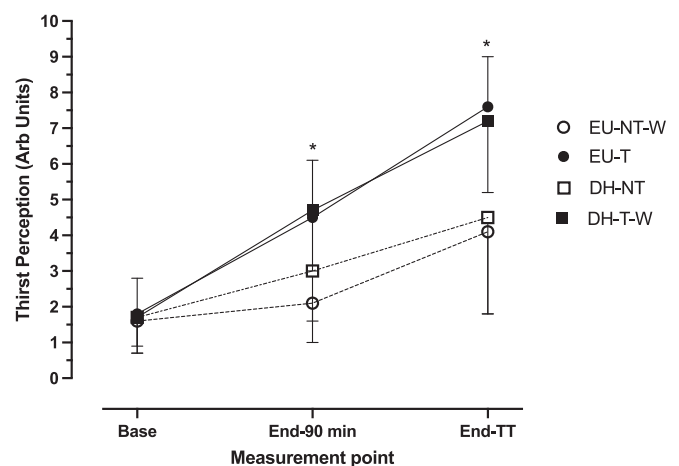


Fig. 6. Shows the rating of thirst perception at baseline (Base), at the end of the 90 min exercise heat stress for dehydration (End-90 min) at 50 % peak oxygen uptake and at the end of the 20 km time trial (End-TT) while either euhydrated (EU) or dehydrated (DH) dehydrated. Hydration was maintained and blinded in the TT by either saline infusion or sham when participants were either thirsty (T) or not thirsty (NT) and W indicates mouth water rinse available *ad libitum*. Note that *ad libitum* mouth rinse was available to NT. **P* < 0.001 compared to NT. Data redrawn from Table 2 in Cheung et al. (2015).

consequence, although this represents an upper limit. Some evidence points to the thirst sensation rising as osmolality rises (Fig. 3). Overall, evolution endowed *Homo* with appropriate tolerances for both water deficits and thirst perception which provide a reasonable safety margin before physical and cognitive performance is severely compromised. This likely provided a selective advantage not only to search for water but also to continue to function adequately during periods of water lack.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

CRedit authorship contribution statement

Frank E. Marino: Writing – review & editing, Writing – original draft, Project administration, Formal analysis, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

None.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

The author acknowledges the long standing support of Charles Sturt University in providing funding for research and the Spitfire Association for contribution to research on hydration and human performance.

References

- ACSM, 1975. American college of sports medicine position stand. Exercise and fluid replacement. *Med. Sci. Sports Exerc.* 3, 194–196.
- Adams, J.D., Sekiguchi, Y., Suh, H.G., Seal, A.D., Sprong, C.A., Kirkland, T.W., Kavouras, S.A., 2018. Dehydration impairs cycling performance, independently of thirst: A blinded study. *Med. Sci. Sports Exerc.* 50, 1697–1703.
- Adams, W.M., Vandermark, L.W., Belval, L.N., Casa, D.J., 2019. The utility of thirst as a measure of hydration status following exercise-induced dehydration. *Nutrients* 11, E2689.
- Adan, A., 2012. Cognitive performance and dehydration. *J. Am. Coll. Nutr.* 31, 71–78.
- Adolph, E.F., 1938. Heat exchanges of man in the desert. *Am. J. Physiol.* 123, 486–499.
- Adolph, E.F., 1947. *Physiology of Man in the Desert*. Interscience Publishers, Inc, New York.
- Adolph, E.F., Dill, D.B., 1938. Observations on water metabolism in the desert. *Am. J. Physiol.* 123, 369–378.
- Allen, W.E., Chen, M.Z., Pichamoorthy, N., Tien, R.H., Pachitariu, M., Luo, L., Deisseroth, K., 2019. Thirst regulates motivated behavior through modulation of brainwide neural population dynamics. *Science* 364, eaav3932.
- Armstrong, L.E., Kavouras, S.A., 2019. Thirst and drinking paradigms: evolution from single factor effects to brainwide dynamic networks. *Nutrients* 11, E2864.
- Armstrong, L.E., Hubbard, R.W., Jones, B.H., Daniels, J.T., 1986. Preparing Alberto Salazar for the heat of the 1984 Olympic Marathon. *Phys. Sports Med.* 14, 73–81.
- Armstrong, L.E., Ganio, M.S., Klau, J.F., Johnson, E.C., Casa, D.J., Maresh, C.M., 2014. Novel hydration assessment techniques employing thirst and a water intake challenge in healthy men. *Appl. Physiol. Nutr. Metab.* 39, 138–144.
- Bankir, L., Bichet, D.G., Morgenthaler, N.G., 2017. Vasopressin: physiology, assessment and osmosensation. *J. Int. Med.* 282, 284–297.
- Barney, C.C., Folkerts, M.M., 1995. Thermal dehydration-induced thirst in rats: role of body temperature. *Am. J. Physiol. – Reg. Integ. Comp. Physiol.* 269, R557–R564.
- Bear, I.J., Thomas, R.G., 1964. Nature of argillaceous odour. *Nature* 201, 993.
- Beis, L.Y., Wright-Whyte, M., Fudge, B., Noakes, T., Pitsiladis, Y.P., 2012. Drinking behaviors of elite male runners during marathon competition. *Clin. J. Sports Med.* 22, 254–261.
- Belinskaia, D.A., Voronina, P.A., Goncharov, N.V., 2021. Integrative role of albumin: evolutionary, biochemical and pathophysiological aspects. *J. Evol. Biochem. Physiol.* 57, 1419–1448.
- Bourque, C.W., 2008. Central mechanisms of osmosensation and systemic osmoregulation. *Neuroscience* 9, 519–531.
- Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. *Nature* 432, 345–352.
- Brown, A.H., 1947. Water shortage in the desert. *Physiol. Man Desert* 136–159.
- Bushdid, C., Magnasco, M.O., Voshall, L.B., Keller, A., 2014. Humans can discriminate more than 1 trillion olfactory stimuli. *Science* 343, 1370–1372.
- Camps, G., Veit, R., Mars, M., de Graaf, C., Smeets, P.A., 2018. Just add water: effects of added gastric distention by water on gastric emptying and satiety related brain activity. *Appetite* 127, 195–202.
- Capitán-Jiménez, C., Aragón-Vargas, L.F., 2021. Awareness of fluid losses does not impact thirst during exercise in the heat: A double-blind, cross-over study. *Nutrients* 13, 4357.
- Carrier, D.R., 1984. The energetic paradox of human running and hominid evolution. *Curr. Anthropol.* 25, 483–495.
- Chang, Y.K., Labban, J.D., Gapin, J.I., Etnier, J.L., 2012. The effects of acute exercise on cognitive performance: a meta-analysis. *Brain Res.* 1453, 87–101.
- Cheung, S.S., McGarr, G.W., Mallette, M.M., Wallace, P.J., Watson, C.L., Kim, I.M., Greenway, M.J., 2015. Separate and combined effects of dehydration and thirst sensation on exercise performance in the heat. *Scand. J. Med. Sci. Sports* 25 (Suppl. 1), 104–111.
- Cheuvront, S.N., Carter III, R., Sawka, M.N., 2003. Fluid balance and endurance exercise performance. *Curr. Sports Med. Rep.* 2, 202–208.
- Cheuvront, S.N., Kenefick, R.W., Montain, S.J., Sawka, M.N., 2010. Mechanisms of aerobic performance impairment with heat stress and dehydration. *J. Appl. Physiol.* 109, 1989–1995.
- Chlíbková, D., Nikolaidis, P.T., Rosemann, T., Knechtle, B., Bednár, J., 2018. Fluid metabolism in athletes running seven marathons in seven consecutive days. *Front. Physiol.* 9, 91.
- Cian, C., Koulmann, N., Barraud, P.A., Raphel, C., Jimenez, C., Melin, B., 2000. Influences of variations in body hydration on cognitive function: effect of hyperhydration, heat stress, and exercise-induced dehydration. *J. Psychophysiol.* 14, 29.
- Cian, C., Barraud, P.A., Melin, B., Raphel, C., 2001. Effects of fluid ingestion on cognitive function after heat stress or exercise-induced dehydration. *Int. J. Psychophysiol.* 42, 243–251.
- Cohen, S., 1983. After effects of stress on human performance during a heat acclimatization regimen. *Aviat. Space Environ. Med.* 54, 709–713.
- Convertino, A.V., Armstrong, L.E., Coyle, E.F., Mack, G.W., Sawka, M.N., Sherman, W. M., Costill, D.L., Greenleaf, J.E., Montain, S.J., 1996. ACSM position stand: exercise and fluid replacement. *Med. Sci. Sports Exerc.* 28, i–ix.
- Costill, D.L., Sparks, K.E., 1973. Rapid fluid replacement following thermal dehydration. *J. Appl. Physiol.* 34, 299–303.
- Cotter, J.D., Thornton, S.N., Lee, J.K., Laursen, P.B., 2014. Are we being drowned in hydration advice? Thirsty for more. *Extreme Physiol. Med.* 3, 18.
- Eckhardt, R.B., 1987. Was plio-pleistocene hominid brain expansion a pleiotropic effect of adaptation for heat stress. *Anthropol. Anzeig.* 193–201.
- Edmonds, C.J., Crombie, R., Gardner, M.R., 2013. Subjective thirst moderates changes in speed of responding associated with water consumption. *Front. Hum. Neurosci.* 7, 363.
- Ely, B.R., Sollanek, K.J., Cheuvront, S.N., Lieberman, H.R., Kenefick, R.W., 2013. Hypohydration and acute thermal stress affect mood state but not cognition or dynamic postural balance. *Eur. J. Appl. Physiol.* 113, 1027–1034.
- Engell, D.B., Maller, O., Sawka, M.N., Francesconi, R.N., Drolet, L., Young, A.J., 1987. Thirst and fluid intake following graded hypohydration levels in humans. *Physiol. Behav.* 40, 229–236.
- Filingieri, D., 2015. Humidity sensation, cockroaches, worms, and humans: are common sensory mechanisms for hygrosensation shared across species. *J. Neurophysiol.* 114, 763–767.
- Filingieri, D., Fournet, D., Hodder, S., Havenith, G., 2014. Why wet feels wet? A neurophysiological model of human cutaneous wetness sensitivity. *J. Neurophysiol.* 112, 1457–1469.
- Finlayson, C., 2013. The water optimisation hypothesis and the human occupation of the mid-latitude belt in the Pleistocene. *Quat. Int.* 300, 22–31.
- Finlayson, C., 2014. *The Improbable Primate: How Water Shaped Human Evolution*. Oxford Uni Press, Oxford, UK.
- Fitzsimons, J.T., 1972. Thirst. *Physiol. Rev.* 52, 468–561.
- Fitzsimons, J.T., 1979. *The Physiology of Thirst and Sodium Appetite*. Cambridge Uni Press, Cambridge, UK.
- Frederick, K.D., Major, D.C., 1997. Climate change and water resources. *Clim. Change* 37, 7–23.
- Ganio, M.S., Armstrong, L.E., Casa, D.J., McDermott, B.P., Lee, E.C., Yamamoto, L.M., Marzano, S., Lopez, R.M., Jimenez, L., Le Bellego, L., Chevillotte, E., Lieberman, H. R., 2011. Mild dehydration impairs cognitive performance and mood of men. *Br. J. Nutr.* 106, 1535–1543.
- Geelen, G., Keil, L.C., Kravik, S.E., Wade, C.E., Thrasher, T.N., Barnes, P.R., Pyka, G., Nesvig, C., Greenleaf, J.E., 1984. Inhibition of plasma vasopressin after drinking in dehydrated humans. *Am. J. Physiol. Reg. Integ. Comp. Physiol.* 247, R968–R971.
- Gizowski, C., Bourque, C.W., 2018. The neural basis of homeostatic and anticipatory thirst. *Nat. Rev. Nephrol.* 14, 11–25.
- Goodman, S.P.J., Marino, F.E., 2021. Thirst perception exacerbates objective mental fatigue. *Neuropsychology* 150, 107686.

- Gopinathan, P.M., Pichan, G., Sharma, V.M., 1988. Role of dehydration in heat stress-induced variations in mental performance. *Arch. Environ. Health* 43, 15–17.
- Greenleaf, J.E., 1992. Problem: thirst, drinking behavior, and involuntary dehydration. *Med. Sci. Sports Exerc.* 24, 645–656.
- Gurera, D., Bhushan, B., 2020. Passive water harvesting by desert plants and animals: lessons from nature. *Phil. Trans. Royal Soc. A* 378, 20190444.
- Guyton, A.C., Hall, J.E., 2006. *Textbook of Medical Physiology*. WB Saunders Company, Philadelphia, USA.
- Halsey, L.G., Bryce, C.M., 2020. Are humans evolved specialists for running in the heat? Man vs. horse races provide empirical insights. *Exp. Physiol.* 106, 258–268.
- Hew-Butler, T., Rosner, M.H., Fowkes-Godek, S., Dugas, J.P., Hoffman, M.D., Lewis, D.P., Maughan, R.J., Miller, K.C., Montain, S.J., Rehrer, N.J., 2015. Statement of the third international exercise-associated hyponatremia consensus development conference, Carlsbad, California, 2015. *Clin. J. Sports Med.* 25, 303–320.
- Hoffman, M.D., Snipe, R.M.J., Costa, R.J.S., 2018. Ad libitum drinking adequately supports hydration during 2 h of running in different ambient temperatures. *Eur. J. Appl. Physiol.* 118, 2687–2697.
- Hora, M., Pontzer, H., Wall-Scheffler, C.M., Sládek, V., 2020. Dehydration and persistence hunting in *Homo erectus*. *J. Hum. Evol.* 138, 102682.
- Hubbard, R.W., Mager, M., Kerstein, M., 1982. Water as a tactical weapon: A doctrine for preventing heat casualties. *Army Sci. Conf. Proceed.* 2, 125–139.
- Jacobs, L.F., Arter, J., Cook, A., Sulloway, F.J., 2015. Olfactory orientation and navigation in humans. *PLoS One* 10, e0129387.
- Kenefick, R.W., Sawka, M.N., 2007. Heat exhaustion and dehydration as causes of marathon collapse. *Sports Med.* 37, 378–381.
- Kummu, M., Ward, P.J., de Moel, H., Varis, O., 2010. Is physical water scarcity a new phenomenon? Global assessment of water shortage over the last two millennia. *Environ. Res. Lett.* 5, 034006.
- Lavin, C., Melis, C., Mikulan, E., Gelormini, C., Huepe, D., Ibañez, A., 2013. The anterior cingulate cortex: an integrative hub for human socially-driven interactions. *Front. Neurosci.* 7, 64.
- Leib, D.E., Zimmerman, C.A., Poormoghaddam, A., Huey, E.L., Ahn, J.S., Lin, Y.C., Tan, C.L., Chen, Y., Knight, Z.A., 2017. The forebrain thirst circuit drives drinking through negative reinforcement. *Neuron* 96, 1272–1281.e4.
- Liebenberg, L., 2006. Persistence hunting by modern hunter-gatherers. *Curr. Anthropol.* 47, 1017–1026.
- Liebenberg, L., 2013. *The Origin of Science*. Cybertracker, Cape Town, Sth Africa.
- Lieberman, D.E., 2015. Human locomotion and heat loss: an evolutionary perspective. *Comp. Physiol.* 5, 99–117.
- Lind, R.W., Thunhorst, R.L., Johnson, A.K., 1984. The subfornical organ and the integration of multiple factors in thirst. *Physiol. Behav.* 32, 69–74.
- Maebashi, M., Yoshinaga, K., 1967. Effect of dehydration on plasma renin activity. *Jpn. Circ. J.* 31, 609–613.
- Mandelblat-Cerf, Y., Kim, A., Burgess, C.R., Subramanian, S., Tannous, B.A., Lowell, B.B., Andermann, M.L., 2017. Bidirectional anticipation of future osmotic challenges by vasopressin neurons. *Neuron* 93, 57–65.
- Marino, F.E., Kay, D., Cannon, J., 2003. Glycerol hyperhydration fails to improve endurance performance and thermoregulation in humans in a warm humid environment. *Pflügers Arch.* 446, 455–462.
- Matsusaka, T., Nishie, H., Shimada, M., Kutsukake, N., Zamma, K., Nakamura, M., Nishida, T., 2006. Tool-use for drinking water by immature chimpanzees of Mahale: prevalence of an unessential behavior. *Primates* 47, 113–122.
- Maughan, R.J., Owen, J.H., Shirreffs, S.M., Leiper, J.B., 1994. Post-exercise rehydration in man: effects of electrolyte addition to ingested fluids. *Eur. J. Appl. Physiol.* 69, 209–215.
- Maughan, R.J., Leiper, J.B., Shirreffs, S.M., 1996. Restoration of fluid balance after exercise-induced dehydration: effects of food and fluid intake. *Eur. J. Appl. Physiol.* 73, 317–325.
- McGann, J.P., 2017. Poor human olfaction is a 19th-century myth. *Science* 356, eaam7263.
- McKinley, M.J., Johnson, A.K., 2004. The physiological regulation of thirst and fluid intake. *News Physiol. Sci.* 19, 1–6.
- Nielsen, B., 1996. Olympics in Atlanta: a fight against physics. *Med. Sci. Sports Exerc.* 28, 665–668.
- Noakes, T.D., 2010. Is drinking to thirst optimum. *Ann. Nut. Metab.* 57 (Suppl. 2), 9–17.
- Noakes, T.D., 2012a. Waterlogged: The Serious Problem of Overhydration in Endurance Sports. *Human Kinetics*, Champaign, IL.
- Noakes, T.D., 2012b. Commentary: role of hydration in health and exercise. *BMJ* 345, e4171.
- Noakes, T.D., Sharwood, K., Collins, M., Perkins, D.R., 2004. The dipsomania of great distance: water intoxication in an ironman triathlete. *Br. J. Sports Med.* 38, e16.
- Nose, H., Mack, G.W., Shi., X. R., 1988. Involvement of sodium retention hormones during rehydration in humans. *J. Appl. Physiol.* 65, 332–336.
- Périard, J.D., Eijssvogels, T.M.H., Daanen, H.A.M., 2021. Exercise under heat stress: thermoregulation, hydration, performance implications, and mitigation strategies. *Physiol. Rev.* 101, 1873–1979.
- Phipson, T.L., 1891a. On the cause of the odour emitted by the soil of a garden after a summer shower. *Chem. News.* 63, 179.
- Phipson, T.L., 1891b. The odor of the soil after a shower. *Sci. Am.* 64, 308.
- Pitts, G.C., Johnson, R.E., Consolazio, F.C., 1944. Work in the heat as affected by intake of water, salt and glucose. *Am. J. Physiol.* 142, 253–259.
- Polak, E.H., Provasi, J., 1992. Odor sensitivity to geosmin enantiomers. *Chem. Sen.* 17, 23–26.
- Robinson, M.M., McLennan, G.P., Thunhorst, R.L., Johnson, A.K., 1999. Interactions of the systemic and brain renin-angiotensin systems in the control of drinking and the central mediation of pressor responses. *Brain Res.* 842, 55–61.
- Rogers, P.J., Kainth, A., Smit, H.J., 2001. A drink of water can improve or impair mental performance depending on small differences in thirst. *Appetite* 36, 57–58.
- Rolls, B.J., Rolls, E.T., 1981. The control of drinking. *Br. Med. Bull.* 37, 127–130.
- Rolls, B.J., Rolls, E.T., 1982. *Thirst*. Cambridge University Press, Cambridge, UK.
- Rosinger, A.Y., 2021. The human thirst. *Sci. Am.* 325, 32–37.
- Rosner, M.H., 2008. Exercise-associated hyponatremia. *Phys. Sports Med.* 36, 55–61.
- Rowland, N.E., 2022. *Thirst and Body Fluid Regulation: From Nephron to Neuron*. Cambridge University Press, Cambridge, UK.
- Saker, P., Farrell, M.J., Adib, F.R., Egan, G.F., McKinley, M.J., Denton, D.A., 2014. Regional brain responses associated with drinking water during thirst and after its satiation. *Proc. Nat. Acad. Sci.* 111, 5379–5384.
- Sawka, M.N., Young, A.J., Francesconi, R.P., Muza, S.R., Pandolf, K.B., 1985. Thermoregulatory and blood responses during exercise at graded hypohydration levels. *J. Appl. Physiol.* 59, 1394–1401.
- Sawka, M.N., Burke, L.M., Eichner, E.R., Maughan, R.J., Montain, S.J., Stachenfeld, N.S., 2007. American College of Sports Medicine position stand. Exercise and fluid replacement. *Med. Sci. Sports Exerc.* 39, 377–390.
- Schmidt-Nielsen, K., 1979. *Desert Animals: Physiological Problems of Heat and Water*. Dover Pub Inc, NY.
- Schmit, C., Hausswirth, C., Le Meur, Y., Duffield, R., 2017. Cognitive functioning and heat strain: performance responses and protective strategies. *Sports Med.* 47, 1289–1302.
- Serwah, N., Marino, F.E., 2006. The combined effects of hydration and exercise heat stress on choice reaction time. *J. Sci. Med. Sport* 9, 157–164.
- Sharwood, K.A., Collins, M., Goedecke, J.H., Wilson, G., Noakes, T.D., 2004. Weight changes, medical complications, and performance during an ironman triathlon. *Br. J. Sports Med.* 38, 718–724.
- Sladek, C.D., McNeill, T.H., Gregg, C.M., Blair, M.L., Baggs, R.B., 1981. Vasopressin and renin response to dehydration in aged rats. *Neurobiol. Aging* 2, 293–302.
- Smit, I.P.J., Grant, C.C., Devereux, B.J., 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biol. Conserv.* 136, 85–99.
- Sobocińska, J., 1978. Gastric distention and thirst: relevance to the osmotic thirst threshold and metering of water intake. *Physiol. Behav.* 20, 497–501.
- Speedy, D.B., Noakes, T.D., Rogers, I.R., Thompson, J.M., Campbell, R.G., Kuttner, J.A., Boswell, D.R., Wright, S., Hamlin, M., 1999. Hyponatremia in ultradistance triathletes. *Med. Sci. Sports Exerc.* 31, 809–815.
- Stricker, E.M., Hoffmann, M.L., 2007. Presynaptic signals in the control of thirst, salt appetite, and vasopressin secretion. *Physiol. Behav.* 91, 404–412.
- Tam, N.D., Zouridakis, G., 2015. Differential temporal activation of oxy- and deoxy-hemodynamic signals in optical imaging using functional near-infrared spectroscopy (fNIRS). *BMC Neuro.* 16 (1), P245.
- Tan, X.R., Low, I.C.C., Byrne, C., Wang, R., Lee, J.K.W., 2021. Assessment of dehydration using body mass changes of elite marathoners in the tropics. *J. Sci. Med. Sport* 24, 806–810.
- Thomas, D.R., Cote, T.R., Lawhorne, L., Levenson, S.A., Rubenstein, L.Z., Smith, D.A., Stefanacci, R.G., Tangalos, E.G., Morley, J.E., Dehydration, C., 2008. Understanding clinical dehydration and its treatment. *JAMDA* 9, 292–301.
- Thompson, C.J., Bland, J., Burd, J., Baylis, P.H., 1986. The osmotic thresholds for thirst and vasopressin release are similar in healthy man. *Clin. Sci.* 71, 651–656.
- Valtin, H., 2002. “Drink at least eight glasses of water a day.” Really? Is there scientific evidence for “8 × 8”. *Am. J. Physiol.-Reg. Integ. Comp. Physiol.* 283, R993–R1004.
- Vargas, N.T., Chapman, C.L., Johnson, B.D., Gatchcole, R., Schlader, Z.J., 2018. Skin wettedness is an important contributor to thermal behavior during exercise and recovery. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 315, R925–R933.
- Vineis, P., Chan, Q., Khan, A., 2011. Climate change impacts on water salinity and health. *J. Epidemiol. Glob Health.* 1, 5–10.
- Vogt, B.A., 2016. Midcingulate cortex: structure, connections, homologies, functions and diseases. *J. Chem. Neuroanat.* 74, 28–46.
- Vorosmarty, C.J., Green, P., Salisbury, J., Lammers, R.B., 2000. Global water resources: vulnerability from climate change and population growth. *Science* 289, 284–288.
- Wall, B.A., Watson, G., Peiffer, J.J., Abbiss, C.R., Siegel, R., Laursen, P.B., 2015. Current hydration guidelines are erroneous: dehydration does not impair exercise performance in the heat. *Br. J. Sports Med.* 49, 1077–1083.
- Wang, C., Trongnetrunya, A., Samuel, I.B., Ding, M., Kluger, B.M., 2016. Compensatory neural activity in response to cognitive fatigue. *J. Neurosci.* 36, 3919–3924.
- Wang, G.J., Tomasi, D., Backus, W., Wang, R., Telang, F., Geliebter, A., Korner, J., Bauman, A., Fowler, J.S., Thanos, P.K., Volkow, N.D., 2008. Gastric distention activates satiety circuitry in the human brain. *NeuroIm* 39, 1824–1831.
- Wolf, A.V., 1958. *Thirst: Physiology of the Urge to Drink and Problems of Water Lack*. Charles C Thomas, Springfield, IL.
- Zimmerman, C.A., Lin, Y.C., Leib, D.E., Guo, L., Huey, E.L., Daly, G.E., Chen, Y., Knight, Z.A., 2016. Thirst neurons anticipate the homeostatic consequences of eating and drinking. *Nature* 537, 680–684.
- Zouhal, H., Groussard, C., Minter, G., Vincent, S., Cretual, A., Gratas-Delamarche, A., Delamarche, P., Noakes, T.D., 2011. Inverse relationship between percentage body weight change and finishing time in 643 forty-two-kilometre marathon runners. *Br. J. Sports Med.* 45, 1101–1105.
- Zurovsky, Y., Shkolnik, A., Ovadia, M., 1984. Conservation of blood plasma fluids in hamadryas baboons after thermal dehydration. *J. Appl. Physiol.* 57, 768–771.