Printzlau, F. A. B., Bourganos, A., Fukuda, K., & Mack, M. L. (2025). Learning-dependent modulation of working memory. *Memory & Cognition*, 1–14.
Sligte, I. G., Scholte, H. S., & Lamme, V. (2009). V4 activity predicts the strength of visual short-term memory representations. *Journal of Neuroscience*, *29*(23), 7432–7438.
Supèr, H., Spekreijse, H., & Lamme, V. A. F. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, *4*(3), 304–310.
Vogel, E. K., Woodman, G. F., & Luck, S. J. (2006). The time course of consolidation in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *32*(6), 1436–1451.
Xu, Y. (2023). Parietal-driven visual working memory representation in occipito-temporal cortex. *Current Biology*, *33*(20), 4516–4523.e4515.
Zhou, C., Lorist, M. M., & Mathôt, S. (2022). Categorical bias as a crucial parameter in visual working memory: The effect of memory load and retention interval. *Cortex*, *154*, 311–321.

Evolution, time, and the observer

Heather Browning[a]* and Walter Veit[b,c]

[a]Department of Philosophy, University of Southampton, Southampton, UK; [b]Department of Philosophy, University of Reading, Reading, UK and [c]Munich Center for Mathematical Philosophy, Ludwig Maximilian University of Munich, Munich, Germany
drheatherbrowning@gmail.com
wrwveit@gmail.com

*Corresponding author.

doi:10.1017/S0140525X25102926, e170

Abstract

Fleming and Michel propose that conscious vision evolved as a result of the water-to-land transition of animal life, enabling what they call "reality monitoring." Here, we challenge their account by drawing on evolutionary arguments and the sensory capacities of aquatic life. Consciousness, we suggest, may have deeper evolutionary roots with significant roles for "slow" decision-making.

The target article by Fleming and Michel offers a novel evolutionary account of conscious vision, arguing that it emerged during the transition from water to land due to the broader sensory horizons. From the role of conscious vision in model-based learning and action selection, they develop a theory of consciousness facilitating the higher order process of "reality monitoring": "the capacity to determine whether internal signals reflect external reality or endogenous activity uncoupled from sensory input".

While we find their arguments for the role of consciousness in reality monitoring compelling, we worry about the limitations that come from an excessive focus on vision. While F&M acknowledge that they are really just offering an account of *visual consciousness*, the inferences and theorising at times suggest otherwise. While they recognise that there is more to consciousness, including other types of perceptual processing and affective states, they are addressed only incidentally.

In this commentary, we'll examine how these factors may challenge their evolutionary proposal, requiring one to think about the range of activities and perceptual experiences available to many animals. In particular, we'd like to highlight two limitations of the account presented. The first is the claim that visual consciousness is too slow for immediate action selection. The second is the possibility for reality monitoring across a far wider range of perceptual modalities, which may undermine the significance of the transition from water to land.

In arguing that conscious visual processing is too slow to guide immediate action selection, F&M have assembled a rich and convincing collection of empirical evidence about the speed of visual consciousness. As they note, Dennett & Kinsbourne (1992) have argued in their influential "Time and the observer" that there is a difference between the time a mental state occurs and the time of an event represented by the mental state. From an evolutionary perspective, F&M's insistence that conscious vision is too slow for rapid actions, such as fleeing from an ambush predator, or responding to fast-moving prey is almost certainly correct. However, we think they over-emphasise the importance of these specific rapid actions within an animal's entire behavioural repertoire. Part of the problem here is the very nature of experiments on vision, which are almost always highly restrictive, limiting options, time, and conflicting variables for human and animal subjects (Veit 2023). Many decisions made by animals occur at slower speeds: e.g. moving between foraging patches, finding shelter, interacting with conspecifics. These behaviours could be guided by visual input without the need for a rapid response. It is therefore unclear why visual consciousness needs to explain something beyond traditional action selection of this type. Indeed, there is already a lot of evidence that conscious vision can help animals to survey environments and build mental models of the location of key resources, and use this to guide behaviour over longer timescales.

Second, there is no reason to think that reality monitoring is necessarily or uniquely visual. F&M briefly note at the end of the paper that the same abilities could indeed arise for other sensory modalities, which could be the subject of other similar projects. While we appreciate that they deliberately focused on vision alone, we think some of the conclusions are weakened when this possibility is explored seriously. Animals, particularly aquatic animals, have a wide range of perceptual capacities beyond vision. These include hearing, lateral line vibration sensing, electroreception, and chemoreception. These modalities give the animals a far broader underwater sensory horizon than vision does, and therefore, if the sensory horizon is as important as the authors argue, they are highly likely to contribute to model-based learning and behavioural control leading to reality monitoring capacities and, presumably, consciousness.

Both of these give reasons to think the transition to land may not be as significant as the authors seem to imply. Slower-scale visual processing could play a role in much of the behaviour of aquatic animals, who could also be surveying their environments to gather information to feed into decision-making. As they note, "the cluttered terrestrial-like environments of coral reefs and tide pools may be unusually rich environments for the evolution of model-based visual cognition". Additionally, some fish rely on visual processing for complex decisions: cleaner fish will visually detect parasites and even recognize marks on their own body with a mirror (Kohda et al., 2022). Pelagic fish who rely on stalking and ambush tactics rather than pursuit, such as many sharks (Munroe, Meyer, & Heithaus, 2022), could reasonably use conscious visual input to guide their decision-making while hunting. Widening the scope of perceptual modalities also means that even pelagic fishes, who may not often rely on vision, could still have complex mental models that require real-time reality monitoring across other senses. Even if it were true that these types of aquatic animals specifically lack conscious vision, the likelihood of them having conscious processing across the other modalities decreases the significance of this difference. While the Cartesian theatre will always remain a tempting model, it is one we need to continue to resist (Dennett & Kinsbourne, 1992), and this includes its emphasis on vision (Veit, 2022a). While vision may be central to human conscious experience, the evolutionary history of consciousness is likely to be much older (Veit, 2022b).

Financial support. No funding to report.

Competing interests. None.

References

Dennett, D. C., & Kinsbourne, M. (1992). Time and the observer: The where and when of consciousness in the brain. *Behavioral and Brain Sciences*, *15*(2), 183–201.

Kohda, M., Sogawa, S., Jordan, A. L., Kubo, N., Awata, S., Satoh, S., Kobayashi, T., Fujita, A., & Bshary, R. (2022). Further evidence for the capacity of mirror self-recognition in cleaner fish and the significance of ecologically relevant marks. *PLoS Biol*, *20*(2), e3001529.

Munroe, S., Meyer, L., & Heithaus, M. R. (2022). Elasmobranch foraging strategies and tactics. In *Biology of sharks and their relatives* (pp. 323–355). CRC Press.

Veit, W. (2022a). The origins of consciousness or the war of the five dimensions. *Biological Theory*, *17*, 276–291. https://doi.org/10.1007/s13752-022-00408-y

Veit, W. (2022b). Complexity and the evolution of consciousness. *Biological Theory*, *18*, 175–190. https://doi.org/10.1007/s13752-022-00407-z

Veit, W. (2023). *A philosophy for the science of animal consciousness*. Routledge.

Multisensory horizon

Tony Cheng[a]* and Philip Tseng[b]

[a]Waseda Institute for Advanced Study, Waseda University, Tokyo, Japan and [b]Department of Psychology, National Taiwan University, Taipei, Taiwan
h.cheng.12@alumni.ucl.ac.uk
ptseng@ntu.edu.tw

*Corresponding author.

doi:10.1017/S0140525X2510280X, e171

Abstract

This comment critiques the concept of "sensory horizon" for focussing narrowly on vision, overlooking aquatic animals' rich multisensory integration. Aquatic vertebrates possess sophisticated auditory, mechanosensory, olfactory, and tactile systems that support essential behaviours. Evidence indicates that multisensory integration evolved in water, challenging visual-centric views. We thus urge replacing "sensory horizon" with "multisensory horizon" to more accurately reflect ecological and evolutionary realities.

In our comment, we suggest that the notion of "sensory horizon" risks overlooking the *multisensory* nature of animal minds. According to the authors, "an organism's sensory horizon is the spatial limits of *a particular* sensory modality" (p. 6; emphasis added). This might be fine as an abstract definition, but such a unimodal notion flies in the face of actual aquatic dynamics.

To begin with, many aquatic vertebrates, especially teleost fish, possess sophisticated *auditory* systems that are well adapted for underwater sound propagation (Popper & Fay, 1999). These auditory systems support vital behaviours such as predator evasion, prey detection, communication, and navigation – all of which imply a significant degree of sensory integration. The lateral line system, which is present in most aquatic vertebrates, exemplifies a specialised *mechanosensory* modality that detects water movements and vibrations; it plays a crucial role in spatial orientation and environmental perception (Coombs, Görner, & Münz, 1989). Moreover, there is strong evidence that aquatic animals are capable of visuo-auditory *integration*. For example, goldfish (*Carassius auratus*) exhibits enhanced startle responses when exposed simultaneously to visual and auditory stimuli, demonstrating multisensory enhancement effects that parallel those observed in mammals and birds (Fay, 2005). In zebrafish (*Danio rerio*), calcium imaging studies have revealed that brain regions such as the optic tectum and torus semicircularis respond to both visual and auditory inputs, showing clear cross-modal modulation (Truszkowski et al., 2017). These brain structures functionally resemble the mammalian superior colliculus, suggesting a conserved neural architecture supporting *multisensory integration* across vertebrate species.

Evolutionary evidence also points to the direction that multisensory integration likely began in aquatic environments. Clack (2012) emphasises the gradual modification of aquatic auditory systems into structures adapted for terrestrial hearing, highlighting an evolutionary continuity rather than a sudden innovation. Auditory localisation, a crucial ability for spatial cognition, is well documented not only in aquatic but also in amphibious species (Edds-Walton & Fay, 2008), posing a challenge to the view that vision alone enabled unconscious multisensory integration. From a more ecologically grounded perspective, cross-modal integration may have evolved incrementally, shaped by the sensory demands of aquatic organisms. Ghazanfar and Schroeder (2006) argue that multisensory integration is a fundamental feature of neural processing, reflecting the variety of ecological pressures animals face. While terrestrial life certainly expanded the functional role and complexity of vision, it may not have been the original source of *conscious* vision, as the target article seems to suggest.

Even *without* multisensory integration, although aquatic animals vary in their reliance on vision and hearing for prey detection and predator avoidance depending on species and environmental conditions, many species rely more heavily on *auditory* cues, particularly sound localisation and echolocation, to detect prey and evade predators, especially in environments where visibility is limited (Au, 1993; Fay & Popper, 2000). Hearing provides aquatic animals with 360-degree environmental information and can penetrate visual blind spots. Since sound travels farther underwater, it enables these animals to effectively detect environmental sounds, prey movements, and predator locations. Given all these, the authors' divide-and-conquer strategy *beginning from vision* seems all the more inapt.

More positively, we urge that *multisensory horizon* should be in place right at the beginning of the analysis. The main reason is that most (if not all) creatures that can perceive at all do have more than one sensory modality. In the authors' account, it works as if those aquatic animals first anchor their sensory horizons with *vision*