



# The evolution of wetness perception: A comparison of arachnid, insect and human models

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## ABSTRACT

Hygroreceptors are a type of humidity sensor that have been identified in several invertebrate classes including *Insecta* and *Arachnida*. While their structure has been well researched, the nature of the mechanisms behind their function is debated as being either mechanical, evaporative, or psychrometric in insects and potentially also olfactory in arachnids. There is evidence that can be used to support or oppose each of these concepts, which also invites the possibility of multiple unified mechanisms occurring together. The integration of multiple sensory modalities has also formed the foundation of wetness perception in humans, led by thermal and tactile cues with supplementary information from vision and sound. These inputs are integrated by a vast neural network in the brain, which also occurs on a smaller scale in insects and arachnids. It is possible that as cerebral capacity increased throughout human evolution, this facilitated a preferable system of wetness perception via multisensory integration and rendered hygroreceptors obsolete. While this cerebral development hypothesis is only speculative, it gives a framework for further investigation. Additional research needs to be conducted to correctly classify hygroreceptor types in invertebrates and their relative prevalence before evolutionary associations can be made with vertebrate species. This integratory premise also applies to the human system, as knowing the relative contribution and compounding effects of each sensory modality on wetness perception will aid the overall understanding of the system and help to uncover the evolutionary development pathways underpinning each sense.

## 1. Introduction

From the first *Homo sapiens* to modern day humans, we have all been subject to a regular cycle of changing seasons and environments. Whether this was our nomadic ancestors suffering from cracked, dry skin in the dead of winter or modern travel introducing us to the warm muggy nights following the wet season, all of these perceptions are highly reliant on humidity and wetness sensations. Our ability to sense humidity and wetness on the skin gives life to our perceptions, bringing a vivid new perspective that enhances the way we interpret the world around us. However, it could be argued that this sensory experience is taken for granted. The reason is that humans do not seem to possess hygroreceptors; specific receptors for wetness sensations (Clark and Edholm, 1985). Despite their apparent absence in humans these receptors have been identified in several invertebrates, with research focussing on insects such as the fruit fly, *Drosophila melanogaster* (Enjin et al., 2016), stick insects, *Carausius morosus* (Tichy, 1987), and honeybees, *Apis mellifica* (Altner and Loftus, 1985). This hygroreceptor bearing group has undergone a divergent evolution from their

vertebrate counterparts, and both the reasons why and the underlying sensory mechanisms are currently unexplained. It is this issue which this review aims to address, by proposing morphological, behavioural and environmental differences that may have acted as adaptive stressors in the evolutionary process.

## 2. Hygroreception

The ability of certain animals to react to changes in air humidity was first detailed over one hundred years ago (Shelford and Deere, 1913). The mechanism behind this response then began to be isolated, first noted almost forty years later by an entomologist who described a type of 'moist air receptor' in the antennae of the honey bee, *A. mellifica* (Altner and Loftus, 1985; Lacher, 1964). Their dry counterparts were subsequently identified, and an antagonistic relationship between the two was established. Both wet and dry hygrometers are housed in hygroreceptive sensilla, which appear as small fixed styloconical protrusions on insect antennae or in small pits on the cuticle surface. The cell bodies lay below the sensilla surface, with unbranched dendritic

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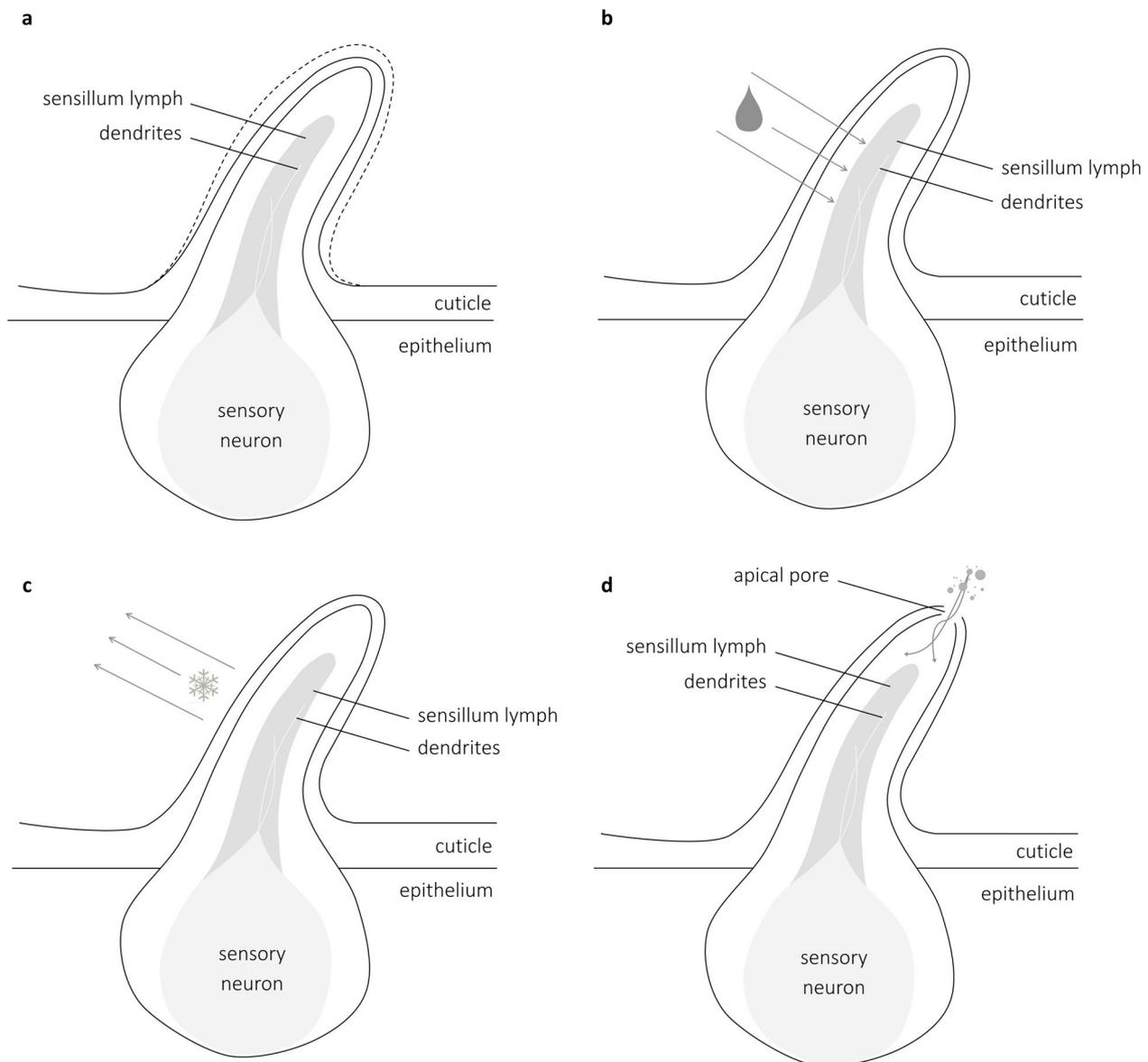
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**Fig. 1.** A series of proposed hygroreceptor concepts. **a** – ‘mechanical hygrometer’ found in insects, which responds to cuticle expansion or contraction due to changes in humidity; **b** – ‘evaporimeter’ found in insects, which quantifies humidity based on the rate of moisture evaporation and the resultant change in concentration of sensillum lymph electrolytes; **c** – ‘psychrometer’ found in insects, which responds to magnitude of cooling cues that result from moisture evaporation; **d** – ‘olfactory hygrometer’ found in arachnids, which responds to both moisture and vapour molecules entering the apical pore and reacting with dendrite membranes.

segments extending into the lumen of the protruding sensilla. This lumen also contains a lymph reservoir, which is similarly connected to a larger lymphatic system below the sensilla surface (Steinbrecht and Müller, 1991). Finally, the sensilla also contain a network of thermo-receptive cold neurons, which along with the wet and dry hygrometers form a sensory triad (Altner et al., 1983). The functional mechanism behind the components of hygroreceptive sensilla, or hygroreceptors, has not yet been confirmed. There are currently four central concepts which can begin to explain the mechanism, with the first three models relating to insects and the final relating to arachnids. These can each be applied to existing species but require additional research and refinement. It is also a possibility that the concepts can be integrated, as multiple hygroreceptor types seem to occur in the same species (Liu et al., 2007).

### 2.1. Mechanical hygrometer

The first model assumes a type of mechanical hygrometer, in

which humidity levels can be inferred by the shrinking and swelling of the hygroreceptive sensilla cuticle due to moisture transfer (Fig. 1a) (Tichy and Kallina, 2010). This mechanism is supported by the morphology of the cuticle, which is highly innervated such that sensory terminals are easily deformed by humidity-induced geometric changes in membrane structure. This concept has been validated by the physical manipulation of sensilla cuticles in crickets, *Gryllus bimaculatus*, fruit flies, *D. melanogaster*, and cockroaches, *Periplaneta americana*, which results in neural stimulation analogous to that induced by humidity (Itoh et al., 1984; Liu et al., 2007; Yokohari and Tateda, 1976). However, when applying similar investigatory methods in the honey bee, *A. mellifica*, and physically monitoring mechanical changes in situ at the apex of the sensilla, there was no notable difference in cuticle morphology changes (Resch et al., 1998). This being said, apical stimulations using direct pressure as opposed to tangential movement in the cabbage moth, *Mamestra brassicae*, were successful (Becker, 1978). This implies that the structure and corresponding sensitivity may vary between species and could provide further evidence towards the

integration of multiple concepts.

## 2.2. Evaporimeter

The second model assumes the hygroreceptor to be a form of evaporimeter which quantifies the level of external humidity based on the rate of moisture evaporation from the sensillum cuticle and the resultant change in concentration of sensillum lymph electrolytes (Fig. 1b) (Steinbrecht and Müller, 1991). It has been proposed that there are small channels leading from the main internal lymphatic cavity within the sensilla to the exterior cuticle which pass via the dendrite membranes. This would provide an avenue for moisture to reach the surface for evaporation, and would additionally allow the continuous monitoring of ions within the lymph fluid (Tichy and Kallina, 2013). This has been identified in the silk moth, *Bombyx mori*, in which critically low external humidity has been seen to result in reversible morphological changes to dendrite terminals, thought to be a protective mechanism against desiccation damage (Steinbrecht and Müller, 1991). However, it should be noted that for this system to work effectively, the ions, viscosity and flow rate of lymph will need to be kept within a suitable homeostatic range to fulfil other functions within the sensilla and wider organism (Tichy and Kallina, 2013). It would therefore be a prominent area of further research to establish the extent of lymph characteristic changes at different humidities. These lymphatic changes may affect other bodily systems to varying extents across different species, which may limit the viability of the model to only a small number of taxa that can tolerate such large-scale systemic changes.

## 2.3. Psychrometer

The third concept focusses on psychrometer ability. These infer humidity levels based on the cooling cues that result from moisture evaporation, which will depend on the humidity gradient between organism and environment (Fig. 1c). In this case, the aforementioned wet and dry hygrometers act predominantly as thermoreceptors, analogous to wet-bulb and dry-bulb thermometers respectively. Studies in the cockroach, *P. americana*, have shown that the temperature changes involved are sufficient to validate the psychrometer theory in slow continuous test conditions (Tichy and Kallina, 2013). It could be hypothesised that this is the closest sensory mechanism to that which drives human wetness perceptions, as these both rely heavily on cooling cues (Filingeri et al., 2014). However, humans do not have specific isolated sensilla upon which they experience such sensations. Instead, their sensations may link to the wider organism morphology, as the absence of an exoskeleton and a large skin surface area can facilitate a much larger number of receptors with a greater spatial representation, potentially providing a preferential sensory experience.

## 2.4. Olfactory hygrometer

The fourth and final concept has been identified in wandering spiders of the *Cupiennius* genus, and suggests that hygroreception is effectively superimposed on olfactory chemoreceptors (Fig. 1d). The mechanism appears to be similar to that of insects, with an antagonistic pair of wet and dry cells positioned in receptive sensilla on the cuticular surface (Ehn and Tichy, 1994). However, sensilla in spiders have a pore at the apex which allows vapours to enter and reach dendritic membranes (Fölix, 1970). If this pore is blocked, both olfactory and hygrometry responses are significantly diminished, implying some level of interaction (Blumenthal, 1935). Furthermore, the hygroreceptors can be excited by highly pungent, volatile or polar vapours typically associated with olfaction (Ehn and Tichy, 1994). Despite these associations the olfactory hygrometer premise is not favoured, with many citing the stark contrast between the fine structure of insect hygroreceptive sensilla and the more robust, coarser arachnid olfactory sensilla. It should

also be noted that the hygroscopic properties of the pore may vary between arachnid species such that the relative relationship with interacting compounds may be affected (Steinbrecht and Müller, 1991). As there is such a high structural diversity in sensilla both within and between invertebrate species (Tichy and Gingl, 2001), this suggests that there is likely to be a range of transduction systems and again reinforces the possibility of multiple interacting mechanisms.

As is the case in the majority of the aforementioned research, variables in a natural environment would differ considerably from research conditions. For example, magnitude, direction and rate of changes in temperature, ambient humidity and air flow may affect results, as would the physical activity of the organism. This was illustrated in *D. melanogaster*, which were allowed to move between several locations of differing humidity levels, with the location in which they settled being considered preferable. This firstly demonstrated the ability of hygroreceptors to quantitatively assess humidity, as opposed to just inferring a presence or absence, and also the importance of hygroreceptors in influencing thermal behaviour. However, as well as highlighting the complexity of the quantitative system, it also showed that the preferred humidity condition related to the origin of the *D. melanogaster*, with each test population preferring the humidity level most analogous to that found in its native climate (Enjin et al., 2016). While this implies a highly sophisticated mechanism underpinned by a complex neural network, it also highlights the flexibility of the system and the role it may have played in allopatric speciation throughout evolution.

## 3. Multisensory integration in humans

While the sensation of wetness has been a crucial evolutionary factor throughout the animal kingdom across thousands of years, hygroreceptors have not been found in humans and are not documented in other mammals (Filingeri, 2016; Filingeri and Havenith, 2017). Several alternative strategies for sensing wetness in humans have been proposed. The first investigations were conducted by Bentley over a century ago, who hypothesised that a sensory blending phenomenon was the primary driver behind the ability to sense wetness (Bentley, 1900). This is effectively focussed on a combination of thermal and tactile inputs, with the former later being identified as the primary driver in wetness perception (Filingeri et al., 2014). In addition to thermal and tactile inputs, some additional supplementary pathways have been identified, although the relative magnitude of each input has not been fully investigated. This includes visual cues, such as the visible formation of perspiration droplets on the skin, the darkening of clothes that have been in contact with a wet stimulus, or the glossy sheen and additional weight of damp hair (Bergmann Tiest et al., 2012; Sawayama et al., 2017). Additionally, the auditory cortex of the brain can process and associate certain frequencies or patterns of sounds to wetness, such as when comparing the interactions between dry and wet hands (Jousmäki and Hari, 1998). It could be argued that the primary stimuli of thermal and tactile inputs are an inherent perceptible ability, whereas the inputs provided by audio and visual cues are supplementary learned behaviours (Filingeri and Havenith, 2018).

### 3.1. Bayesian multisensory integration

With such an extensive neural network in place, a multisensory integration mechanism must exist across the nervous system. There are several hypotheses that propose mechanisms behind this, with one of the most widely accepted following a Bayesian approach. This effectively states that the brain is able to construct a feasible external scenario from perceived stimuli, and actively updates the probability of it occurring based on the addition and weighted integration of new information (Deneve and Pouget, 2004; Fetsch et al., 2013). For example, an individual may hear the patter of rain beginning to fall, feel a cold sensation on their arm and then look at the area to see if water is

present. This process from the initial receipt of signals to the formation of a complete and coherent representation has been likened to that of computer modelling (Pouget et al., 2002). There are several branches of research that may contribute to multisensory integration via the Bayesian approach. These typically rely on the premise of crossmodal perception, in which there are direct interactions between multiple sensory modalities. For example, it has been proposed that some multisensory neurons which serve different sensory pathways, such as those in the visual and vestibular systems, are capable of almost optimal stimuli integration via the linear sub-additive summation of their external inputs. This is consistent with the computational modelling theories that have been used to investigate the likelihood of Bayesian inference. However, it is restricted by the fact that small fluctuations in stimuli reliability can alter the respective weights that neurons use to prioritise information, and so may only partially contribute to the construction of a fully unified percept (Angelaki et al., 2009).

### 3.2. Multimodal convergence

An alternative to Bayesian multisensory integration is that of multimodal convergence, which is also a type of crossmodal perception. When multiple sensory modalities provide the same information pertaining to a particular stimulus, they are deemed to be convergent and therefore can be considered as a reliable representation of the outside world. Additionally, the convergence of multiple modalities may account for their ability to influence each other in their apparent unimodal states, such as by dampening or amplifying them to produce a dominant modality that makes the most sense of a situation (Driver and Spence, 2000). For example, the ventriloquism effect shows the convergence of speech and sound, with vision being the overriding component used in determining the location of the audio source (Bertelson, 1999).

### 3.3. Correlation detection

A similar premise to that of convergence is correlation detection, which again is a form of crossmodal perception. This approach factors in all sensory modalities, but selectively combines data from those sources that seem to correlate the most effectively. It is an adaptive and dynamic process, which takes into account the temporal lags between different sensory pathways and diffuses spatiotemporal conflicts in order to promote sensory synchronisation (Parise and Ernst, 2016). It is possible that research by Beauchamp supports this theory, as he was able to identify some neural pathways that were previously thought to be exclusive to one modality to be weakly active or below baseline resting voltage in response to stimuli from other modalities. This dampening or amplifying effect may assist in the aforementioned selective combination of stimuli, but is notably similar to the modulating effects previously associated with multimodal convergences (Beauchamp, 2005). Instead of regarding these as separate entities, it is perhaps more likely that the Bayesian approach integrates both convergent and correlative stimulation pathways and is able to modulate these accordingly.

### 3.4. Visual dominance theory

An additional model is the visual dominance theory. As the name suggests, this assumes that vision becomes the dominant modality in all perceptive scenarios in which it is available (Shams et al., 2000; Witten and Knudsen, 2005). Research into this is predominantly focussed on the interaction of visual and auditory stimuli, but has also been seen to apply in haptic situations (Botvinick and Cohen, 1998; Gori et al., 2008). The theory also draws upon the previously mentioned ventriloquism effect, citing the fact that visual is always the dominant modality as opposed to being situationally determined as proposed by the multimodal convergence hypothesis (Bertelson, 1999). However,

this has been contradicted by the double flash illusion, in which a series of visual flashes and auditory beeps were presented to participants, who were instructed to count them. When flashes outnumbered beeps, these were generally perceived correctly. However, when beeps outnumbered flashes, many participants overestimated the number of flashes such that they were equal to beeps. This effectively shows that they had experienced illusionary visual stimuli, and therefore shows that auditory stimuli was more prevalent in this case (Shams et al., 2000).

### 3.5. Intersensory bias hypothesis

Finally, the intersensory bias hypothesis proposed by Welch and Warren suggests that the most appropriate modality in any given scenario will form the dominant neural input. However, this is also based somewhat on the quality of the modality, as a stimulus of greater magnitude can override a poorer quality stimulus that may have been deemed more task appropriate (Welch and Warren, 1980). For example, when attempting a conversation in a loud environment such as a concert stadium, visual lipreading can take precedence over the auditory cues that would typically be used, as it is a stimulus of a greater quality and magnitude (Sumby and Pollack, 1954). This is an example of the inverse effectiveness rule that is commonly associated with multisensory integration, in which the degree of integration is inversely proportional to the ambiguity of the stimulus (Holmes, 2007). This relationship has recently been highlighted by Kuang and Zhang, who were able to influence ambiguous directional instructions using previously conditioned scent pairings such as banana with leftwards motion and fennel with rightwards (Kuang and Zhang, 2014). Despite all central integration theories providing supporting evidence, very few of them focus directly on wetness perception or the modalities that have the greatest influence on it. It is therefore a key area of research to be further investigated, both in determining the importance of each modality in human wetness perception and establishing how they interact to provide a fully integrated and coherent experience of wet stimuli.

## 4. Multisensory integration in invertebrates

The presence and extent of each sensory modality varies significantly across invertebrate species, including insects and arachnids. As can be expected, the typical brain capacity of invertebrates is significantly smaller than that of humans, with genera such as *Drosophila* having less than 0.1 million neurons (Henry et al., 2012) ranging up to *Apis* species with almost 1 million neurons (Menzel and Giurfa, 2001). While these appear to be large numbers, they are tiny in comparison to the vast networks found in human brains that contain roughly 86 billion neurons (Azevedo et al., 2009). Additionally, the invertebrate brains themselves vary in structure and function. For example, different species of spider have evolved varying behavioural approaches to predation when subject to different environmental stressors, which is reflected in their brain structure. Those that build webs to trap prey are more sensitive to inputs such as air flow and humidity, which form part of location choice, and to tactile inputs such as vibrations that serve as alerts when prey has been successfully trapped. These spiders have larger corresponding ganglia in the posterior of the brain compared to those which have evolved to hunt with vision, which instead prioritise ocular pathways (Culin et al., 2018; Fölix, 1996; Long, 2016). This shows that there is a variation in potential hygroscopic ability and methods of cortical transduction and integration.

Further structural differences can be seen in insect brains, which are divided into three lobes - the protocerebrum, the deutocerebrum, and the tritocerebrum. The first lobe is where visual transduction occurs. The second lobe is most relevant to hygroreception as it innervates the antennae and processes information from them (Boyan et al., 2003). Along with information regarding humidity, this also includes olfactory, gustative, thermal and tactile cues which may supplement

information regarding humidity (Schneider, 1963). The third lobe is responsible for the integration of information from the two other lobes, and also serves as a transducer for sensory information from the visceral nervous system. Interestingly, this visceral system is almost considered to be a secondary brain as it is responsible for so many vital organ functions and intrinsic insect behaviours, some of which may relate to actions based on humidity (Bitsch and Bitsch, 2010). This gives further evidence to the importance of multisensory integration in invertebrates, even though it is on a significantly smaller scale than humans.

## 5. Evolutionary drivers

### 5.1. Insects and arachnids

While there is a clear divide between hygroreceptor bearing and devoid species, it should be noted that the evolutionary stressors shaping their hygroreceptive abilities have significantly varied. This can be regarded in broader terms, such as the main function of hygroreception, and also in more specific cases, such as the changes resulting from hygroreception in different environments. In both insects and arachnids one of the main functions of hygroreception is to maintain body water balance within optimal limits, and hence ensure correct physiological functioning across the body (Arlian and Veselica, 1979; Canals et al., 2015). While this sounds somewhat vague, the ability to correctly manage water balance affects many aspects of the organisms' lives and can greatly influence habitat choice. For example, water balance underpins the ability of insects to metabolise food, maintain cell functions, excrete waste materials and control cuticle permeability in different environments; if not done correctly this can result in death within a matter of hours (Arlian and Veselica, 1979). Similarly, wolf spiders of the genus *Hygrolycosa* are endemic to habitats with a highly specific humidity range, and exhibit behavioural changes to enforce this environmental preference and help maintain water balance (Dahl, 1908).

Hygroreception is also a critical factor in breeding rituals. For example, some insect species have been shown to choose their habitats and egg laying locations based on humidity, such as in the mosquito, *Aedes aegypti*. Additionally, fluctuations in humidity can interfere with larval cycles. If insects could not sense and respond appropriately to humidity differences, it is likely that they would either not survive to a breeding age or fail to successfully mate (Pedroso de Almeida Costa et al., 2006). In pollinating insects such as bees, hygroreception also affects pollination ecology. For example, the water evaporating from a flower is proportional to its nectar concentration, and so the associated humidity gradient can be considered an indicator of floral profitability. If this mechanism failed and successful pollinations declined, there would then be a greater impact on the wider ecosystem and ramifications in other species at trophic levels across the food web (von Arx, 2013). Therefore, it is not just the insects themselves that rely on hygroreceptors. This would have been critical as the Earth changed and forced natural selection pressures on insects and all other related flora and fauna.

### 5.2. Humans

In humans, the ability to sense wetness plays a role in both comfort and survival. For example, physical skin wetness and the associated perceptions have been shown to influence thermal behaviour during exercise and recovery conditions. This helps to maintain the body within the thermal neutral zone such that comfort is improved and less energy is required for thermal balance (Vargas et al., 2018). This link between wetness perception and comfort is prevalent from an early age, such as in nursing infants, where the use of damp clothes has been shown to trigger skin discomfort such that infants seek assistance from carers (Costa, 2011; Prasad et al., 2003).

On an autonomic level, this can be summarised using homeostatic

models. For example, humans must balance their bodily water content such that they maintain ion concentrations in blood, lymph, endocrine and other systems to maintain whole body functions (Vokes, 1987). As wetness perception is primarily controlled by cold thermal inputs (Filingeri et al., 2014), the role of survival can also be extended to the ability to sense temperatures. In terms of conscious survival this may be associated with the ability of humans to choose their habitats and avoid environmentally exacerbated illnesses, as can be seen in extant primate species (Hill et al., 2004). Environmental awareness applies both in short and long term contexts and was especially important during nomadic periods. Itinerant populations relied on the avoidance of immediate danger associated with adverse weather conditions, such as landslides and flooding. However, they also relied on water for their long term survival, as it was essential in daily life for drinking, food preparation, hygiene and even primitive forms of animal husbandry, all practices which are reflected in modern populations (Robinson, 2017).

The ability to sense rain is also noted in extant humans who, like their ancestors, detect rain via olfaction (Polak and Provasi, 1992). The smell of rain is described as being distinctively musty, organic and earthy, and is referred to as petrichor (Bear and Thomas, 1964). It is comprised predominantly of the compound geosmin, which is a metabolite of certain microbial, fungal and algal species (Polak and Provasi, 1992). Geosmin is produced throughout these species' lives but leaches into the soil in larger quantities upon death (Liato and Aider, 2017). It is subsequently released from soil upon disturbance, such as that caused by rain, and so is frequently associated with wet, humid environments (Bear and Thomas, 1964). Geosmin is typically mixed with other volatile organic compounds trapped in soil pockets to produce the characteristic petrichor odour (Jiang et al., 2018). Current studies estimate human sensitivity to the naturally occurring enantiomer of geosmin to be as low as 9.5 parts per trillion (Polak and Provasi, 1992), which gives further evidence towards the likely absence of hygroreceptors in modern humans given that other highly sensitive alternative functions exist.

Human wetness perception also plays a role in evolutionary aspects that assist with ease or even enjoyment of life. For example, it has been noted that the ability to perceive wetness plays a significant role in precision grip and object interaction (Augurelle, 2002). The first species reported to have manipulated objects in their environment was *Homo habilis*, which existed between 1.8 and 2.3 million years ago (Wood, 2014). They were able to use semi-sophisticated stone tools for tasks such as cooking, hunting and construction (Carroll, 2003). This species was the successor of *Australopithecus afarensis*, which had a smaller cerebral rubicon that is characteristic of the genus. While the boundary in brain size between the genera is disputed at around 600 cm<sup>3</sup> (Wood and Collard, 1999), this still gives further evidence to the likelihood of a multisensory integration mechanism that relies heavily on complex neural systems found in higher capacity brains.

This allows the introduction of a speculative cerebral development hypothesis, highlighting the potential coevolution between cerebral development and the multisensory integration of wetness. As brain capacity increased and a larger range of senses could be integrated to form a sophisticated and efficient perceptual network, this may have been preferable to hygroreceptors such that they became obsolete. Consequently, they do not appear to exist in modern humans (Clark and Edholm, 1985), or may have been rendered vestigial like the appendix is today. As insect brains are much smaller, such a thing would not have been feasible and therefore hygroreceptors have prevailed to this day. Further evidence can be seen in the comparison to mammals, which have larger brain sizes and also seem to lack hygroreceptors. However, there are some other animals that lack hygroreceptors and still have small brains such as the free living round worm, *Caenorhabditis elegans*, but this seems to be an exception (Filingeri et al., 2014).

The larger capacity of *H. sapiens* brains compared with their evolutionary precursors and other coexisting mammal species may have also led to the conscious and more logical interpretation of stimuli, and

the ability to learn certain behaviours and cues linked to wetness perceptions (Boesch, 2007). This opens the field up to the long-argued nature versus nurture debate. In the case of humans, there are likely to be integral natural instincts that are a part of survival, which will likely be mirrored in other mammals, and also learned behaviours which focus more on supplemental enjoyment and experience (Eisenberg, 2004; Stotz, 2008). For example, from birth babies will cry when they experience wetness at the interface between their skin and clothes in sensitive areas. While this will initially only cause forms of minor discomfort, there is an underlying mechanism which induces the crying to reduce the risk of further problems such as contact dermatitis (Prasad et al., 2003).

On the other hand, there may be learned behaviours in the perception of wetness such as the darkening of fabric or shine on a surface once it has become wet, which can be observed from birth (Sawayama et al., 2017). However, the majority of mechanisms cannot easily be attributed to either nature or nurture, and are likely to be a mixture of multiple concepts (Eisenberg, 2004; Stotz, 2008). For example, when cold and warm liquids are poured at identical rates into identical beakers, over 70% of individuals could correctly identify which corresponded to each temperature despite no prior knowledge of this ability (Velasco et al., 2013). Would this have been a subconsciously learned identification mechanism, or is there an integral ability present from birth that recognises changes in liquid pitch and tone? There are several sensory experiences and appropriate examples that would do well in answering such questions, but the most significant issue is in infant communication, which centres around the conveying of needs as opposed to the supplying of information (Grosse et al., 2010).

### 5.3. Common ancestry

Another aspect to consider regarding the evolutionary pathway behind hygroreceptors is their presence or absence in a common ancestor. The shared ancestor between vertebrates such as *Mammalia* and arthropods including *Insecta* and *Arachnida* is termed the urbilaterian. In fact, this is the last common ancestor of all animals with a bilateral symmetry, but is currently only hypothesised as physical evidence has not been recorded (Bailly et al., 2013). Two main theories surround the urbilaterian. The first is the most widely accepted, and is termed the 'complex urbilaterian hypothesis' (Manuel, 2009), whereas the second is termed the 'planuloïd urbilaterian hypothesis' (Hejnol and Martindale, 2008). These are effectively the extremes of its potential existence, with the former assuming an organism with a developed brain, nervous system, circulatory system, digestive tract and motility system (Manuel, 2009). The latter suggests a more basic life form, including a blind digestive tract, diffuse nervous system and limited sensory or motility organs (Hejnol and Martindale, 2008).

In the context of hygroreception, the most important aspect to note is the hypothesised presence of appendages in the complex urbilaterian hypothesis. This would include the development of antennae, which are used in many sensory processes including hygroreception (Panganiban et al., 2002). It could therefore be hypothesised that hygroreceptors, even in a primitive form, were present in these organisms and have subsequently been lost throughout human evolution. This further supports the proposed cerebral development hypothesis, showing the potential relationship between the development of the brain and associated multisensory integration abilities with the loss of the hygroreceptor, both in humans and other mammals. Furthermore, genetic analysis has shown similarities in key expressive genes in embryonic brain development between protostomes and deuterostomes. This implies a monophyletic origin such that brains at this early stage were highly similar, implying that there was not sufficient capacity for other sensory strategies to have yet evolved as an alternative to hygroreceptors (Bailly et al., 2013; Sprecher and Reichert, 2003).

### 5.4. Future evolutionary mechanisms

We are likely to experience a slowed physiological evolution of hygroreceptors in the coming centuries, especially in more developed countries. This is mostly due to the fact that genetic anomalies that would have previously been subject to natural selection are now more easily and readily treatable, leading to greater recovery and survivability such that the genes can be passed on. For example, if a mutation in the wetness sensing pathways of early hominids led to an improper habitat choice, for instance a cold humid dwelling, this may create health issues such as respiratory infections. While this would have greatly compromised immune systems or even resulted in death, modern medicine could easily resolve issues such that the affected individuals could survive to reproduce, passing on their mutated genes and reducing the influence of natural selection (Torrance, 2009). Additionally, modern advances in many other aspects of our daily lives make us less subject to environmental stressors that may emphasise certain biological adaptations, further slowing down the rate of physiological evolution (Stock, 2003). It is noteworthy that some advances may slightly promote evolution. For example, growing populations increases the likelihood that mutations are introduced, both adverse and beneficial, and the ease of global travel increases worldwide genetic distribution. However, any true biological adaptations would still be unlikely unless they represent highly significant changes. As there is a large diversity of environments, wealth and social systems across the globe, there is potential for these extreme physiological changes and even speciation to begin, but this is still improbable and would take several hundreds of years, relying on a stable continuous change and spread to become established (Templeton, 2010).

## 6. Conclusions

It is proposed that four types of hygroreceptors have evolved within extant *Insecta* and *Arachnida* species, existing independently or as an integrated hygroreceptive system. In these species the exact nature of the hygroreceptors depends on their exposure to environmental stressors and the associated morphological and behavioural adaptations developed throughout evolutionary history. This differs to humans, in which the multisensory integration of different sensory modalities is highly reliant on the large cerebral capacity of the species. It is therefore likely that increases in brain size throughout human evolution have allowed the development of a more sophisticated and efficient neurosensory network as opposed to the predominant use of hygroreceptors, which is seen in invertebrates and may have been retained from our last common ancestor, the urbilaterian. Further evolution of the human mechanism by natural selection is likely to be reduced due to the lessened physiological stressors and increased relative survivability of modern life. However, further research into both invertebrate hygroreceptor types and human multisensory integration is required before a more detailed evolutionary pathway, both past and future, can be predicted.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2019.102412>.

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